Linear Infrastructure Networks with Ecological Solutions

Edited by

Sara Santos, Clara Grilo, Fraser Shilling,
Manisha Bhardwaj, Cristian Remus Papp

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Sofia–Moscow

Nature Conservation 47 (Special Issue)

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First published 2022
ISBN 978-619-248-067-7 (paperback)

Pensoft Publishers
12 Prof. Georgi Zlatarski Street, 1700 Sofia, Bulgaria
Fax: +359-2-870-42-82
info@pensoft.net
www.pensoft.net

Printed in Bulgaria, April 2022

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Nature Conservation 47: 1–8 (2022)
doi: 10.3897/natureconservation.47.81795
https://natureconservation.pensoft.net

EDITORIAL

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Ecological Solutions for Linear Infrastructure Networks: The key to green infrastructure development

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Received 7 February 2022 | Accepted 8 February 2022 | Published 25 March 2022

http://zoobank.org/DC920D21-0948-44F5-A0C0-300E6CE81814

Citation: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (2022) Ecological Solutions for Linear Infrastructure Networks: The key to green infrastructure development. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 1–8. https://doi.org/10.3897/natureconservation.47.81795

Introduction

The rapid expansion of linear infrastructure networks poses a global threat to biodiversity and ecosystem services (Laurance and Balmford 2013; van der Ree et al. 2015). Over the last few decades, research and careful planning have led to solutions which begin mitigating the negative effects of these infrastructures (Lesbarrères and Fahrig 2012; van der Grift et al. 2013; Rytwinski et al. 2016). Transport monitoring protocols and data are becoming more widely available, and novel actions are being tested and promoted (Vercayie and Herremans 2015; Schwartz et al. 2020). Robust protocols, landscape genetics, ecological connectivity modeling, remote sensing including GPS animal tracking, among other tools, are being frequently used in infrastructure planning and management (Balkenhol and Waits 2009; Carvalho et al. 2018; Shilling et al. 2020; Valerio et al. 2020; Zeller et al. 2020). The approach towards linear infrastructure planning is also transforming. Linear infrastructure-related habitats are increasingly valued for the biodiversity conservation opportunity they provide and have become a key contributor to Green Infrastructure development (Dániel-Ferreira et al. 2020; Ouédraogo et al. 2020). There is also a growing awareness of the need for coexistence between infrastructure and biodiversity, and citizens participate in this process (Périquet et al. 2018; Waetjen and Shilling 2018).

IENE (Infrastructure & Ecology Network Europe) is a network of experts on linear infrastructures (LI) and biodiversity from Europe and across the world. The main aim of IENE is to provide a platform to promote cross-boundary cooperation in research, mitigation and planning of LI (Seiler and Helldin 2015), facilitated by frequent national and international meetings. IENE organizes an international conference every two years, focusing on biodiversity and transportation (IENE 2021). These conferences provide a way to present innovative research, identify critical questions and problems, discuss ways to increase the efficiency of solutions, and improve communication among decision makers, planners, and researchers. IENE is also a founding member of the Global Congress on Linear Infrastructure and Environment, which brings together experts from every continent to discuss globally important issues of the interaction between linear infrastructure and the environment. Furthermore, IENE, together with other international transport and ecology conference organizations, the World Wide Fund for Nature (WWF) and the International Union for Conservation of Nature (IUCN), has helped to develop The Global Strategy for Ecologically Sustainable Transport and other Linear Infrastructure, a strategy to support biodiversity conservation and enhance ecological connectivity at the governance, policies, planning and implementation stages of transport projects around the world (Georgiadis et al. 2020).

The IENE2020 International Conference "LIFE LINES – Linear Infrastructure Networks with Ecological Solutions" aimed to improve environmental sustainability of infrastructure by bringing together and sharing the experiences of experts involved in the planning, research and administration of linear infrastructures around the world. The Conference focused on transportation infrastructures, but it also included other linear infrastructures, such as electric power lines. The Conference was held online from 12 to 14 January 2021, and was organized by the University of Évora, LIFE LINES project (LIFE14 NAT/PT/001081 https://lifelines.uevora.pt/), and IENE. The Conference was attended by over 300 participants from 31 countries, representing different stakeholders including ecologists, road and linear infrastructure technicians, NGOs, and policymakers. Participations were highly diverse, with 197 presentations, 13 workshops and two side events (LIFE SAFE CROSSING workshop and LIFE LINES Final Seminar), covering several important topics such as: (1) Innovative Solutions for Linear Infrastructure Impact assessment, Mitigation and Monitoring; (2) Challenges and Opportunities for Infrastructure-Related Habitats; (3) Linear Infrastructure Ecology; (4) Citizen Science and the Involvement of Civil Society; and (5) Legislation and Policy (IENE 2020 Organising and Programme committees, 2021).

About this collection

This Special Issue, entitled "Linear Infrastructure Networks with Ecological Solutions", is a collection of studies that address the main themes of the IENE 2020 conference. Fifteen papers in this volume present research carried out on linear infrastructures, namely roads (8 papers), railways (1 paper), roads and railways (3 papers), power lines (2 papers) and waterways (1 paper). These meaningful contributions were brought from Europe (11 papers), South America (1 paper), North America (2 papers) and Asia (1 paper), and discuss legislation and policy, wildlife-mortality patterns, citizen science, barrier effects, mitigation planning and testing the efficiency of mitigation.

Important insights on **legislation and policy** are highlighted by experiences from Germany and the Carpathians. Steege et al. (2022) present us with a review of projects, political programmes, and progressive legislation on German federal waterways. While, Papp et al. (2022) provide specific recommendations to mainstream ecological connectivity into the planning and design of linear transport infrastructure to maintain the long-term viability of large carnivores in the Carpathians region. These studies contribute with guidance for other authorities striving towards similar goals.

The patterns of **wildlife mortality on roads (roadkill)** were assessed in Brazil, India and Greece. The roadkill of four mammal species were related with landscape use in Brazil. Generalist species such as the crab-eating fox (*Cerdocyon thous*) and the six-banded armadillo (*Euphractus sexcinctus*), showed higher roadkill probabilities in human-modified regions; however, habitat specialist mammals, such as the giant anteater (*Myrmecophaga tridactyla*) and the collared-anteater (*Tamandua tetradactyla*), showed higher roadkill risk with increasing fragmentation of forest or savanna areas, respectively (Cirino et al. 2022). From India, Sur et al. (2022) present the first patterns of vertebrate roadkill assessed in a National Park, demonstrating that roadkill rates were highest during the monsoon season, particularly for amphibians. The analysis of long-term mortality of the brown bear (*Ursus arctos*) in Greece revealed 60% of roadkills were concentrated in four hotspots, occurring most often in periods of increased animal mobility, under poor light conditions and reduced visibility (Psaralexi et al. 2022). All of these results are crucial for identifying the risk to different taxonomic groups, and defining proper mitigation measures specific to each region and communities.

There is an interesting contribution from a **citizen science** project from Belgium, which collected almost 90,000 roadkill records in 12 years. Although collected roadkill data was biased towards larger and more charismatic species, the data suggests that the number of roadkill is decreasing in recent years (Swinnen et al. 2022). This contribution highlights the benefit of getting the public to actively participate in biodiversity conservation.

The role of species behaviour on the **barrier effect of roads** was studied in Portugal. Roads were a behavioural barrier to the movement of small-sized carnivores, although they also take advantage of road proximity as feeding areas (Ferreira et al. 2022). In another study, Fernandes et al. (2022) also found Cabrera voles (*Microtus cabrerae*), an endangered small mammal, had different space use and movement patterns when living on road verges compared to living away from the road. Both studies highlight the need to integrate species behaviour into road permeability projects.

There were also novel approaches to inform **mitigation planning** on roads, railways and powerlines. Helldin (2022) discusses the advantages and disadvantages of single large crossing structures versus several small crossing structures for decreasing barrier effects of roads and railways on wildlife. This debate is of utmost importance as this knowledge improves the efficiency of mitigation planning and the communication between environmental planners and transport agencies. Bird distribution data was used in spatial models to derive a high-resolution map of risks of collisions between birds and power lines across Belgium, identifying locations where mitigation measures should be placed (Paquet et al. 2022). Both of the above approaches can be applied to different contexts, improving spatial planning and design for mitigation across linear infrastructure networks.

The final theme of the papers in this collection focuses on the **effectiveness of mitigation measures,** giving practical recommendations on specific strategies. Accommodating co-use by wildlife and humans may be possible when the mammal species are tolerant of human presence; however, wildlife passages intended to be used by species that are sensitive to human presence should avoid human co-use (Warnock-Juteau et al. 2022). Commonly implemented wire netting fences are not efficient at stopping small animals from climbing over and onto the roadway, thus fences made of alternative materials (e.g., concrete, PVC) may be more efficient (Conan et al. 2022). Short fencing segments can increase the risk of Florida Key deer (*Odocoileus virginianus clavium*) vehicle collisions, especially near fence-ends, thus mitigation measures must be implemented on an appropriate scale to be effective (Huijser and Begley 2022). Wildlife warning reflectors are not an effective method to modify roe deer (*Capreolus capreolus*) behaviour and reduce risk of wildlife-train collisions (Jasińska et al. 2022). Similar results were found from deflectors used to reduce bird-power line collisions (Kornhuber et al. 2022). These authors recommend the use of the animal deflector to a polymeric insulator, since no danger to small birds and small animals could be identified. However, more research and tests on different insulator types need to be conducted before solid recommendations can be made. Testing of mitigation strategies allows for their limitations to be identified and provides a foundation for improving the techniques.

Conference conclusions

The IENE 2020 International Conference presented the impacts and opportunities that Linear Infrastructure brings to nature conservation, allowed the discussion of successes and failures in mitigation and monitoring, and showed novel approaches to harmonize infrastructures and the surrounding environment. The contents of this volume underlines how important ecological solutions are to minimize the negative impacts of Linear Infrastructure and to achieve increasingly greener infrastructures.

Acknowledgements

We wish to thank all colleagues who presented their important work at IENE2020 and to those who also submitted their works to this Special Issue. Thanks to the reviewers for offering their time and constructive suggestions. We additionally thank the Editorial Office of Nature Conservation, and especially to Boriana Ovcharova, the Managing Editor, for their kind assistance during the entire process. We are also grateful to the University of Évora, LIFE LINES project (LIFE14 NAT / PT / 001081), and IENE - Infrastructure and Ecology Network Europe.

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Nature Conservation 47: 9–13 (2022)
doi: 10.3897/natureconservation.47.81621
https://natureconservation.pensoft.net

EDITORIAL

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Promoting ecological solutions for sustainable infrastructure

Anders Sjölund[1], Yannick Autret[2], Marita Boettcher[3], Julie de Bouville[4], Lazaros E. Georgiadis[5], Elke Hahn[6], Agnès Hallosserie[4], Adam Hofland[7], Jean-François Lesigne[8], Antonio Mira[9], Charlotte Navarro[4], Carme Rosell[10], Tony Sangwine[11], Andreas Seiler[12], Paul Wagner[13]

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Received 2 February 2022 | Accepted 3 February 2022 | Published 25 March 2022

http://zoobank.org/7091EC98-9F95-4870-BBD0-A58A487A9600

Citation: Sjölund A, Autret Y, Boettcher M, de Bouville J, Georgiadis LE, Hahn E, Hallosserie A, Hofland A, Lesigne J-F, Mira A, Navarro C, Rosell C, Sangwine T, Seiler A, Wagner P (2022) Promoting ecological solutions for sustainable infrastructure Promoting ecological solutions for sustainable infrastructure. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 9–13. https://doi.org/10.3897/natureconservation.47.81621

Linear infrastructure networks such as roads, railways, navigation and irrigation canals, and power lines have grown exponentially since the mid-20th century. Most of these networks built before the 1990s have a significant impact on the environment. While there is no doubt that humanity needs infrastructure to ensure safe, secure and sufficient access to food, water and energy, it is essential to prevent the loss of biodiversity and ecosystems which are also at the basis of the provision of such fundamental services. Those complex, interconnected issues cannot be tackled without research and innovation, both in the fields of biodiversity and of infrastructure.

IENE (Infrastructure Ecology Network Europe) was set up in 1996 to meet this need. Its mission is to promote the exchange of knowledge, experience and best practice in safe and sustainable pan-European transport infrastructure. With a status of an association today, this independent network has more than 400 members consisting of researchers, engineers, decision makers and infrastructure operators. IENE functions as an international and interdisciplinary forum. It supports cross-border cooperation in research, mitigation, planning, design, construction and maintenance in the field of biodiversity and transport infrastructure.

Every two years, IENE organises an international conference to present cutting-edge research, identify pressing issues and problems, discuss effective solutions and map out future activities in the field of transport ecology and infrastructure. In this special issue we are very glad to present you with some of the best scientific outcomes of the IENE 2020 conference, hoping that it will contribute to further breakthroughs in science and uptake in policy-making and practices on the ground. We commend the organising team of the University of Évora, Portugal, for their excellent programming of the conference and for having gathered exceptional scientists on the topic of biodiversity and infrastructure. They managed to host a high-quality event, despite the many adjustments that had to be done because of Covid-19, including postponing the conference to January 2021 and holding it entirely online.

The topic of IENE conference 2020 was "Linear Infrastructure Networks with Ecological Solutions" and the motto was "working together". This means that every stakeholder has a role to play, and that biodiversity should be considered at all governance scales and during all phases of the set-up of infrastructure. The papers selected here are of particular interest to follow the path set forth in the conference's final declaration, which is included in this issue.

To keep the exchange of knowledge going between conferences, these discussions feed into the Wildlife and Traffic handbook that IENE has been curating since 2003. This handbook highlights solutions and measures aimed at mitigating the fragmentation of habitats and animal mortality due to transport infrastructures. It compiles the knowledge accumulated over the past decades on ecological mitigation, as well as best practices identified through a literature review and expert contributions. Its objective is to promote solutions to reconcile biodiversity and transport infrastructure that are evidence-based, action-oriented, feasible, cost-effective and innovative. The handbook aims to be up to date with the latest findings in research and best practise, but will still rest on solid and generally accepted conclusions and experiences.

The handbook will also be further expanded through the European BISON project, in which IENE is a technical leader. This project, the first of its kind supported by the European Union, is funding a €3 million Coordination and Support Action (CSA) on transport and biodiversity. In particular, the project aims to identify future research and innovation needs, sustainable and resilient construction, maintenance and inspection methods and materials that can be used by different transport modes to mitigate pressure on biodiversity. It builds on more than a decade of IENE conferences and will publish a Strategic Research and Deployment Agenda on the topic of biodiversity and infrastructure in 2023.

The knowledge gathered by IENE is also intended to help the private and semi-public sector. By launching the Transport4nature initiative at the IUCN Congress in September 2021, IENE is inviting transport companies operating at the European level to make commitments to biodiversity. This initiative is accompanied by the work of the IENE Scientific and Expert Committee, and builds on the wide knowledge accumulated in the community for several decades.

At a time when many States are investing massively in infrastructure to stimulate the economy and job creation, the knowledge provided by the IENE network is more than ever essential to put in place sustainable solutions and prevent infrastructure from causing natural and climatic damage that could last for decades and lead to points of no return. We hope that the reading of this special issue will be inspiring, for researchers, practitioners and decision-makers to continue their efforts to reconcile biodiversity protection and infrastructure planning and to implement efficient solutions on the ground.

IENE

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IENE 2020 International Conference Declaration

Sustainable infrastructure needs ecological solutions – it's time to work together!

We, the participants of the IENE 2020 International Conference, acknowledge that:

1. We are facing a significant worldwide expansion of transportation networks; this is especially the case in countries with developing economies.
2. If no action is taken, this global expansion will entail a substantial increase in greenhouse gas emissions, wildlife mortality and landscape fragmentation and change, with devastating effects on climate, biodiversity and ecosystem services.
3. Globally, ecosystem services are estimated to yield more than the Gross World Product of 2019 (https://www.worldometers.info/gdp/).
4. Despite the development and implementation of environmental impact assessment legislation, many existing transportation infrastructure networks are not

environmentally friendly. These impacts are far-reaching with a debt being paid daily through unnecessary risks extendable to human health and well-being.

5. The economic, social, and ecological consequences of biodiversity loss and the role of transportation infrastructure is increasingly acknowledged worldwide:

- Conservation and restoration of ecological connectivity is a major flagship in the preparation of the upcoming United Nations "Post-2020 Global biodiversity framework" following the recognised failure of the Aichi Targets associated with the loss and fragmentation of natural habitats (Target 5) (https://www.cbd.int/gbo5).
- The European Green Deal and the new European Biodiversity Strategy for 2030, adopted by the European Commission in May 2020, stresses the need to develop a resilient Trans-European Nature Network supported by ecological corridors allowing the free flow of genes and individuals (https://ec.europa.eu/info/sites/info/files/communication-annex-eu-biodiversity-strategy-2030_en.pdf).
- The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) states that since 1970, transportation infrastructure is an important driver of land use change and associated loss of terrestrial biodiversity (https://ipbes.net/global-assessment).
- The World Economic Forum 2020 recognised that biodiversity loss is one of the major threats with 'plausible higher than average impact' on Global Economies (https://www.weforum.org/reports/the-global-risks-report-2020).

6. To achieve sustainability, infrastructure development must be decoupled from its negative effect on biodiversity. This requires immediate, stringent action and shared responsibilities from all stakeholders.

7. Regional, national, and worldwide networks of experts, including researchers, practitioners, landscape designers, and managers, address such concerns through knowledge-sharing platforms that promote effective ecological solutions.

8. The scarcity of collective and coordinated efforts, such as joint decision-making processes involving environmental, transportation, energy, policy and financing agencies, is still a major obstacle to achieve sustainability in transportation infrastructure projects.

Therefore, we, the participants of the IENE 2020 International Conference, call for an individual and collective endeavour to:

1. Improve robust, science-driven methodologies and decision-support tools to aid sustainable transportation infrastructure planning, based on the no-net loss recommendations, considering cumulative anthropogenic impacts.

2. Mainstream biodiversity and ecological connectivity across all phases of infrastructure planning, development, construction, and maintenance.

3. Enhance collaboration among all relevant actors in transportation infrastructure development through the creation of a multilevel and multidisciplinary group including representatives from the sectors of transportation (e.g. DG Move, TEN-T), energy (e.g. DG Energy) and environment (e.g. DG Environment, TEN-G), as well as from all other relevant stakeholders.

4. Acknowledge that further development of new infrastructure needs to consider cumulative impacts within a larger landscape context; this requires integration with existing infrastructure to guarantee overall habitat integrity and connectivity, thus accounting for potential synergistic interactions between biodiversity impacts and ecological solutions.
5. Accelerate the ecological adaptation of rapid, transparent, and fair transference of scientific evidence-based knowledge to practitioners, managers and infrastructure designers, to avoid negative impacts of transportation infrastructure development on biodiversity.
6. Assure that investments in new transportation infrastructure projects are conditioned to an assessment of their sustainability, considering the no-net loss recommendations to meet biodiversity conservation targets.
7. Guarantee new transportation infrastructure projects, allocate further funding for research and innovation, monitoring and evaluation, as well as knowledge-sharing.
8. Strengthen platforms that support cooperation among scientists, practitioners, and agencies, encouraging international studies that promote direct, rapid exchange of knowledge in a "learning together" environment as opposed to a "learning from each other" process.
9. Establish the foundation for an International "Observatory for the Ecological Effects of Transportation Infrastructure and related mitigation works and policies", to compile standardized information from which new insights can be gained and new remedies can be developed.

These proposed actions are the responsibility of all of us, but the support and incentive of decision-makers is the main foundation upon which the provision, implementation and dissemination of the actions can take place, safeguarding a sustainable earth where biodiversity and people may thrive together.

What are IENE Declarations?

Since 1996, IENE operates as an international and interdisciplinary forum to encourage and enable cross-boundary cooperation in research and mitigation and planning in the field of ecology and transport infrastructures. The IENE biannual international conference provides interdisciplinary discussion panels for these activities with the aim to present cutting-edge research, identify urgent questions and problems, discuss effective solutions, and outline the paths for upcoming activities in transport and infrastructure ecology. Since 2012, a Declaration has been produced during each conference and focused on a topic that requires particular attention from transportation and nature conservancy stakeholders. This message represents a common statement by the participants and addresses decision makers, planners, technicians and researchers as well as the general public, by calling for actions that contribute to finding solutions to old and emerging conflicts, filling the research gap and, overall, minimising the impact that transport infrastructure exerts on nature.

IENE Governance Board

Nature Conservation 47: 15–33 (2022)
doi: 10.3897/natureconservation.47.70732
https://natureconservation.pensoft.net

REVIEW ARTICLE

A peer-reviewed open-access journal
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Germany's federal waterways – A linear infrastructure network for nature and transport

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Academic editor: Manisha Bhardwaj | Received 27 June 2021 | Accepted 17 September 2021 | Published 25 March 2022

http://zoobank.org/6437C907-FB47-45D5-8A09-BECAB97DFB60

Citation: Steege V, Engelbart D, Hädicke NT, Schäfer K, Wey JK (2022) Germany's federal waterways – A linear infrastructure network for nature and transport. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 15–33. https://doi.org/10.3897/natureconservation.47.70732

Abstract

Major rivers are unique linear structures because they serve different purposes simultaneously: A habitat and dispersal route for flora and fauna as well as a navigation route, the site for recreational and economic activities and a source for drinking water and irrigation. In recent years, it has become increasingly clear that waterways must be developed in an environmentally and economically sustainable and socially responsible manner. The Federal Ministry of Transport and Digital Infrastructure (BMVI) and its specialised agencies – the Waterways and Shipping Administration of the German Federal Government (WSV), the Federal Institute of Hydrology (BfG) and the Federal Waterways Engineering and Research Institute (BAW) – are aiming to achieve this goal by integrating environmental issues into the development and maintenance of waterways. This paper aims to fill the gap on the one hand between scientific analyses of ecological freshwater status and proposals for its improvement, and, on the other hand, bringing this knowledge into practical realisation. Recent activities at the German federal waterways are exemplarily reviewed on the basis of applied research projects, local projects, political programmes and progressive legislation.

Keywords

Biodiversity, bioengineering, Germany's Blue Belt, German waterways, river restoration, Water Framework Directive

Introduction

Major rivers are unique linear structures because they serve different purposes simultaneously: Habitat and dispersal route for flora and fauna as well as navigation route, site for recreational and economic activities and source for drinking water and irrigation (Fig. 1). They link up cities and ports. The energy of their running water is used to generate power.

People have travelled on and used rivers to transport goods for thousands of years. For a diversity of reasons, including safety, they also began very early to alter the natural course of flowing water and, over time, built the engineering features which they considered necessary and desirable. Bogs and marshes were drained and reclaimed, weirs and dams were constructed, rivers and streams diked and straightened. The result is an ecological status of rivers and floodplains, which is not satisfactory from our current perspective.

Nature and its vital contributions to people, providing biodiversity and ecosystem functions and services, are deteriorating worldwide. Regarding freshwater ecosystems, this is stated on a global scale currently e. g. by IPBES (2019), Van Rees et al. (2020) and Vari et al. (2021). How to improve this status on a global scale is subject to intense scientific and political discussion within the Post-2020 Global Biodiversity Framework (https://www.cbd.int).

An overview of the ecological status of Europe's waters and wetlands and EU policies aiming to improve water quality is documented by EEA (2019). 40% of Europe's surface water bodies achieve good ecological status based on an assessment of the second river basin management plans (published 2015) required under the EC Water Framework Directive (WFD). Enhanced activities of EU member states are recommended to reach the quality goals of WFD until the timeline 2027.

Figure 1. River Rhine near Maxau (Source: BAW).

On the same data base (WFD, second cycle) in Germany just about 7% of streams and rivers were in at least "good" ecological condition in 2015 (UBA 2021). An assessment of the current state of floodplains on behalf of the Federal Agency for Nature Conservation (BfN) shows that, overall, just under 1% of recent (floodable) river floodplains are very slightly modified (floodplain condition class 1) and 8% are slightly modified (floodplain condition class 2) and thus still largely ecologically functional. 33% of the floodplains are assigned to floodplain condition class 3 (significantly altered), but still have "floodplain character," i.e. the flooding potential still exists, but is limited by alterations to the watercourse. The predominance of floodplain condition classes 4 (heavily modified) and 5 (very heavily modified) at 32% and 26%, respectively, reflects the intensive use of riverine landscapes. However, due to the historically evolved situation of the floodplains as centres of settlement and economic development along the rivers, these changes are only partially reversible (BMU & BfN 2021).

Consequently, today we know that our waterways must be developed in an environmentally and economically sustainable and socially responsible manner. The great challenge now is to establish a balance between transport systems and nature. How can all these functions be integrated with as little conflict as possible?

A scientific overview on knowledge and possibilities to put expertise on river functioning, river management and rehabilitation into practice is given by Buijse et al. (2005). They recommend river rehabilitation to be part of integrated river management to search for win-win options as well as to find compromises where conflicts with other functions arise. Van Rees et al. (2020) conclude that policies and strategies must have a greater focus on the unique ecology of freshwater life and its multiple threats and should reflect on how this may be achieved.

This paper aims to fill the gap on the one hand between scientific analyses of ecological freshwater status and proposals for its improvement, and on the other hand bringing this knowledge into practical realization. The paper documents how the German Federal Ministry of Transport and Digital Infrastructure (BMVI) and its specialised agencies – the Waterways and Shipping Administration of the German Federal Government (WSV), the Federal Institute of Hydrology (BfG) and the Federal Waterways Engineering and Research Institute (BAW) – are aiming to achieve this goal by integrating environmental issues into the development and maintenance of waterways. This happens on the basis of political programmes, progressive legislation, applied research projects and local projects. Building fish passes, creating bypasses in floodplains, riverbank restoration (where possible), and the development of innovative groynes as well as training walls are some practical examples under the umbrella of the so-called "building with nature" approach.

Short overview of the German federal waterways and their connecting function within the national and European biotope network

Fig. 2. gives an overview of the system of German federal waterways within the Central European network of waterways. It is a network that connects the transport of goods and people not only within Germany, but also with neighbouring countries and

Figure 2. Overview of the system of German federal waterways within the Central European waterways network (Source: WSV).

overseas. The volume of goods transported on German inland waterways amounts to about 220 million tons per year. This is currently about 11% of the cargo in the modal split; the remaining large majority is transported by rail and road. The network of federal waterways in Germany comprises about 7,300 kilometres of inland waterways, of which rivers account for about 75 percent of the route and canals for the other 25 percent. The federal waterways also include about 23,000 square kilometres of sea waterways (https://www.gdws.wsv.bund.de/DE/wasserstrassen/wasserstrassen-node.html). Almost all major rivers in Germany serve as waterways.

At the same time, the major German rivers are of course also central connecting axes of the nationwide and the European biotope network (Fig. 3).

Today, it is generally expected that there should be a balance between transport functions of the German federal waterways and consideration of contemporary ecological standards. This expectation has also altered the way in which those in business and administration look at this issue and understand their own roles. Many things which seemed unthinkable just a short time ago are now firmly established in practice and planning. Improving the ecological status of federal waterways is a process which

Figure 3. Connecting axes of the German (rivers: blue lines) and the European (coloured arrows) biotope network (Source: BfN 2016).

always calls for a fine sense of judgement as well as cautiously testing the ground in the search for the possible, followed by reflective assessment of what is subsequently achieved. Important general ecological framework conditions are the Water Framework Directive (WFD), the Marine Strategy Framework Directive (MSFD) and the Birds and Habitats Directives of the EU.

Practical examples of ecological measures and research projects on German federal waterways

Alternative concepts for the protection of river banks

In 2004, the Federal Institute of Hydrology (BfG) and the Federal Waterways Engineering and Research Institute (BAW) launched a joint research programme on the technical and ecological suitability of alternative concepts for the protection of river banks (Schmitt et al. 2018). Studies of hydraulic loads and the ecological potential of this type of construction, taking into account the impact of navigation, are being undertaken along selected stretches of waterways. At the same time, researchers are performing in-depth laboratory studies as well as model studies. Close cooperation between various departments of the BAW (earthworks and bank protection, navigation) and the BfG (landscape conservation, vegetation science, animal ecology) enables interdisciplinary project work from a technical and ecological point of view. Currently, this research has been extended to the waterways at German North Sea estuaries (Fig. 4).

Various biotechnical approaches to bank protection at inland waterways are currently being tested in cooperation with the Oberrhein Waterways and Shipping Office in a large-scale trial on a one kilometre long river section on the right bank of the Rhine near Worms (km 440.6 to km 441.6), i.e. on the largest and busiest waterway in Germany. In the study area, around 120 freight ships per day are operating. Depending on the discharge, the water level fluctuates by over 6 m. The embankments are also relatively steeply inclined. In four test fields, the stone embankments above the mean water level were replaced by willow spreaders, pre-cultivated reed gabions and plant mats or stone mattresses. In another four fields, the stone fill was preserved and ecologically upgraded by various measures. The bank was planted with grazing poles and machines, with bushes and hedges, the bank structure was improved with gravel, large individual stones and deadwood; in addition, protected areas were created by a bank stabilisation of stones in front of the embankment. For comparison, one test field remained without protection (Schilling et al. 2013).

The results of research and best practise examples are presented on the internet: https://ufersicherung.baw.de. The aim of this project is to develop recommendations and basic principles to facilitate an application of the newly-developed methods for bank protection of inland waterways (Söhngen et al. 2018).

Figure 4. Biotechnical approaches to bank protection at German North Sea estuaries (Source: BAW).

Rees flood spillway

Another example of successful and integrated planning, with the early involvement and inclusion of stakeholders, is the flood spillway project near the city of Rees on the lower Rhine (Fig. 5, WSV 2012; BUND 2013). Since the purpose of this federal project is to provide flood protection in addition to preventing erosion of the river bed, it is also co-financed by the state of North Rhine-Westphalia. The Rees flood spillway helps to counteract the lowering of the groundwater level and improves the habitats for wetland fauna and flora. New shallow water and mud areas enliven the wetland fauna. As a result, the species diversity of grassland birds in the floodplain landscape can increase again. The project has gained recognition at European level and has been included in the EC Guidance Document on Inland Waterway Transport and Natura 2000 (EC 2018). In 2014 the bypass on the Rhine was awarded the "Working with nature Award" at the 33rd PIANC (World Association for Waterborne Transport Infrastructure) World Congress (PIANC 2014).

Figure 5. Rees flood spillway (Source: BAW).

Paving the way for migratory fish

In Germany, the WFD was primarily transposed into national law by the Federal Water Act (WHG) and taken up in the laws of the Federal States. With the 2010 amendment to the Federal Water Act, the WSV has taken over responsibility for maintaining and restoring ecological patency at the dams it constructs or operates on federal waterways.

220 weirs in the federal waterways require measures, i.e. structures must be newly constructed or repaired to enable accessibility for fish and macrozoobenthos in order to reach the goals of the WFD. This requires resources to the order of (a currently-estimated) 1 billion euros. In addition, regionally varying management responsibilities need to be coordinated and a variety of economic, ecological and political requirements need to be taken into account. For example, the sometimes complex and technically demanding integration of new fishways into existing structures makes it difficult to implement measures in a timely manner and may lead to conflicts with other objectives (of utilisation) such as energy production by hydropower plants. In addition to the co-ordination of different interests, the planning processes themselves can be lengthy. At the same time, however, the WFD's timeframe for achieving the objectives is tight. For this reason, synergies with already-planned measures (such as the restoration or replacement of defective weirs) are increasingly sought in the implementation of the measures.

Another challenge is the great need, especially for fishways on large water bodies, to close gaps in our knowledge of fish behaviour in relation to topography, geometry and hydraulics in the access area and within ladders in order to be able to guarantee sufficient functionality of the new facilities. A pilot project for monitoring and research is the Mosel fishway near Koblenz (Fig. 6). The successful cooperation between the WSV

Figure 6. Mosel fishway near Koblenz (Source: BfG).

and the state of Rhineland-Palatinate was crowned by the opening of the modern fishway in September 2011. In March 2012, the first upstream-migrating salmon was registered and in July 2013 a shad was seen for the first time in 60 years to ascend the river Mosel. All in all, the fishway has proven to be passable for most fish species and sizes, leading to notably high yearly numbers of ascending fish (e.g. more than 230.000 in 2015 (BfG 2017)). The state of Rhineland-Palatinate has moreover built a visitor centre, the "Mosellum", where visitors can immerse themselves in the world of migratory fish.

To approach all the aforementioned challenges, an implementation strategy, which takes into account different ecological and economic requirements, reflecting political and administrative boundaries and providing a strategy for closing knowledge gaps through research projects, was developed at the federal level (BMVBS 2012; BMVI 2015; BfG & BAW 2017). The prioritisation for the implementation of measures (BMVI 2015) is currently updated and will be integrated into Germany's management plans for the third implementation cycle of the WFD.

Synergies between different actors

These examples are only a small selection from the wide range of measures with which the WSV in Germany contributes to the preservation and promotion of biodiversity on watercourses as linear landscape structures within the framework of maintaining the waterways, but also in the course of compensation measures for expansion projects and in the fulfilment of legal obligations.

However, the fulfilment of legal tasks is only one side of the coin for achieving water-ecological objectives. If someone wins one hundred percent (e.g. nature conservation) there are usually also losers (often e.g. agricultural land). In our participatory and federal society, there is no progress in the implementation of measures on waterways without taking into account the users and social groups as well as institutions concerned. For this reason, the BMVI together with the WSV are increasingly focusing on dialogue and communication and integrated project planning, e.g. LIFE projects, funded by the EU.

LIFE+ project "My favourite river" Zugwiesen

A new floodplain has been created from 2011–2013 along the river Neckar near Stuttgart: the "Zugwiesen". The "Zugwiesen" project became the responsibility of several stakeholders, who normally have different fields of activity and whose interests are occasionally in conflict. The WSV, on the one hand, is responsible for the river Neckar and its utilisation as a traffic route; the city of Ludwigsburg, on the other hand, has responsibility for the larger river bank areas. Both sides put forward convincing arguments and showed creativity which resulted in a joint concept. As the concrete slabs on the left Neckar embankment exhibited considerable damage, the Waterways and Shipping Office Stuttgart decided to integrate reconstruction works into the ecological redevelopment of the "Zugwiesen" floodplain. The embankment was levelled over a length of 800 metres. The former wall was removed, the river and the floodplain were reunited (Fig. 7).

Figure 7. LIFE+ project "My favourite river" Zugwiesen (Source: Jochen Faber, INFO & IDEE GmbH).

The Zugwiesen-project clearly shows that the banks of a river can offer exemplary habitat conditions, even if there is high traffic from ships. Diverse habitats for plants and animals invite visitors to observe and learn while getting some fresh air. Federal and local government have engaged in an unprecedented level of cooperation to realise the project. The new "Zugwiesen" floodplain covers an area of 17 hectares and includes a new water body with an area of 40,000 sqm. The former bank reinforcement was broken up and vegetation planted for a near-natural bank protection, resulting in the restoration of the entire large area along the Neckar bend. Meadows, an alluvial forest with willow and alder trees, still-water bodies with islands, wetlands and ponds as well as a brook winding its way through the area provide a habitat for animals and plants. An observation platform, the "Stork's Nest" enables visitors to observe even those protected parts of the area that are not allowed to enter (https://neckar.ludwigsburg.de/start/Projekte/Zugwiesen.html).

Integrated EU-LIFE-project "Living Lahn"

Some minor waterways in Germany are no longer used for the transport of goods as they had been before. For some of these waterways, development strategies to reduce infrastructures that are no longer required and the enhancement of opportunities for ecological development and recreational activities are discussed. The integrated European Union's LIFE-project "Living Lahn - one river, many interests" (2015–2025), conducted by the federal state of Hesse together with the federal state of Rhineland-Palatinate, the WSV and the BfG aims at helping to restore the "good ecological potential" of the federal waterway Lahn. At the same time, the interests of shipping and other competing uses will be integrated in accordance with ecological requirements. This project creates best-practice examples for other rivers. "Living Lahn" was the first integrated LIFE-project, which has been funded in Germany by the European Commission (HMUKLV 2021) (https://www.lila-livinglahn.de/en/start).

The project partners are:

- Hessian Ministry for the Environment, Climate Protection, Agriculture and Consumer Protection;
- Ministry for Climate Protection, Environment, Energy and Mobility of Rhineland-Palatinate;
- Directorate for Infrastructure and Approval North;
- Governmental Authority of Gießen;
- Waterways and Shipping Office Mosel-Saar-Lahn;
- German Federal Institute of Hydrology.

The first main objective of the Living Lahn project is to enhance the ecological status and connectivity of the river itself while simultaneously enriching the quality of life along the river. This aim will be reached through practical projects such as

- Restoration of natural retention areas and their self-regulation.
- Identification of pollution sources and their elimination in order to improve the water quality.
- Improving structural diversity in weir-regulated river stretches.
- Implementation of measures for restoring the linear patency in different types of locks and weirs, thus leading to a direct improvement of the water-bound habitats and their different animal and plant species.
- Promotion of sustainable tourism offers e.g. in the field of canoeing/rowing by constructing new portage sites as well as by providing a “Lahn App” for better planning of leisure activities.

The second main objective is to develop an overall concept, the so-called “Lahn-Concept”, which takes into account its further ongoing use as a federal waterway as well as water ecology and revitalisation aspects and flood protection. Ever since 1981, the Lahn has no longer been used for freight transport. The weir buildings partly need substantial restoration and maintenance works, calling for urgent action from the responsible authorities.

The Lahn-Concept pursues a holistic approach, in order to integrate the numerous interests, usages, and stakeholders, and, of course, the Lahn River itself, into the development process. With the participation of all project partners and the interested public, the Lahn-Concept offers a unique opportunity to ‘re-invent’ the technical maintenance of the Lahn, to enhance the ecological health and connectivity of the river itself, to improve the potential for tourists, to implement the goals of the Water Framework Directive and to consider further relevant correlations. The challenge will be to balance competing interests as there are flood protection, nature conservation, shipping, water conservation, economic efficiency, hydropower, tourism, agriculture, fisheries, and more.

For this purpose, the responsible project partner Waterways and Shipping Office Mosel-Saar-Lahn involved the public in a dialogue process at an early stage. Transparency and acceptance among the population will be fostered by regular publications, working groups and workshops, wherever necessary in order to collect feedback from relevant stakeholders.

The question of retaining or tearing down weirs to reach different objectives is often at the heart of the discussion process. As a way to rationalize discussions (and, possibly, decisions) concerning this topic, a study was set up to examine the effects of the removal of selected weirs on ecosystem services (ES). In this study, which is in its final stage, the RESI (River Ecosystem Services Index, Podschun et al. 2018) approach is utilised. The case study has already been used to refine parts of the ES concept (Albert et al. 2020). Moreover, the BMVI is currently discussing the use of certain ecosystem services indicators for future decision processes concerning traffic projects.

The WSV is responsible for approx. 2,800 km of secondary waterways. They have lost their importance for freight traffic due to changing transport flows and ship sizes and are now mainly used for tourism. Thus, it will be a key issue to elaborate concepts and perspectives in order to face challenges arising from the development described above. The common elaboration of the Lahn-Concept is considered a pilot activity for the WSV and can serve as a blueprint for further sustainable development concepts of other federal waterways of the same category.

Overall concept Elbe (Gesamtkonzept Elbe)

In the past, various demands for use of the Elbe River, such as shipping, nature conservation, flood protection, tourism and port management, have led to controversial disputes between the actors involved. The Binnenelbe upstream from the weir Geesthacht is home to valuable natural and cultural landscapes as well as original habitats of outstanding importance. The Elbe River landscape is a model landscape for sustainable development of the United Nations on more than 400 kilometres of the river as the oldest German UNESCO-biosphere reserve (https://www.flusslandschaft-elbe.de/start/?changelang=2).

Against the background of the different utilisation claims with legal obligations and the transferred responsibilities, the German Federal Ministry of Transport and Digital Infrastructure (BMVI) together with the Ministry for the Environment, Nature Conservation and Nuclear Safety (BMU), agreed at the federal level at the end of 2010 on a paper of key issues for an overall concept for the Elbe. In subsequent years, the overall concept Elbe (Fig. 8) was consolidated and institutionalised in a broad dialogue with federal states and various stakeholders in numerous conferences and consultations. Today, it has rules of procedure and bodies for cooperation at steering and working level. It forms the foundation for the long-term development of the Elbe upstream of Geesthacht, both as a shipping route and as a valuable natural area, taking into account other interests of use (https://www.gesamtkonzept-elbe.bund.de/Webs/GkElbe/DE/Home/home_node.html).

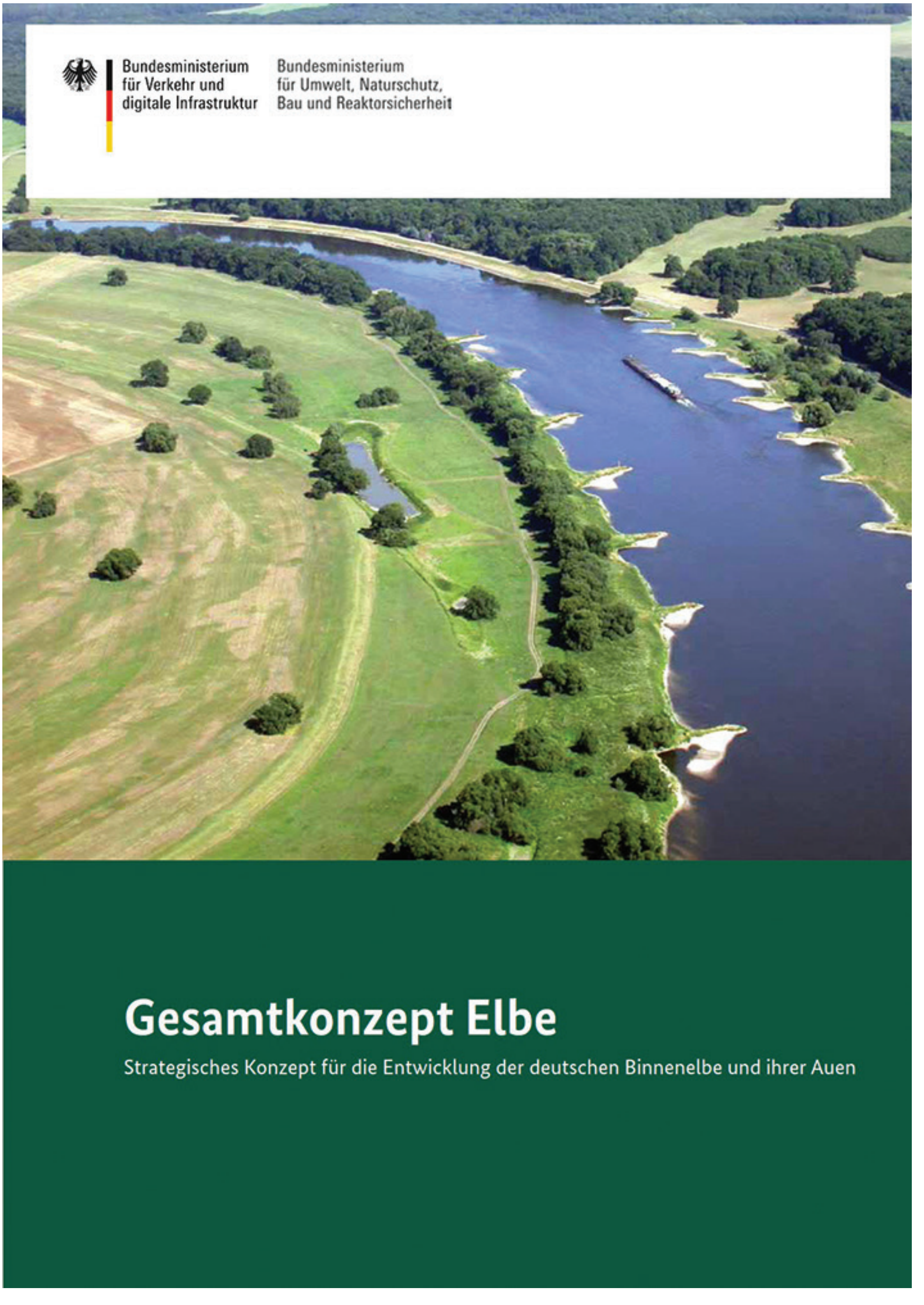

Figure 8. Overall concept Elbe (Gesamtkonzept Elbe) (Source WSV).

The overarching objectives are to combat erosion, improve flood protection, reduce inputs of contaminants, improve shipping conditions and maintain and restore habitats and habitat types in waters, banks and floodplains.

The implementation of the overall concept is not the sole responsibility of the German federal government. The federal states also have some essential responsibilities - such as flood protection as part of water management, nature conservation, tourism and port management. In its course and with its tributaries, the Elbe River touches ten of Germany's 16 federal states. This is a task for the next decades.

Germany's Blue Belt and new legislation

"Germany's Blue Belt" is one of the BMVI's new flagships. It is a Federal Government programme in cooperation with the BMU. After the initial impulse from the coalition agreement of the Federal Government in 2013, and some years of political activities and conceptual preparatory work, the operational phase of the „Blue Belt" programme started in 2019 (https://www.blaues-band.bund.de/Projektseiten/Blaues_Band/DE/neu_01_Bundesprogramm/bundesprogramm_node.html). It aims at developing a system of interlinked biotopes of national significance along Germany's federal waterways within the next decades and provides an opportunity to link adapted infrastructure standards to ecological objectives. This will also help to make these regions more attractive for leisure and recreational activities.

One important part of the implementation is the Federal Floodplain Programme which is managed by the Federal Agency for Nature Conservation (BfN). Measures strengthening lateral connectivity between rivers and floodplains are of special significance within the programme. In parallel, the objectives of the WFD and the Natura 2000 Directives are supported.

"Germany's Blue Belt" establishes a framework for action over the coming decades. Although it focuses on the network of minor waterways, it also defines "ecological stepping stones" for the very busy federal waterways. Such renaturalisation measures may include the reconnection of abandoned meanders and flood channels or the levelling of banks, provided that this is also compatible with the transport of freight. However, if rivers, banks and floodplains are developed as a holistic entity, also areas will be affected that are not owned by the Federal Government. Here, a financial-assistance programme of BfN creates incentives for supporting the restoration of habitats typically found on floodplains. The budget of the Federal Ministry for the Environment for 2020 e.g. provides 6.8 million euros for the Floodplain Programme. For the years 2021 to 2023 there are commitment appropriations of around 25 million euros (https://www.bfn.de/blauesband/foerderprogramm-auen.html).

Most of the watercourses in question, namely the federal waterways, are owned by the German Federal Government. It is thus a good idea to task the WSV with implementation of this programme, especially as it already has the necessary expertise and experience.

In 2016, the Federal Waterways Administration launched five model-projects (BMVI & BMU 2020) (https://www.blaues-band.bund.de/Projektseiten/Blaues_Band/DE/neu_04_Projekte/Aktuelle_Projekte/Projekte_node.html).

One model-project, the bank renaturation "Kühkopf-Knoblochsaue" on the river Rhine (Fig. 9), was hailed as a successful example as part of the UN Decade of Biological Diversity in 2020.

While launching the Blue Belt programme, it quickly became clear that the existing legal obligations of the WSV were not sufficient to carry out major renaturation measures that are to be classified as water management expansion. To enable the WSV to manage all these tasks in an appropriate manner, the BMVI and the BMU pursued an extension of legal tasks to allow the WSV to support the goals of the WFD to an extended degree. A corresponding amendment to the law was prepared by the German Federal Government in coordination with the Water Management Administration of the Federal States. On 09 June 2021, the new law came into force. The Federal Waterways Administration is now given the sovereign task of implementing water management expansion measures to achieve the hydromorphological objectives of the WFD. This kills two birds with one stone: the implementation of Germany's Blue Belt will be fully enabled administratively and the WSV can contribute actively to the achievement of the WFD objectives. This new legal task for the WSV will significantly advance and help to accelerate the implementation of the WFD on German federal waterways in the upcoming years and decades.

Figure 9. Germany's Blue Belt model project "Kühkopf-Knoblochsaue", River Rhine km 474.0–476.5.

Conclusion and perspectives, monitoring

The examples given in this overview illustrate how the German Federal Ministry of Transport and Digital Infrastructure (BMVI) and its specialised agencies are aiming to achieve the goal of integrating environmental issues into the development and maintenance of waterways. Important triggers for this process have been the EU environmental directives, where a starting point was the Directive 85/337/EEC of 27 June 1985 on the assessment of the effects of certain public and private projects on the environment.

As a result of many years of efforts to improve the performance of WSV for the ecological development of rivers used as federal waterways, the following key factors can be highlighted for successful implementation:

1. Support for this expansion of tasks by political decision makers and NGO's;
2. Contributions to the achievement of environmental goals as statutory responsibility (→ legal responsibility for ecological patency and hydromorphological measures to reach the objectives of the WFD in federal waterways);
3. Organisational units and staff for environmental tasks (→ new environmental division within the waterways administration, > 100 new employees within the last years);
4. Allocation of budgetary funds (→ still insufficient; helpful funding by EU (LIFE-projects Lahn, Neckar) and by BMVI and BMU (Germany's Blue Belt));
5. Cooperation projects between waterways administration and environmental authorities at national, federal and local levels as well as cooperation agreements with NGO's (→ Germany's Blue Belt, LIFE-projects, Overall concept Elbe);
6. Organisational consolidation of the forms of cooperation over many years (→ Germany's Blue Belt, Lahn concept, Overall concept Elbe);
7. Land availability (→ Prerequisite for all renaturation measures in the riparian area and in the floodplains);
8. Continuous input of scientific expertise, consulting and monitoring (→ by specialised BMVI agencies BfG, BAW);
9. Visibility (→ Public relations and combination with nature leisure experience) – closes the loop to policies (1.).

The implementation of these measures on the German waterways will be accompanied and documented in the long term by monitoring, where the BfG will have a special task. Since an improvement in the ecological status/potential of water bodies or the floodplain status in larger spatial units cannot be expected within a few years, it is important to highlight the special value of even small-scale measures accordingly and to make them visible to the public. The following rather general aspects should here be emphasised:

- aim for measures that are as effective as possible;
- bring together several partners and causes to large-scale projects (e.g. link compensation measures with renaturation measures or ecological flood protection measures, use of eco-accounts);

- bring ecosystem services more into focus as part of cost-benefit considerations (Pusch et al. 2018; Hornung et al. 2019; Funk et al. 2020);
- implementation of integrated management plans (Navigation, sediment management, WFD, MSFD, Natura 2000, Floods Directive 2007/60/EC).

Closing remarks

Integrating ecological objectives more strongly into administrative action is an ongoing but crucial process which will last several decades. Planning processes and realisation of projects – including projects for nature conservation – require a great deal of time and coordination due to diverse legal requirements and social demands, interdependencies and trade-offs. Nevertheless, more integrated planning is necessary. For this purpose, however, appropriate and substantial resources are needed – money, staff, and time. Another key bottleneck, especially for larger projects, is the availability of suitable areas. Managing land tenure is difficult and time-consuming. Hence, in our densely-populated region of Central Europe it will not be able to achieve all ambitious environmental goals at large rivers within a few years. Following these goals through a long-term perspective therefore requires a certain amount of patience and endurance. BMVI, together with the WSV, are nevertheless en route to achieve these goals.

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Nature Conservation 47: 35–63 (2022)
doi: 10.3897/natureconservation.47.71807
https://natureconservation.pensoft.net

REVIEW ARTICLE

A peer-reviewed open-access journal
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Rapid linear transport infrastructure development in the Carpathians: A major threat to the integrity of ecological connectivity for large carnivores

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Academic editor: Clara Grilo | Received 5 October 2021 | Accepted 29 January 2022 | Published 25 March 2022

http://zoobank.org/2BC333A8-8934-4C47-AC74-35E12A0A92BE

Citation: Papp C-R, Dostál I, Hlaváč V, Berchi GM, Romportl D (2022) Rapid linear transport infrastructure development in the Carpathians: A major threat to the integrity of ecological connectivity for large carnivores. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 35–63. https://doi.org/10.3897/natureconservation.47.71807

Abstract

The development of sustainable transport is a key challenge in societies where there is an accelerated need for socio-economic development. This is the case for seven countries from central and south-eastern Europe that share the Carpathian Mountains. The challenge of developing sustainable transport requires transdisciplinary, or at least cross-sectoral cooperation, between the transport development and nature conservation sectors. Such cooperation is not in the culture of the Carpathian countries, which together host some of the most remarkable biodiversity values in Europe, including the largest populations of brown bear, grey wolf and Eurasian lynx. The overall length of motorways in these countries more than quintupled in the last 30 years and the rapid expansion of Linear Transport Infrastructure (LTI) continues at exacerbating rates. The rich biodiversity habitats are being fragmented and the concept of ecological connectivity is poorly understood and implemented by the national authorities. Ecological networks for large carnivores are not defined nor officially recognised in the Carpathian countries, with little exceptions. The legislation is not consistent across the strands of ecological connectivity and is not harmonised between the countries to effectively support transnational conservation efforts. Thus, the critical intersections between planned or even existing LTI and ecological corridors for large carnivores cannot be identified, in most cases leading to increasing habitat fragmentation and isolation of wildlife populations in the region. We summarised all this key context-related information for the Carpathians in relation to LTI development and ecological connectivity. To counteract this trend in the Carpathian ecoregion, we propose a set of recommendations to: improve and harmonise the legislation; develop and endorse methodologies for designating ecological corridors; address the cumulative impact on ecological connectivity; define other threats on landscape permeability; improve stakeholder engagement, cooperation and communication; develop comprehensive and transparent biodiversity and transport databases; monitor wildlife and transport for implementing most appropriate mitigation measures and strategies; build capacity to address the issue of sustainable transportation; and foster transnational cooperation and dialogue. Bringing these elements together will support the design of ecological networks in a way that considers the needs and location of both current and future habitats and contribute to efforts to address the climate crisis. These specific recommendations are relevant also for other areas of the world facing similar problems as the Carpathians.

Keywords
Connectivity conservation, conservation, ecological corridors, environmental impact, habitat fragmentation, large mammals, LTI, policy actions, sustainable transport

Introduction

Habitat loss and fragmentation is considered as one of the main causes of biodiversity loss worldwide (Rands et al. 2010; Barnosky et al. 2011; Hilty et al. 2020), threatening with extinction over a quarter of the world's mammalian species (Butchart et al. 2010), including large carnivores (Noss et al. 1996; Crooks 2002; Crooks et al. 2017). Habitat fragmentation usually refers to a landscape-scale process of transforming a large and continuous habitat into smaller patches of different sizes, spatially separated from each other by a matrix of generally human-modified land use types (Wilcove et al. 1986; Fahrig 2003; Rogan and Lacher 2018) and it involves habitat loss, deterioration and subdivision (see Fischer and Lindenmayer 2007).

The development of linear transport infrastructures (LTI) and networks are one of the main reasons for habitat fragmentation (Geneletti 2003, 2004; Trocmé et al. 2003; Rhodes et al. 2014), particularly in mountain areas and it negatively affects large carnivores (Forman and Alexander 1998; Fahrig and Rytwinski 2009; Morales-González et al. 2020) not only at local, but also at landscape level (Proctor et al. 2012; Bischof et al. 2017; Finďo et al. 2018). Large LTI are usually overlapping, altering or sometimes even interrupting wildlife/ecological corridors, especially if the infrastructures are not permeable, in the absence of properly designed and placed underpasses, overpasses and other crossing structures (Van der Ree et al. 2009). Considerable efforts are, thus, being made to maintain ecological connectivity at the landscape level (Hilty et al. 2019; Keeley et al. 2019) in order to allow species movement. Dedicated ecological connectivity studies are needed in this respect (Loro et al. 2015; Mimet et al. 2016) and to integrate their results into early planning processes.

In the mountainous areas of North America, western or northern Europe, LTI mitigation is more commonly implemented (Van der Grift et al. 2013) than in the Carpathian ecoregion. Moreover, differences exist in implementation of LTI between the eastern and western part of the Carpathians. This is mainly due to the political and institutional past and socio-economic differences between the countries of the Carpathian ecoregion.

The lower development of LTI and the relatively smaller human pressure, in general, in the Carpathians, compared to, for example, western Europe, supports the greatest populations of large carnivores in Europe, outside Russia (Chapron et al. 2014). However, habitat fragmentation started to increase lately across the whole Carpathians because of the growing and legitimate need for socio-economic development (Hlaváč et al. 2019) and is likely to affect the large carnivore species that are present in the ecoregion, namely the brown bear (*Ursus arctos* L.), grey wolf (*Canis lupus* L.) and the Eurasian lynx (*Lynx lynx* L.). This is already reflected in the overall length of motorways developed in the Carpathian countries which more than quintupled in the last three decades. This dramatically increased building of road infrastructure in the region, with further infrastructure to be planned or rapidly expanded and/or upgraded, is happening without implementation of suitable mitigation measures. The main reason is a long-term negligence of wildlife-traffic-collision problems in the past, absence of studies on wildlife movement and absence of proper ecological assessment in the area of planned infrastructure. It is absolutely necessary to plan and implement wildlife mitigation measures on planned roads/railways (Fedorca et al. 2019) and also enhance migration permeability during the upgrading process of existing ones.

Our focus in the paper is to document the negative effects of LTI on wildlife, more specifically on the ecological corridors in the Carpathian ecoregion (as the area of interest) used by the large carnivores present here. We selected this group of animals as focus species, considering that we gathered data and knowledge related to it in conjunction with transport in a systematic way from 2017 to 2021 through different conservation projects. Last but not least, large carnivores are umbrella species and their conservation brings benefits to several other large mammals and vertebrates in general (Hlaváč et al. 2019).

The aim of the paper is to provide a comprehensive review of the LTI development (as grey infrastructure), ecological corridors conservation (as part of green infrastructure) and solutions for harmonising grey and green infrastructure in the Carpathians. These two fields, transportation and nature conservation, need concrete policy actions for their reconciliation and we sought to provide the basis for this in the region.

We provide a brief overview of: (1) the Carpathian ecoregion to better understand the regional context, (2) relevant legislation governing nature conservation and transport infrastructure development, (3) status of transport infrastructure in the region, (4) key ecological aspects including status of ecological connectivity and identification of ecological corridors for large carnivores, (5) effects of current road and rail transportation on ecological corridors in the Carpathians, (6) positive and negative examples of transport infrastructure development in the Carpathians and (7) knowledge, practice and other gaps in avoiding fragmentation by transport infrastructure development. Furthermore, we propose a set of recommendations to maintain ecological connectivity while developing transport infrastructure in the Carpathians, which are also applicable in other areas of the world with similar problems.

Methods

We collected information on projects and studies/reports carried out on our topics of interest especially in the Carpathian ecoregion. Qualitative research of data and information was sought for exploring and synthesising the key results obtained in previously conducted relevant research and nature conservation projects and activities.

Datasets on transport and biodiversity have also been gathered and databases investigated and interrogated to select the most appropriate pieces of information. We reviewed the most relevant legislation in connection with biodiversity conservation, ecological connectivity, strategic environmental assessment, environmental impact assessment, appropriate assessment, spatial planning etc. at European, Carpathian and national levels.

The main source of information related to transport infrastructure and ecological corridors in the Carpathians originated from the TRANSGREEN (DTP1-187-3.1), ConnectGREEN (DTP2-072-2.3) and SaveGREEN (DTP3-314-2.3) projects (e.g. Hlaváč et al. 2019; Papp and Berchi 2019; Okániková et al. 2021), which first addressed, in a systematic way, the overlapping between LTI development and connectivity conservation in this region.

To complete the picture of transport development and ecological connectivity at the national levels, as well as to provide country-specific information regarding different practices, stakeholder engagement in the form of meetings was carried out.

The most relevant international and scientific literature available regarding our topics of interest was consulted, in order to better understand and position the Carpathian issues, in relation to the global context. In this respect, we searched for publications in databases/research tools, such as Web of Science, Scopus, CrossRef, Google Scholar etc. We used the following keywords and combinations: habitat fragmentation, linear transport infrastructure, transport infrastructure and ecological connectivity, threats to ecological connectivity, conservation of large carnivores, ecological connectivity and large carnivores. We searched the 1960–2021 interval and we considered the most cited and newest articles of interest as main conditions/criteria.

Maps were developed using ArcGIS 10 (ESRI 2011) by collecting and integrating data from both reliable literature and results generated through the TRANSGREEN, ConnectGREEN and SaveGREEN projects.

Results and discussion

The Carpathian ecoregion

The importance and vulnerability of the Carpathian mountains

Mountain environments cover only about 25% of the total land area on the globe, but are shelter to over 85% of the planet's species of, for example, amphibians, birds and mammals, many of them being restricted to mountains. Mountains play a multitude of roles for Earth's biodiversity and influence surrounding lowlands through biotic interchange, changes in regional climate and nutrient runoff (Rahbek et al. 2019a, 2019b). They occur in half of the world's biodiversity hotspots (Jacobs et al. 2021).

Climate change is affecting the mountain ecosystems at a faster rate than other terrestrial ecosystems (Jacobs et al. 2021) and temperature rises tend to be positively correlated with elevation (Pepin et al. 2015) and is expected to be more prevalent in the northern latitudes (Nogués-Bravo et al. 2007). The Carpathian Mountains are included in this trend, being exposed to multiple other stressors besides climate change that can affect the exceptional biodiversity values present here, especially the rapid expansion of LTI and other types of infrastructure.

The Carpathian ecoregion (Fig. 1) covers 209,256 km^2 (CERI 2001) and is shared by seven countries: Czech Republic, Slovakia, Poland, Hungary, Ukraine, Romania and Serbia. The studies on climate change affecting biodiversity in the Carpathians are scarce (Gurung et al. 2009; Werners et al. 2014a, 2014b; Hlásny et al. 2016; Kruhlov et al. 2018) and the combined effects of both climate change and habitat fragmentation due to LTI development has not been addressed and quantified yet.

Our broader focus on the Carpathian ecoregion is relevant in the context of large carnivores' conservation, considering their need for extensive territories on one hand and, on the other, of LTI development which is more prevalent in the lower lands of the Carpathians.

Natural values and geography

Thanks to their exceptional natural values, including a great variety of endemic plants and animals, but also vulnerability, the Carpathians are included in WWF's "Global 200" list of major ecoregions in need of biodiversity and habitat conservation (WWF 2001).

More than 60,000 native species, excluding microorganisms, are estimated to be present in the Carpathians (UNEP 2007). The Carpathians are home to approximately 4,000 vascular plants (Tasenkevich 1998), 35,000 invertebrate species, mainly insects, soil mites and spiders and over 500 vertebrate taxa, including mammals, nesting birds, amphibians, reptiles and fish and lampreys (UNEP 2007).

Three out of the five large carnivore species from Europe are present in the Carpathian ecoregion, namely the brown bear (*Ursus arctos*), grey wolf (*Canis lupus*) and the Eurasian lynx (*Lynx lynx*) (CERI 2001; UNEP 2007). Chapron et al. (2014) estimated 7,200 brown bears, 3,000 grey wolves and 2,300–2,400 Eurasian lynxes. Currently the overall size of these large carnivore populations in the Carpathians might be higher as a result of different conservation efforts and projects implemented in the region, as well as of favourable legislative framework at the EU level. Considering that these species are sensitive to habitat fragmentation caused by LTI (Proctor et al. 2012; Bischof et al. 2017; Find'o et al. 2018) and need extensive territories to satisfy their needs, concrete and intensive conservation efforts and harmonised management measures need to be put into action in the Carpathian ecoregion in a concerted way (Papp et al. 2020).

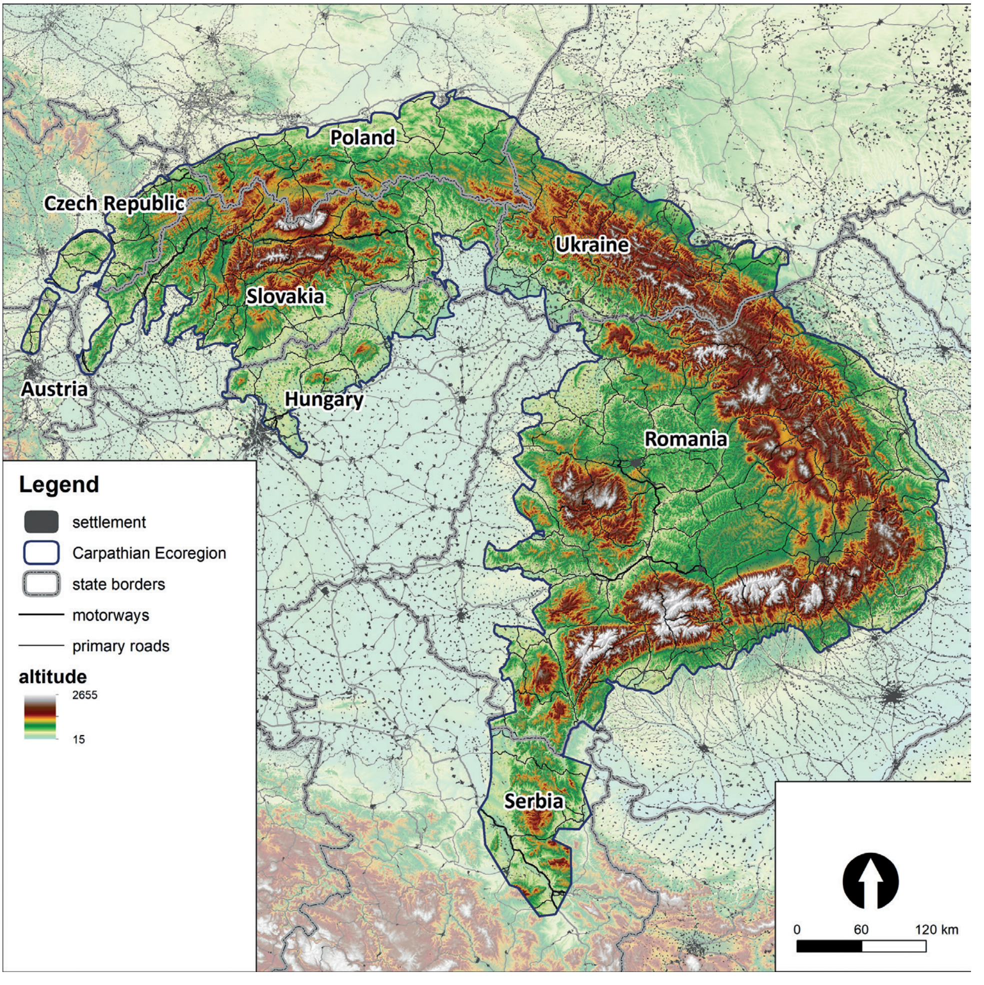

Figure 1. The Carpathian ecoregion.

The Carpathians have a length of 1,500 m, an average altitude of 850 m, the highest parts being in the northwest and south, with the greatest elevation in Slovakia, 2,655 m (UNEP 2007).

Rising temperatures have been recorded in all seasons for the period 1961–2010, with substantial warming of up to 2.4 °C in summer seasons and the model projections suggest a future temperature increase of up to 1.8 °C for 2021–2050 (EEA 2017).

The Carpathians are an important water source for three major rivers, namely the Danube and Dniester, flowing into the Black Sea and the Vistula River, flowing into the Baltic Sea.

The Carpathians are not only home to wildlife, but also to over 17 million people living in both small remote villages and major cities (UNEP 2007).

As a result of the political transformation of 1989, accelerated changes in land-use and land-cover started to occur in Central and Eastern Europe, especially due to profound changes in agriculture, improvements in people's welfare, growth in the tertiary sector and migration from rural to urban areas (Turnock 2003). Farmland abandonment increased in this period most probably in relation to institutional changes and restructuring of property rights (Munteanu et al. 2017). In addition, farmland abandonment in the Carpathian region threatens cultural landscapes and their associated biodiversity, although this can, in turn, increase carbon sequestration (Kuemmerle et al. 2008).

Relevant legislation for ecological connectivity in the Carpathians

Relevant legislation at international level and implications for the Carpathian countries

The first European nature conservation convention, the Bern Convention, signed in 1979, is the European contribution to the sustainable conservation of the world's biodiversity. The Bern Convention developed the Emerald Network, a group of selected natural areas hosting crucial and threatened biodiversity in Europe (CoE 2021).

The contribution of EU member states to the pan-European Emerald Network is represented by the creation and management of the Natura 2000 Network (European Commission 1992, 2009), which is the largest coordinated network of protected areas in the world (EEA 2021). However, the Natura 2000 Network is only applicable in the EU member states, meaning that, in the Carpathian region, it is the main conservation tool in Czech Republic, Slovakia, Poland, Hungary and Romania (Fig. 2). A total of 1,178 Natura 2000 sites were designated by these countries in their Carpathian Mountain area. In the other two non-EU Carpathian countries, Ukraine and Serbia, the Emerald Network is the key conservation instrument (Fig. 2), having 49 Emerald sites designated in their Carpathian area.

The European Commission (2021a) also promotes the conservation of the five large carnivore species found in Europe and its guiding documents are used by the Carpathian countries to improve their conservation efforts of the three species that are present in the area and to develop national action plans.

The EU's Biodiversity Strategy for 2030 (European Commission 2021b) is favouring both large carnivores and ecological connectivity conservation. The EU Strategy on Green Infrastructure is another EU-wide strategy relevant in the context of ecological connectivity and sustainable transport development.

The Convention on Environmental Impact Assessment (EIA) in a Transboundary Context or the ESPOO Convention, adopted in 1991, is another important legislative instrument. Given that seven nations share the Carpathian Mountain range and that large infrastructure projects including LTI are often developed between countries as part of different major transport corridors of international importance, the ESPOO can represent a valuable tool when mitigation measures, for instance, are not properly planned by a certain country, especially as a non-EU country.

The most important transport related policy of the European Commission (2021c) is the Trans-European Transport Network (TEN-T), directed towards the implementation and development of a Europe-wide network of roads, railway lines, inland waterways, maritime shipping routes, ports, airports and rail-road terminals. Three of the nine core transport network corridors are crossing the Carpathian area: Baltic Adriatic, Orient/East Mediterranean and Rhine-Danube (European Commission 2021d). The existing LTI, developed within these large transport corridors, is impacting to some extent the ecological connectivity in the Carpathian region. In the eastern part of the Carpathians, especially in Romania, the LTI, corresponding to the Orient/East Mediterranean and Rhine-Danube transport corridors, is still under development and concrete measures have to be taken in order to either avoid, mitigate or ultimately compensate for the potential environmental impacts.

The only multi-level governance mechanism covering the whole of the Carpathian area is the Framework Convention on the Protection and Sustainable Development of the Carpathians (Carpathian Convention), adopted in 2003 by the seven parties. It has two specifically relevant protocols to our topic: Protocol on Conservation and Sustainable Use of Biological and Landscape Diversity and Protocol on Sustainable

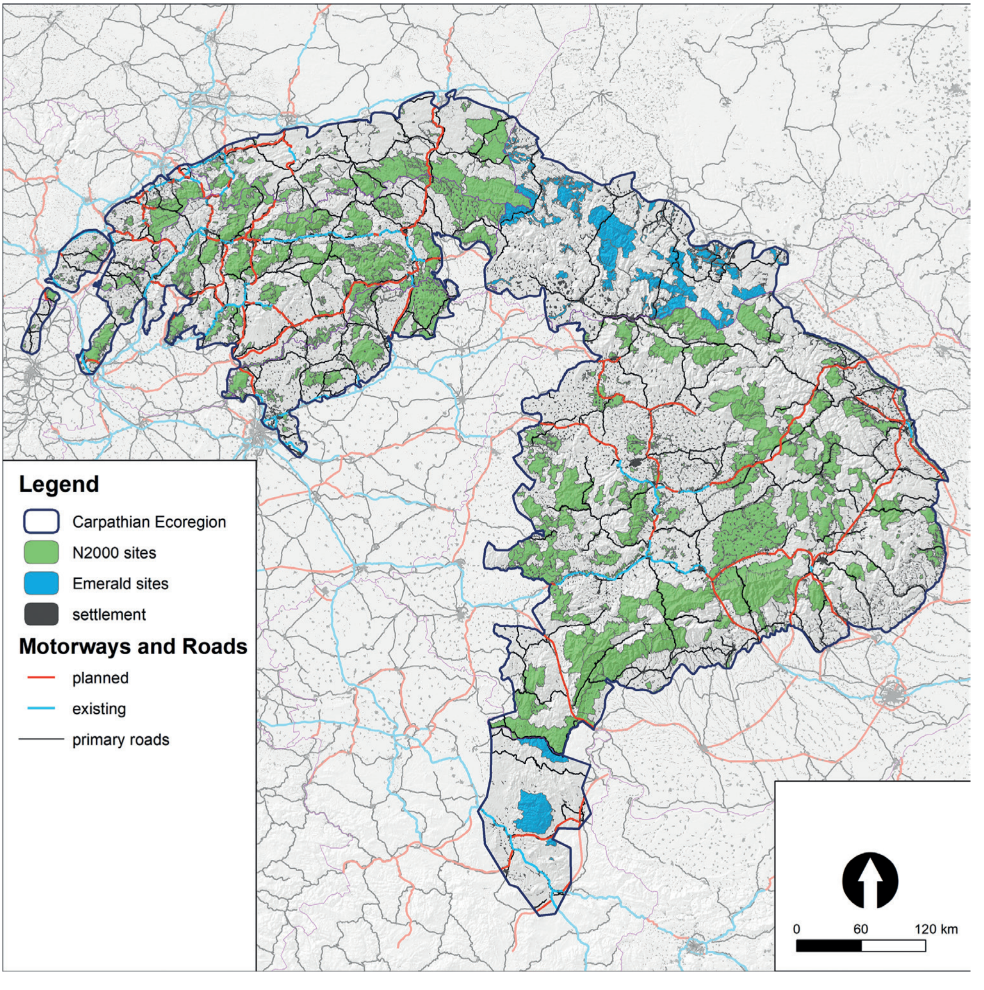

Figure 2. Natura 2000 and Emerald sites and transport network (motorways and roads) in the Carpathians.

Transport (UNEP Vienna Programme Office 2021). These two protocols set basically the framework for conserving biodiversity and maintaining ecological connectivity, while developing transport infrastructures in the Carpathians. In addition, the parties to the Carpathian Convention adopted the International Action Plan on Conservation of Large Carnivores and Ensuring Ecological Connectivity (Papp et al. 2020; UNEP Vienna Programme Office 2020), which is framing a unique and innovative example of a participatory and coordinated effort at transboundary level for implementing a population-based conservation of large carnivores, benefitting not only the Carpathians and the broader Danube Region, but also other regions in Europe and beyond. The second strategic objective of the Plan is to "Prevent habitat fragmentation and ensure ecological connectivity in the Carpathians" and contains a major action for mainstreaming biodiversity into transport planning and development.

Biodiversity and connectivity conservation is a priority action also under the macro-strategy European Strategy for the Danube region (EUSDR 2020), the Carpathians being part of the wider Danube region.

Relevant legislation at national levels related to ecological corridors

Since joining the EU, Czech Republic, Slovakia, Poland, Hungary and Romania gradually harmonised their national legislations with the EU regulations. Some of these countries (e.g. Czech Republic) have a higher level of compliance with EU legislation than others (e.g. Romania), at least from a transport and environmental point of view. On the other hand, the non-EU countries, namely Ukraine and Serbia, are preparing for this harmonisation as part of their EU accession process. This means that, in the Carpathian region, there are consistent differences in the national legislation from EU to non-EU countries, but there are also differences even within the same country category.

In all Carpathian countries, there is relevant nature conservation related legislation which provides the framework for conserving ecological corridors. However, all countries are lacking in official methodologies for the identification and designation of ecological corridors, which, in practice, makes connectivity conservation difficult and often ineffective.

Czech Republic and Slovakia are the most advanced countries in terms of connectivity conservation, where it is actually possible to protect ecological corridors and to maintain landscape connectivity through specific national nature conservation instruments.

In Hungary and Poland, there are also regulations regarding ecological corridors; however, the binding framework related to them is not well established, meaning that there are no uniform rules to determine corridors and there is no consistent network of corridors at the national level.

In Romania and Serbia, the protection and management of ecological corridors is not yet clearly defined, even though there are provisions related to the ecological network, including definitions. In practice, there are no legal obligations and restrictions imposed to secure ecological corridors. The only country in the Carpathians with a dedicated law on the preservation of the ecological network is Ukraine; however, its practical implementation is facing difficulties due to conflicting sectoral legislation or lack of dedicated funding for the identification of ecological corridors.

Papp and Berchi (2019) collected further information on the most relevant pieces of legislation at national levels in all the seven Carpathian countries.

In the absence of officially designated corridors, clear legal obligations and specific binding management measures to secure ecological connectivity, LTI development will remain one of the greatest threats to the integrity of natural habitats and functionality of existing ecological corridors in the Carpathians.

SEA, EIA, AA procedures and LTI planning in the Carpathians

The Strategic Environmental Assessment (SEA), Environmental Impact Assessment (EIA) and Appropriate Assessment (AA) can additionally contribute to a higher level of biodiversity and ecological connectivity protection by assessing the impact of different strategies, plans, programmes or projects on them.

The Directive on the assessment of the effects of certain plans and programmes on the environment (European Commission 2001), also known as the "SEA" Directive, requires and regulates the environmental assessment of certain plans and programmes which are likely to significantly harm the environment, for example, transport master plans. In the context of TEN-T further development and general transport planning, it is important to reconcile the descriptive and analytical aspects of the SEA and, in this respect, Fischer (2006) proposed a generic SEA framework for evaluating practice and developing further guidance.

The EIA Directive (European Commission 2014) on the assessment of the effects of certain public and private projects on the environment, requires environmental assessments for certain projects like LTI development, which can have a significant impact on the environment by virtue, before a development consent is given by the competent national authority.

AA is required by the Habitats Directive when a plan or project, either alone or in combination with other plans or projects, might impact a Natura 2000 site. The different LTI projects generally have an impact on Natura 2000 sites or other protected area categories, especially if developed in mountain areas like the Carpathians where there are several protected plant and animal species. AA is thus a prerequisite and shall constitute an integral part of SEA and EIA procedures.

The main issue in implementing the SEA, EIA or AA in the Carpathian countries is represented by the fact that the cumulative effect is not calculated properly or not at all. Several assessments of the effects of LTI on biodiversity conclude that there is no significant harm or provide a basic set of minimum mitigation measures and do not consider, for example, nearby electric fences, European road, railway and river (Fig. 3). In Romania, for instance, the ecological corridors are not identified and designated, so it is difficult to consider them in the planning process, which leads to an increase in habitat fragmentation.

In all Carpathian countries, based on previous experience in the construction of LTI, especially motorways, the greatest problems are seen in assessing the impact of the transport corridor on sustainable land development. In the Czech Republic, a key problem that is addressed is the impact of the new infrastructure on the environment, in particular, the elimination of health impacts (noise and vibrations, air pollution),

Figure 3. Cumulative impact of **a** highway sector between Turda and Aiud in Romania **b** Mureș River **c** railway **d** European road E81 and **e** electric fence used to keep wildlife away from the agricultural field, on the permeability of the landscape, not assessed.

the location of the linear construction in the landscape and the solution to the issue of fragmentation, the interruption of ecological corridors.

The benefits of taking an active and conscious part in shaping local spatial policies are generally not properly explained in the Carpathian countries and, therefore, low social awareness in the area of spatial planning and environmental protection can be observed, especially in Poland and Romania.

The problem of habitat fragmentation due to LTI has been underestimated in the Carpathian countries for a long time. In Slovakia, for instance, there are just a few studies aiming at the identification of core areas and ecological corridors. There is, indeed, an EIA analysis carried out during a landscape planning process, but it is rather a theoretical analysis lacking in reliable field data and validation, which is basically common to all Carpathian countries, excepting to some extent, Czech Republic. In Hungary, to regulate or decrease the impacts of LTI on natural habitats, the alignment is chosen in the planning stage, based on the least number of most sensitive areas each alternative is crossing.

In Serbia, as well as in Romania and Ukraine, generally there are no comprehensive habitat and species distribution maps which could provide a sound basis for integrative planning of LTI.

In Ukraine, there are specific provisions and recommendations to construct wildlife crossing structures and fences along certain roads, but they largely remain as recommendations, not as obligations.

In the absence of clear commitments to identify and designate ecological corridors in the Carpathians, many mitigation measures are not properly designed and certainly not implemented in proper places. Moreover, the lack of harmonisation of cross-sectoral policies and strategies is also leading to increased fragmentation in the region.

The evolution of transport infrastructure in the Carpathians

Ancient trade routes have crossed Europe since time immemorial. The Carpathian region is located at the crossroads of east–west (from south-eastern Europe/Asia towards western Europe) and north–south ("Amber road" Baltic-Adriatic). Therefore, the role of transport has always played a crucial role in the economic life of the Carpathian region. The complicated orography of the region predetermined the best routes for transport networks. Their directions followed the deep narrow valleys of main rivers embedded in mountain ranges. Other human activities were also concentrated in these favourable locations and formed barriers, which, in many cases, are hardly permeable for wildlife.

The 19th century laid the foundations for transport networks. Most of the region was under the rule of the Kingdom of Hungary in these times. The modern age country level transport network development concept was created and made official in 1848, which was designed to change the economic, social and political profile of the country. Besides improving the conditions of the most important inland waterways (Danube, Tisza, Dráva Rivers), it contained also the fundamental directives for the radial road and railway network (Oszter 2017).

Rail transportation reached its peak at the beginning of World War I (WWI). New post-WWI States faced the problem of a lack of infrastructure that was not designed to meet their needs, as the new geopolitical structure of Europe radically changed flows of trade and people in the region. The privileged position of railways began to decline in favour of the emerging road transport, which took over the role of main transport system during the 1960s. Its rising importance meant significant increase in motorisation and traffic intensities, which were difficult to be absorbed by existing road systems, especially in the hinterlands of main cities. The plans for the construction of motorway networks have been developed; for example, Czechoslovakia adopted it through a government resolution in 1963 (Lídl et al. 2009). However, the construction of the motorways in Carpathian countries continued very slowly. There were only 1,237

Table 1. Major road network in Carpathian countries and the projection to the future (CZ-Czech Republic, HU-Hungary, PL-Poland, RO-Romania, RS-Republic of Serbia, SK-Slovakia). Data source: MD ČR (2017); own GIS analysis, based on planning documents and maps from individual countries; the planned network figure is purely indicative, as many motorways are not yet spatially stabilised. ‡ In 1990, Czech and Slovak Republics were Czechoslovakia. § Czech Republic included 459 km of expressways into the motorway network from 1 January 2016. † Only part of Poland consisting of Voivodeships: Podkarpackie, Małopolskie, Śląskie and Świętokrzyskie.

	CZ	HU	PL†	RO	RS	SK
Motorways 1990 [km]	326‡	210	44	113	341	203‡
Motorways 2020 [km]	1.324§	1.253	538	904	925	497
Expressways 2020 [km]	373	474	216	-	32	244
Motorway and expressway density 2020 [km per 1000 km^2]	21.5	18.6	13.2	3.8	12.2	15.1
Planned motorways [km]	2.010	1.778	556	2.416	1.530	703
Planned expressways [km]	903	1.210	648	1.784	446	1.124
Density of complete planned network [km per 1000 km^2]	36.9	32.1	21.1	17.6	25.5	37.3
The network completion rate in 2020	58%	58%	63%	22%	48%	40%

kilometres of discontinuous motorway network in operation around 1990. Socio-economic changes after 1989 have brought an extremely rapid growth in traffic, which has spurred increased construction efforts; thus, the overall length of motorways in these countries more than quintupled in 30 years (see Table 1, Fig. 2). Further expansion is expected in upcoming years.

Key ecological aspects

Ecological connectivity, networks and corridors in the Carpathians

Ecological corridors are an important component of functional ecological networks and they primarily connect wildlife habitats and improve the functional connectivity of landscapes. Ecological connectivity, as defined by CMS (2020) "is the unimpeded movement of species and the flow of natural processes that sustain life on Earth". Connectivity is essential for supporting species' movement for individual survival, mating, searching food and other resources, gene flow in metapopulations and for colonisation of new areas.

However, ongoing habitat fragmentation and loss continue to threaten such functions and cause decline of populations and even local extinction (Crooks et al. 2017; Westekemper et al. 2021). Wide-ranging species, such as large carnivores, are more likely to experience negative population-level effects of habitat fragmentation and to exhibit low tolerance for human activity (McClure et al. 2017).

The case of the Carpathian Mountains shows the importance of maintaining landscape connectivity on an international scale.

The ecological corridors keep landscapes permeable and one way to identify them is by the species-specific needs and the movement function they provide. Large carnivores naturally do not respect state boundaries or any other administrative or political frontiers; however, infrastructure and urban development is driven mainly by national strategies. The most efficient tool for maintaining landscape connectivity is the development and protection of ecological networks. In the case of the Carpathians, a robust supranational system of core areas and corridors is the proper solution.

Several projects and studies focused on identifying ecological networks and corridors in the Carpathians for large mammals, for example, the "Mapping conservation areas for carnivores in the Carpathian Mountains" (Salvatori 2004), "Potential habitat connectivity of the European bison (*Bison bonasus* L.) in the Carpathians" (Kuemmerle et al. 2011), "Identification and assessment of the potential movement routes for European bison in the North-East of Romania" (Deju 2011), "Creation of ecological corridors in Ukraine" (Deodatus et al. 2013), BioREGIO Carpathians project (Appleton and Meyer 2014) and Life Connect Carpathians (FFI 2019). No matter the selected focus species, the identification of ecological corridors used different methodologies, making the results non-comparable at the Carpathian level, sometimes not even at the national levels.

Our approach to identify the ecological network for large carnivores in the Carpathians (Papp et al., in prep.) (Fig. 4), was based on the habitat suitability models using the actual occurrence data of large carnivores (bear, wolf and lynx) and a set of environmental variables including abiotic, habitat and anthropogenic factors. According to the habitat suitability models, core areas and stepping stones were identified and their function in the Carpathians was discussed with local and national experts. At the same time, the resistance surface was derived from the habitat suitability model and fragmentation geometry was prepared in order to express landscape permeability for large carnivores. Finally, a connectivity model was prepared presenting a coherent network of core areas, stepping stones and corridors. This output was reviewed with experts and improved, based on their feedback in order to produce the final version of the pan-Carpathian ecological network. This is the first comprehensive ecological network projected at the Carpathian ecoregion level, offering a robust instrument for spatial planners and other stakeholders to identify from the early stages of planning different LTI or other large infrastructure projects, potential conflicts between economic projects and nature conservation. The intersection points between these two can be further explored and solutions tailored to allow both development and conservation.

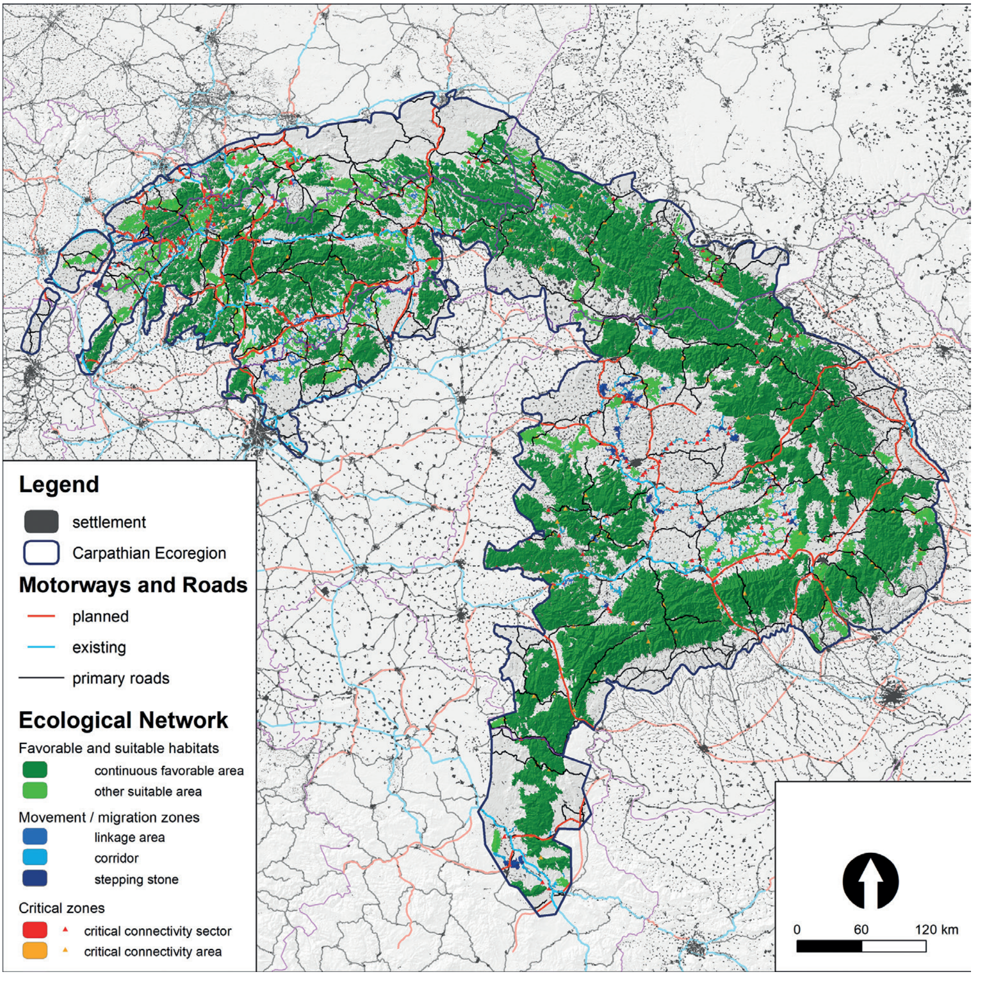

Figure 4. The ecological network for large carnivores in the Carpathians and the overlap with the transport network.

Other threats to ecological connectivity (beside transport) in the Carpathians

Another significant factor, which negatively influences ecological connectivity in the Carpathians, is increasing urbanisation and industrial development. The increasing human disturbance, especially around large cities and/or touristically attractive places, can also negatively influence wildlife, as well as natural habitats. This includes the use of 4×4 vehicles, jogging, biking and hiking, harvesting of non-timber products, hunting, skiing, the operation of ski lifts in the middle of protected areas etc.

Moreover, as a result of increasing intensive agriculture and large-scale forestry in many Carpathian countries, continuous and systematic loss of valuable large carnivore habitats is taking place.

The use of electric fences to prevent human-wildlife conflicts (e.g. to guard livestock, beehives, crops, orchards or properties, in general), although in principle an important and widely recommended conservation tool, can create a serious barrier effect, especially if deployed on a large scale.

The edge effect sometimes could possibly cause increased predation, increased mortality within corridors and the spread of invasive species and diseases. Some investigations confirm it to varying degrees (Haddad et al. 2015).

Last, but not least, climate change is also posing a serious, but hard to quantify threat at the moment to the Carpathian habitats.

Effects of current road and rail transportation on ecological corridors in the Carpathians

Transport development in the Carpathian region has been considerably delayed compared to western European countries. Accelerating the construction of motorways, trans-European roads and railways have brought accession to the EU to most countries (2004 - Czech Republic, Slovakia, Poland, Hungary; 2007 - Romania).

The Carpathians were inhabited by large carnivores continuously several decades ago. Bears, wolves and lynxes could move within mountain complexes with no limits. At that time, there was no need to delimit ecological corridors, because the area was continuously passable. The absence of officially designated ecological corridors and pressure to accelerate construction of transport infrastructure, or of other types of infrastructure, often led to the original ecological corridors being irreversibly interrupted.

Transport infrastructure in the Carpathians is typically located in mountain valleys as already indicated. Constructing new transport infrastructure in such areas always brings expansion of housing development as well. As a result, barriers often accumulate at the bottom of the valley - artificially fortified rivers, roads, motorways and railways - all run here in parallel and supplemented by residential and industrial development. Mountain valleys are, therefore, gradually becoming total barriers for animals. Some mountain complexes within the Carpathians are already surrounded on all sides by such barriers. Originally contiguous pan-Carpathian populations of large carnivores are gradually divided into smaller isolated units hardly capable of long-term survival. Transport infrastructure also involves animal mortality caused by traffic.

The level of fragmentation caused by transport infrastructure (Fig. 4) is, of course, different in various parts of the Carpathians. The western Carpathians along the border of the Czech Republic, Slovakia and Poland belong to the most affected parts. Rapid road and motorway development took place in this area during the past years and mountain ranges, such as Beskydy, Kysuce, Malá Fatra or Beskid Śląski, are almost isolated with a few last passages existing here, often only several tens of metres wide. The issue of fragmentation has already been given a lot of attention in this area for many years. All potential ecological corridors have been identified here and construction of several green bridges over existing roads and motorways is proposed at the most significant places. The situation is serious in other parts of Slovakia as well, but the solution is unfortunately complicated by the fact that a network of ecological corridors for large carnivores is not officially delimited here (Hlaváč et al. 2019).

Transport infrastructure development in Ukraine is, so far, not as fast as in other parts of the Carpathians. However, even here, quick recreational development occurs near existing roads, which creates barriers often tens of kilometres long.

Hungary is not a key country in terms of large carnivore occurrence and movement, but there are several areas in the north near the border to Slovakia (Bükk National Park or Aggtelek National Park), where a migration connection to Slovak populations still exists. In order to ensure the long-term existence of large carnivores in this area, it is necessary to identify and designate all significant ecological corridors and to manage them effectively, especially in places of their crossings with transport infrastructure and with the cross-border links to the Slovak populations that must be carefully taken into account.

Romania has the largest unfragmented forest areas and the largest populations of all three large carnivore species (Chapron et al. 2014). Due to the lack of official designation and recognition of ecological corridors in Romania, the effect of road and rail transportation on wildlife corridors has not yet been properly addressed. The current road network intersects several Natura 2000 sites. The first "green bridge" ever to facilitate the crossings of a highway (Lugoj-Deva) by large carnivores (Fig. 5F) was recently built (2018).

Ecological corridors have not been comprehensively defined in Serbia. There are also no studies trying to define the effect of current transport infrastructure on large carnivore populations in this country.

From the Carpathian countries, only the Czech Republic has officially delimited a network of ecological corridors for large carnivores. Delimiting ecological corridors and ensuring their protection in spatial planning remains a challenge for all Carpathian countries in the upcoming period. Whether the Carpathians can keep hosting viable populations of large carnivores in the future will depend on how well this challenge will be handled.

Positive and negative examples of transport infrastructure development in the Carpathians

Positive examples of transport infrastructure development in the Carpathians

During the railway reconstruction in the Beskydy Protected Landscape Area, eastern Czech Republic, two underpasses (Fig. 5A) were built. They meet the requirements to facilitate the movement of large carnivores. The permeability of the railway sections was improved, a fact that was confirmed by the sand belt monitoring and snow tracking of animals passing through the underpasses. Four ecoducts are currently under construction as part of the extensive modernisation of the D1 motorway between Prague and Brno as a contribution to defragmentation.

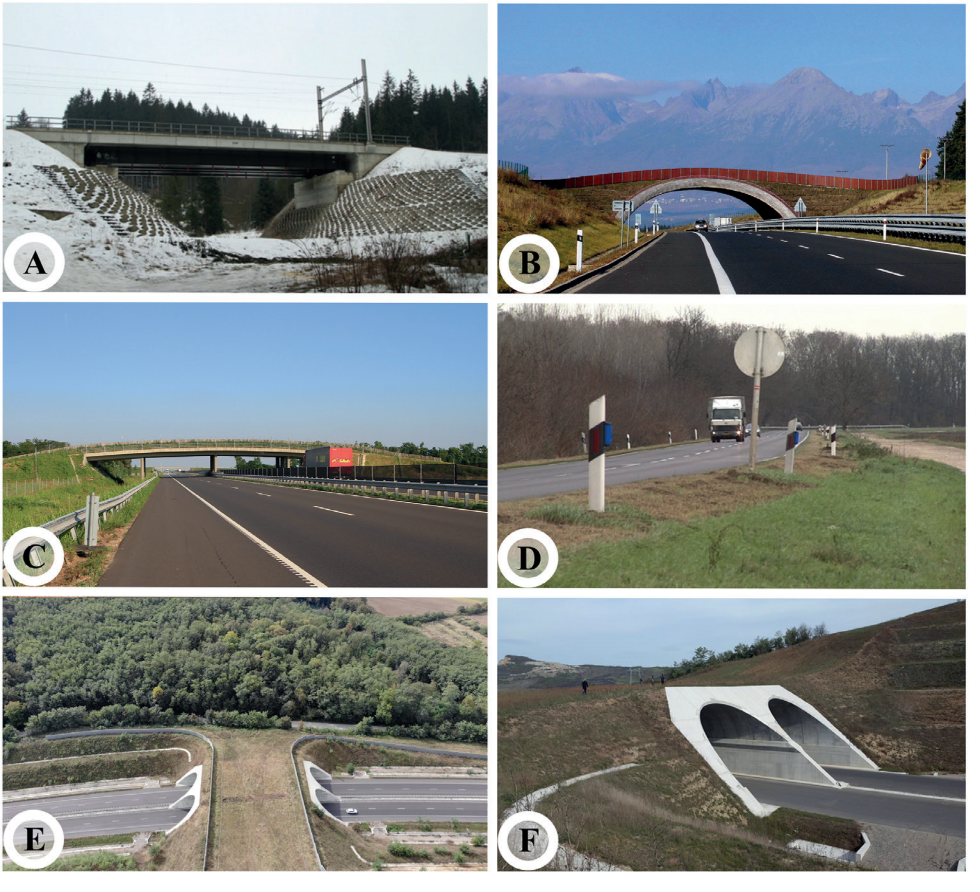

Figure 5. Positive examples of transport infrastructure development in the Carpathian countries **A** underpass constructed on the railway in the cadastre of the Mosty u Jablunkova close to national border in Czech Republic **B** overpass connecting the High and Low Tatra Mountains in Slovakia **C** overpass on M43 between Szeged and Nagylak in Hungary **D** blue retro reflectors installed on odometers on Main Road1 in Hungary **E, F** the first green bridge ever built in Romania on Lugoj-Deva highway, close to Brănișca Village

Besides some prolonged viaducts on some road sections, two green bridges exist in Slovakia. The first is connecting the High and Low Tatra Mountains (Fig. 5B). The second one is the so-called ACC (Alps-Carpathians Corridor) north of Bratislava that should enhance wildlife movements between Slovakia and Austria. This contribution to defragmentation started in 2016, being the first attempt in Central and Eastern Europe to build such a structure over an existing operating motorway.

Along the TEN-T network in Poland, several overpasses (green bridge-type crossings) that allow wildlife movement already exist. Moreover, bridges over watercourses are adapted to the migration/movement of animals. On the motorways, there are also structures for medium size animals, such as underpasses or culverts.

In Hungary, best practices refer to wildlife overpasses built over, for example, motorway M43 in south-east (Fig. 5C) or motorway M85 in the western part. Furthermore, several underpasses for medium-size animals, as well as noise, light-pollution and bird protection walls, have been built. Blue retro reflectors were also installed on odometers on Main Road1 in Hungary to reduce wildlife collisions (Fig. 5D).

As of today, there are no concrete examples of sustainable transport development in Ukraine, but there are intentions in this respect. Some decisions from the past can be considered as being sustainable, taking into account that they create conditions for permeability of motorways and railroads. They refer to the large bridges over Latorytsya River and the Beskydskiy Tunnel in the Carpathians, as well as numerous railroad culverts and bridges.

The first major transport infrastructure project in Romania that incorporated mitigation measures for ensuring connectivity within the landscape is the Lugoj-Deva highway. The original technical project was improved to include a system of solutions (i.e. tunnels, viaducts, green bridges) that allow the movement and dispersal of large carnivore species. Three green bridges have been built in total (Fig. 5E, F), two tunnels and three viaducts are expected to be realised according to the environmental permit.

There are no notable best practice examples in Serbia. At the moment, several highways are in the planning and designing process and possibilities/obligations for the construction of the migration/movement structures are explored; however, there is a perpetual problem of non-existing hard evidence of the ecological corridors at Serbian national level.

Negative examples of transport infrastructure development in the Carpathians

There are obviously many negative examples concerning the infrastructure development in the Carpathian region, even if they are not highlighted or properly documented.

For example, in the Czech Republic, the construction of four ecoducts in the southern and two that were built on the northern road circuit of Prague are very questionable. This is a suburban, very intensively used area, with high human activity. No endangered species can be expected to inhabit here or disperse through the road, which had a negative impression on public opinion about spending money on green bridges.

Zvolen–Kriváň section on R2 is a negative example from Slovakia. The express road has dramatic negative impacts on the movement of wildlife due to the absence of functional wildlife crossing structures. The road section completely isolates the valuable Poľana Mountain range, hosting the three large carnivore species, from the south of the country and further from Hungary.

The number, density and design of animal crossings is not optimal in Poland, not even in protected areas. The functionality of most passages for large and medium size animals is significantly limited by the structures' poor management/maintenance or use of the surrounding areas by humans. One example is the viaduct for large mammals close to Nietoperek, where the inappropriate height is limiting the possibilities of the animals to move from one way to another.

Hungary has a relatively low number of wildlife passages (40 in total, as of 2010) and they are not evenly distributed with regards to the main identified wildlife corridors. Hungary's largest viaduct is at Kőröshegy on the M7 motorway to the south of Lake Balaton. The necessity of this large viaduct was a topic of many debates at the end of the construction in 2007. In the proximity of the viaduct, a wildlife overpass was built in the correct location (leading out from a forest into a dirt road), but in a wrong way. It is basically not functional due to some technical mistakes/details that were overlooked. The monitoring of wildlife tracks revealed that deer and other species turned around.

In Ukraine, there are no dedicated wildlife crossings constructed at the moment and, generally, the movement needs of large mammals were not considered when LTI was developed.

Romania is another negative example where, due to the lack of an integrated approach in the case of Lugoj-Deva highway, a green bridge built in Brănișca area over the highway does not mitigate the negative effects of the adjacent existing county road and ends in the county road instead of passing it and leading the animals to the existing forest patch that borders the road.

In Serbia, there is a general belief amongst conservation groups that the development of LTI is done in a negative way, since the movement needs of animals are not properly addressed, partly because of the lack of ecological corridors designation and recognition. No dedicated wildlife structures have been built yet in Serbia.

Gaps in avoiding fragmentation by transport infrastructure development

We identified several gaps in terms of LTI development and connectivity conservation in the Carpathian ecoregion.

First of all, there are huge gaps in terms of knowledge availability, but also expertise and experience in properly dealing with the mitigation of negative effects of LTI. For countries like Romania, Serbia and Ukraine, this type of mitigation is relatively new and there is no sufficient national level capacity, expertise and experience to properly address and develop mitigation measures.

There are gaps in terms of understanding the effects and impacts of LTI projects in general. This is partly due to the fact that, generally, no studies have been carried out to assess the effects of LTI on wildlife and its movements or the effectiveness of the various mitigation measures, if any. In addition, the calculation and evaluation of cumulative effects is generally done in a very superficial way, in some ways because of the lack of clear criteria and guidance for evaluators and low public interest and participation in the spatial planning processes.

There is a lack of cooperation and open dialogue between many actors involved in the development of grey and green infrastructure. Usually, there is no genuine culture of cooperation between institutions in the countries of the region (this is still an effect of the former communist regime). This is a great barrier which should be overcome for the benefit and safety of both humans and animals.

There are also considerable practice gaps. There is no standard monitoring of the effectiveness of the implemented mitigation measures and already-built objects. There is no clear and documented evidence to understand or recommendations made about what types of mitigation measures work where and in which contexts. This type of monitoring is standard in many other countries and is perceived as a necessary step towards increasing the efficiency of funds spent to ensure the permeability of LTI for animals.

There is also a lack of studies on migration/movement behaviour of large carnivores in the Carpathian ecoregion. There are no harmonised methodologies implemented to perform large carnivores monitoring, sometimes not even at national levels (e.g. in Romania and Ukraine). Some studies were performed, especially in protected areas; however, that is not enough to avoid landscape fragmentation for large carnivores.

Generic biodiversity-related data are available at the EU level through different databases developed by the European Commission and the EEA. However, there are significant differences between the national databases. In some countries, data are typically scarce, especially in Romania, Ukraine and Serbia. In Romania, for instance, there is no national biodiversity database publicly available, which might help in identifying potential conflicts with transport infrastructure development in biodiversity-rich areas as in protected areas.

Open information on spatial distribution of roads and railways and their categories is commonly available from infrastructure managers for all countries, but not necessarily in GIS shape format. There is also a lack of official open spatial data. A good alternative is the OpenStreetMap project, which of course does not provide detailed or technical information such as, for example, green infrastructure elements.

Traffic intensities on roads are usually collected once in five years through detailed traffic censuses to the level of regional roads. Full data in spatial form are not freely available on-line in any country. Some countries present them in a map form in their respective viewer application or as exported raster maps (Czech Republic, Slovakia, Poland, Hungary). For Romania, detailed data are available from CESTRIN137 only as a paid service.

A source of traffic intensities is UNECE's e-Roads census, which only covers major roads included in the European Agreement on Main International Traffic Arteries "AGR". There is no intensity data for road traffic in Ukraine at all.

No data were collected within our projects regarding the level of disturbances from traffic. Information on these effects is generally missing; however, partial information on noise pollution can be obtained from the mapping done by the EU member states to assess exposure to noise from key transport and industrial sources and made available through two initial reporting phases, 2007 and 2012. This was required by the

Environmental Noise Directive (European Commission 2002). This mapping should also cover (besides the other sources) roads with annual traffic exceeding 3 million vehicles. In some countries, such data are available as raster in internet-based viewer applications and not as shape files.

Information about wildlife mortality on roads is quite well collected in Czech Republic from various sources, such as Nature Conservation Agency, police accident database, hunters; a common database is available for viewing on the webpage of the Transport Research Centre. Other countries (Ukraine, Poland) collect roadkill information through police, but Ukrainian data cannot be analysed properly due to the fact that the registration includes both domestic and wild animals. Romania started to implement a similar roadkill application tool as the one from Czech Republic, but not in a coordinated way at the national level. For Serbia, this type of information is not available.

Conclusions

The Carpathians are home to many large mammal species, including the three large carnivore species: brown bear, grey wolf and Eurasian lynx. The LTI network is not fully developed in the area, which gives the countries of the region the chance to plan and implement proper mitigation measures in adequate places to allow wildlife movement across the landscape. Mitigating for LTI at the regional level of the Carpathians will prevent habitat fragmentation and maintain the viability of large mammal populations and their associated ecosystems.

The issue of wildlife movement and transport has been generally underestimated in the ecoregion, so far. Only a few studies on the impact of traffic on wildlife movement and behaviour have been carried out. We emphasise the role and importance of performing high quality studies and recommend them especially in countries where the level of knowledge and experience in reducing the impact of LTI on ecological connectivity and wildlife is low.

The harmonisation of grey and green infrastructure is a long-term and complex process, but essential for both human safety on roads and well-being of large carnivores. Inclusive stakeholder participation, including improved communication, knowledge, data sharing and regular exchange and cooperation between Environmental, Transport and Spatial planning sectors, as well as other relevant parties, within the framework of, for example, stakeholder platforms, is needed from the early planning processes. Moreover, we recommend sustained cooperation with international professional bodies and networks (e.g. IENE - Infra Eco Network Europe) especially in countries with no or low experience and expertise in addressing the need for developing and implementing the most appropriate mitigation measures in the case of new LTI or upgrading process. Besides, other positive and negative examples of LTI development from around the globe should be made widely available especially to road and railway development and construction companies, decision-makers and other key stakeholders.

In terms of legislation related to the protection and implementation of ecological corridors, there are differences in the Carpathian region between the EU and non-EU countries, western and eastern countries and, in general, between countries. In principle, all Carpathian countries have legislation in place for ecological connectivity, but in practice and implementation, there are gaps and discrepancies due to either lack of harmonised legislation across relevant sectors, enforcement, funding or available tools (e.g. absence of the methodology for the official designation of ecological corridors). We recommend to improve and harmonise the legislation related to ecological connectivity and sustainable transport development in the Carpathian countries.

We suggest that the development and endorsement of methodologies for the official designation of ecological corridors in the Carpathian countries should be accelerated to avoid the interruption of ecological connectivity, especially in sensitive areas.

The assessment of cumulative impacts is superficially addressed in the Carpathian ecoregion. We stress the need that the planning and development of LTI, as well as mitigation measures, should also consider other potential barriers and threats to large carnivores at landscape level. In this respect, we also recommend that a transdisciplinary approach to the conservation of large carnivores should be widely applied in the Carpathians to decrease the threats to this group of species, as well as to ensure their sustainable conservation.

We urge the development of national and regional transparent databases where they are absent, including with roadkill information to facilitate the identification of conflicts with large carnivores and the selection of proper mitigation measures and locations where they should be implemented.

Monitoring of both wildlife and transport, including the efficiency of different wildlife crossing types in different contexts, is important to understand and justify the measures that are required for a sustainable transport network in the Carpathians and beyond.

A pool of experts and professionals should be developed in all sustainable transport-related fields. Road ecology needs more attention and development in the Carpathians.

Transboundary and transnational cooperation on improving ecological connectivity and conserving large carnivores is needed for a greater impact and coordination of efforts.

The effects of climate change on large carnivores and their habitats are not closely monitored in the Carpathians. The species' distribution and the location of ecological corridors might change due to habitat transformation and shifts. It is important to closely monitor and observe, respectively, to understand the changes and impacts of future climate changes on large carnivores and ecological corridors so that targeted actions can be identified and implemented in response. This is particularly important since ecological corridors are identified, based on the current distribution of habitats and focal species. However, we also have to consider the projections of the future distribution and changes in terms of habitats. Ideally, ecological networks should incorporate the connectivity needs of both current and future habitats. The same should be considered for any mitigation measures defined, to respond to both the present and predicted future needs of wildlife and society.

Our recommendations can also easily be implemented in other countries and mountain regions of the world, where there are similar main problems: increasing pressures and threats from LTI development on rich biodiversity areas and lack of harmonisation between the green and grey infrastructure. In such regions, the available knowledge and expertise is generally scarce and mistakes can be irreversible without proper documentation and guidance. In addition, improved connectivity between adjacent mountain ranges is crucial, especially when talking about species with large space requirements and in the light of the current global changes.

Acknowledgements

The information that led to the development of this paper was provided by TRANSGREEN (DTP1-187-3.1), ConnectGREEN (DTP2-072-2.3) and SaveGREEN (DTP3-314-2.3) projects, all financed by the Interreg's Danube Transnational Programme. All project partners of these projects were actively involved in delivering specific results which were the building blocks of the paper.

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Nature Conservation 47: 65–85 (2022)
doi: 10.3897/natureconservation.47.73010
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Do the roadkills of different mammal species respond the same way to habitat and matrix?

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Academic editor: C-R Papp | Received 14 August 2021 | Accepted 3 February 2022 | Published 25 March 2022

http://zoobank.org/AE8C4B5D-F47D-490E-A084-D968B99AA7E2

Citation: Cirino DW, Lupinetti-Cunha A, Freitas CH, de Freitas SR (2022) Do the roadkills of different mammal species respond the same way to habitat and matrix? In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 65–85. https://doi.org/10.3897/natureconservation.47.73010

Abstract

While road network expansion connects human settlements between themselves, it also leads to deforestation and land use changes, reducing the connectivity between natural habitat patches, and increasing roadkill risk. More than 30% of registered mammal roadkills in Brazil are concentrated in four species: *Cerdocyon thous* (crab-eating fox); *Euphractus sexcinctus* (six-banded armadillo); *Tamandua tetradactyla* (collared anteater) and *Myrmecophaga tridactyla* (giant anteater), the latter being categorized as vulnerable by IUCN redlist. Our aim was to understand how these animals' roadkills could be related to the land use proportions on landscapes all over the Brazilian territory, and investigate if the roadkill patterns differ among species. We collected secondary data on mammal roadkills (N = 2698) from several studies in different regions of Brazil. Using MapBiomas' data on land use and land cover, we extracted landscape composition around each roadkill sample. Through the proportion of land use and land cover in the area of influence where the roadkill occurred, we built binomial GLM models and selected the best ones by Akaike Information Criteria. For crab-eating fox and the six-banded armadillo, the best models include matrix coverage resulting in increased roadkill risk, while both anteaters' species have a habitat and a matrix component in their best models, with an interaction between the variables. These four species seem to be roadkilled in different landscape arrangements, but in all scenarios, anthropic areas had an important influence over the models. For habitat-dependent and more sensible species, such as *Tamandua tetradactyla* and *Myrmecophaga tridactyla*, the amount of matrix influencing the roadkill risk depends on habitat availability in the landscape. It changes the strength and direction of the effect according to the proportion of natural areas in the region, while with generalist species such as *Cerdocyon thous* and *Euphractus sexcinctus*, the quantity of human-modified coverage increases the risk.

Keywords
Conservation biology, environmental impact assessment, landscape ecology, road ecology, tropics

Introduction

Road ecology is a research area that aims to understand the impact of highways and railways on natural ecosystems, economics, and society. Many studies on this subject focus on one of the most conspicuous effect of roads: wildlife mortality by vehicle collisions (Forman and Alexander 1998; Forman et al. 2003; Laurance et al. 2009; Van Der Ree et al. 2015; Pinto et al. 2020; Teixeira et al. 2020). In temperate regions, such as North America, special attention is given to large mammals, because of the risk associated with collisions, causing fatalities, and human and economic injuries (Huijser et al. 2009). In tropical regions, on the other hand, attention is mostly paid to the high rates of wildlife mortality (Pinto et al. 2020), since the high diversity and high density of natural populations in these habitats lead to an elevated risk of biodiversity loss.

Changes in landscape composition and its structure are some of the main factors leading to biodiversity loss (Dirzo et al. 2014). Roads induce several landscape changes: firstly, the roads are by themselves one type of matrix on the landscape; secondly, this type of matrix causes both population isolation and mortality; and thirdly, roads provide access to remote areas, allowing expansion of agricultural frontiers, causing other major landscape changes (Nagendra et al. 2003; Jaeger et al. 2005; Fahrig and Rytwinski 2009; Laurance et al. 2009; Freitas et al. 2010). All those factors together lead to biodiversity loss (Teixeira et al. 2020). In order to better understand the impact of roads on ecosystems, we need to evaluate the effects of those linear infrastructures from a landscape perspective, searching for patterns that allow us to make guided decisions for biodiversity conservation strategies on large scales.

The majority of studies on road mortality focus on a small region, studying a road or a portion of it. Those studies are important to understand the local impacts of roads, and to search for patterns on specific landscape configuration. When we search for similar studies in Brazil, it is notable that some species are constantly found on roadkill registers (Dornas et al. 2012; Cirino and Freitas 2018; González-Suárez et al. 2018; Grilo et al. 2018). Many mammals in Brazil have large distribution areas, covering a great part of the national territory, and therefore, making it one of the most studied groups (Pinto et al. 2020). It happens because of their response to landscape changes, and their relative risk to human life, since collisions with larger animals can cause human injuries (Huijser et al. 2013; Abra et al. 2019). Landscape influence on mammal road mortality has been accessed by some studies in local scales (Bueno et al.

2013, 2015; Ascensão et al. 2019), but broader scales studies are scarce and needed to identify how different land uses affect the most frequent roadkill mammals on a national scale. Some species have high roadkill rates, such as *Cerdocyon thous* (Linnaeus, 1766), *Euphractus sexcinctus* (Linnaeus, 1758), *Tamandua tetradactyla* (Linnaeus, 1758) and *Myrmecophaga tridactyla* (Linnaeus, 1758) – the latter being considered as Vulnerable (VU) by IUCN, and locally extinct in some regions of Brazil (Miranda et al. 2014a). Those four species are among the most roadkilled animals in the Brazilian territory (Ribeiro et al. 2017; Cirino and Freitas 2018; Grilo et al. 2018). However, they have different degrees of sensitivity to landscape changes and configuration.

The crab-eating-fox (*Cerdocyon thous*) is one of the most frequent species in roadkill registers according to the "Banco de Dados Brasileiro de Atropelamentos de Fauna Selvagem" – BAFS (http://cbee.ufla.br/portal/sistema_urubu/urubu_map.php) and other published researches (Vieira 1996; Prada 2004; Rosa and Mauhs 2004; Cherem et al. 2007; Coelho et al. 2008; Rezini 2010; Lemos et al. 2011; Dornas et al. 2012; Cirino and Freitas 2018). In the evaluation of *C. thous*' extinction risks, one major threat is the roadkill (Beisiegel et al. 2013). Freitas et al. (2014) associated the roadkill of this species to *Pinus* sp. forestry cover in a road in a savanna region of southeastern Brazil. The elevated numbers of *C. thous* roadkill records might be a reflection of its high abundance, generalist habits, and the fact that its occurrence range is in the entirety of Brazil with the exception of the center of the Amazon forest (Lucherini 2015).

The six-banded-armadillo (*Euphractus sexcinctus*) is also a frequent species on roadkill records (Carvalho et al. 2015; Ribeiro et al. 2017). It is a species with fossorial habits, active predominantly at daytime, and mainly inhabiting open areas and forest edges (Medri et al. 2006). The occurrence of this species on forest edges can be an aggravating factor to its high run-over rate, since roads generate edge effect and discontinuities on native vegetation. In a published evaluation of the risks to six-banded-armadillo conservation, the impact of roadkill was listed as a needed research topic for this taxon (Silva et al. 2015).

Both anteater species (*Tamandua tetradactyla* and *Myrmecophaga tridactyla*) are more exigent in terms of habitat quality than the other two species studied in this research. They are less abundant, but also highly roadkilled. The giant-anteater (*Myrmecophaga tridactyla*) is a terrestrial Xernarthra that can move long distances by ground, which can aggravate the roadkill rate of this species. On the other hand, its roadkill is associated with native vegetation proximity to roads in a Cerrado area (Freitas et al. 2014), and to their own movement behavior associated with the proximity of roads to their home ranges and crossing habits (Noonan et al. 2021). The collared-anteater (*Tamandua tetradactyla*) has semi-arboreal habits, and can move both by ground and on tree canopies. It has been recorded in several road monitoring reports (Grilo et al. 2018). The landscape associated with the roadkill of this species in Mato Grosso do Sul state, Brazil, was riparian areas and grassland pastures (Ascensão et al. 2017).

Most road impacts mitigation measures focus on general recommendations, such as implementation of underpasses or fencing in roadkill hotspots, which usually comes in association with native or riparian vegetation, assuming that most animals would use those areas to move and cross the road. However, we cannot assume that all species have the same habitat requirements and patterns of space usage, since it is known that the rate of underpasses usage differs among species (Abra et al. 2020). Furthermore, the roadkill hotspot differs between vertebrate taxa, according to traits such as body size, type of locomotion and time of activity (Teixeira et al. 2013) and such hotspots might change its locations over time (Lima Santos et al. 2017; Teixeira et al. 2017). For a better mitigation of the impacts of roads on animal mortality, patterns and landscape characteristics associated with species' roadkill risk and habitat requirements must be investigated, since species differ in their abundance, occurrences and roadkill rates.

Understanding the landscape patterns linked to road mortality of those species can provide guidance for protection and conservation efforts aiming to mitigate the road impacts on wildlife. Together, these four species presented here represent between 34,7% and 38,8% of the total roadkills of medium-large sized mammals in Brazil (Cirino and Freitas 2018). Most studies on roadkills in Latin America focus on mortality, but just a few focus on how habitat and landscape patterns influence those roadkills occurrences (Pinto et al. 2020). Our aim is to analyze at a national level the effects of habitat and matrix amount on the mortality of those highly roadkilled species, while assessing the year and scale according to each occurrence. Our central hypothesis is that road mortality of different species responds differently to habitat and matrix proportions in the landscape.

Methods

Roadkill data collection

We collected a sample of georeferenced roadkill data from two main sources: (1) monitoring studies across the country; and (2) the "Banco de Dados Brasileiro de Atropelamento de Fauna Selvagem" (**BAFS**). The first one consists of previously published systematic studies in roads of different regions of Brazil; such data was provided by collaborators (see Acknowledgements – Coelho et al. 2008; Freitas 2009; Caceres 2011; Teixeira et al. 2013; Dornelles 2015; Freitas et al. 2015; Ascensão et al. 2017). The second is a dataset obtained at the Brazilian Center of Road Ecology of the University of Lavras, which gathers geo-referenced and validated citizen science roadkill data from a mobile phone app and from other studies across the country. The app works as follows: the user takes a photo of the roadkilled animal, the app then records the location of the photo that is sent for identification down to species level by an expert in the taxonomic group (Castro and Bager 2019). The records used in our analysis were those with adequate species identification, which depended on the quality of the photo and the degradation degree of the carcass. We selected the roadkill data of the four species focused in this study – *Cerdocyon thous*, *Euphractus sexcinctus*, *Tamandua tetradactyla*, and *Myrmecophaga tridactyla* – ranging from 2002 to 2015. We chose these species because they present high rates of mortality in Brazilian roads. For each roadkill occurrence, we created a random point in the same road segment, thus representing the pseudo-absence of roadkill. Thereafter, we used these data to build a roadkill presence (ones) and absences (zeros) matrix for each species, with the same number of absences and presences.

Landscape data and scale of analysis

For land cover and land use, we utilized the serial time data from MapBiomas (Projeto MapBiomas 2021), with a pixel size of 30 m, between 2002 and 2015. To access the exact landscape composition at the time of each roadkill occurrence, we used the land cover map of the correspondent year of the roadkill register. For example, if a *C. thous* was registered as roadkilled in 2006, we would collect the data from MapBiomas of the corresponding year and for the correspondent region. This process was performed to all evaluated species registers throughout the 14 years analyzed.

For each species, we considered a different influence buffer radius starting from the place of the roadkill, since each one has different home ranges, body sizes, and habits requirements. We estimated the mean home range for *C. thous* as 4.9 km^2 (Beisiegel et al. 2013), for *E. sexcinctus* as 0.7 km^2 (Silva et al. 2015), for *M. tridactyla* as 3.6 km^2 (Ohana et al. 2015), and for *T. tetradactyla* as 2.7 km^2 (Miranda et al. 2015). To assess the potential landscape influencing each individual we used a buffer with twice the radius of the home range approximated to a circle shape (A), resulting in the radius of roadkill influence (φ):

If the area of a circle is given by:

$$A = \partial r^2$$

where r is the radius of the circle, so the double of a radius of a circle of a given area is:

$$\varphi = 2\left(\sqrt{\frac{A}{\partial}}\right)$$

We used this radius size because the roadkill point may have occurred on the center of the home range, or on its border (Fig. 1); this way, considering a bigger radius of influence would prevent us from connecting the wrong area, or a smaller area, with the roadkilled individual. The radius for *C. thous* was 2.50 km, for *E. sexcinctus* 0.95 km, for *M. tridactyla* 2.14 km and for *T. tetradactyla* 1.85 km.

For each presence or absence of roadkills we calculated the proportion of land use and land cover inside the buffer based on MapBiomas land cover map for the corresponding year of the roadkill. The classes of land use and land cover considered in the analysis were: (1) forest; (2) savanna; (3) natural open areas; (4) forestry; (5) agriculture; (6) pasture; (7) farming; and (8) water. Farming represents the sum of agriculture and pasture in addition to mosaics or rotation of both classes in the same area. We conduct all landscape analysis and data extraction on ArcGIS v10.3 environment.

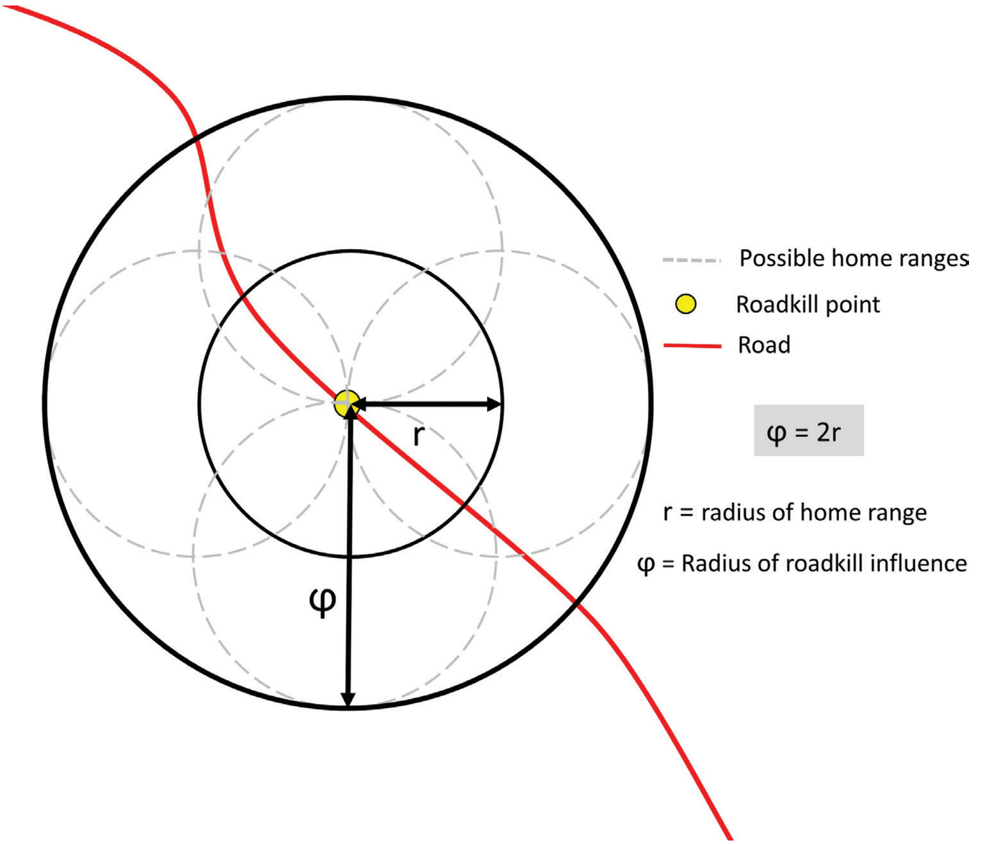

Figure 1. Scheme exemplifying the radius of roadkill influence chosen. For a given roadkill point using the simple radius of home range (r), we might exclude some of the landscape characteristics if the roadkill occurred in the border of the home range. Including the possible home ranges (approximated to a circular shape), and doubling the radius (φ), we ensure that all landscape composition associated with the roadkill occurrence is incorporated within the analysis.

Statistical analysis

To estimate the relative chance of roadkill of each species we constructed binomial generalized linear models (**GLM**), considering the matrix of presences and absences as our response variables, and the proportion of the eight landscape variables inside the radius of roadkill influence as our predictive variables. We built four groups of models, one for each species, with one or two predictive variables by model, combining variables in pairs, and considering the interaction between them. We discarded models with some degree of correlation (> 0.6 or < -0.6) between predictive variables (see Suppl. material 1: Fig. S1). Models with some level of collinearity between the two predictive variables (Variance Inflation Factor > 4.0) were excluded from the analysis (Tay 2017). Overall, we had 45 models for each species (see Suppl. material 1).

All models were ranked by Akaike Information Criteria (AIC) and selected by their corrected AIC value (AICc), with lower values of AICc representing the best models (Burnham and Anderson 2002). Models with AICc distance equal or lower than two ($\Delta AICc \leq 2$), and evidence ratio lower than 2 are considered equally plausible. The statistical analysis was performed on the software R 4.0.2 (R Core Team 2020) using the packages 'bbmle', 'numDeriv', 'effects', 'ggplot2' and 'corrplot' (Fox and Hong 2009; Wickham 2016; Wei and Simko 2021).

Results

Distribution of roadkill occurrences

We collected a total of 2698 georeferenced roadkill records across the country (*Cerdocyon thous* (N = 1282); *Euphractus sexcinctus* (N = 589); *Myrmecophaga tridactyla* (N = 422) and *Tamandua tetradactyla* (N = 405)) (Fig. 2). Overall, the distribution of the observations reflects a potential occurrence and abundance of the four species. Some biases can occur, since the data came from previous studies and citizen science, but to assess the landscape composition in the radius of roadkill influence, we had enough data in terms of quantity and spatial distribution, given the potential distribution of each species.

Model selection

For *Cerdocyon thous* and *Tamandua tetradactyla* only one model was selected as the best model by AIC criteria ($\Delta AICc \leq 2$ and evidence ≤ 2), while the remaining studied species had two equally plausible models. For *Cerdocyon thous* the best model shows a positive effect of agriculture and pasture proportion inside the buffer on the chance of roadkill: for each 10% of pasture cover in landscape the roadkill risk increases by 2.7%, while for agriculture it increases by 4.6%. (Table 1, Fig. 3). For *Euphractus sexcinctus* one selected model shows a positive relationship of roadkill risk with farming and forestry. On the other hand, the other models show a positive relationship with pasture and agriculture, these variables made up the farming class, so we only considered the first model, in which the relative risk of roadkill of *Euphractus sexcinctus* increases 6,5% and 14,7% for each 10% of land cover increment of farming and forestry, respectively (Table 1, Fig. 5). Both anteaters' best models include habitat land cover, matrix land cover and the interaction between them, which will be discussed in the next section (Table 1). For *Myrmecophaga tridactyla*, the best model includes an interaction between pasture and forest areas (Fig. 6), while for *Tamandua tetradactyla* the selected model includes the interaction between savanna and agriculture areas (Fig. 7). The other selected model for *Myrmecophaga tridactyla* includes an interaction between forest and savanna areas, but the effect of both variables on roadkill risk was not significant ($p > 0.05$).

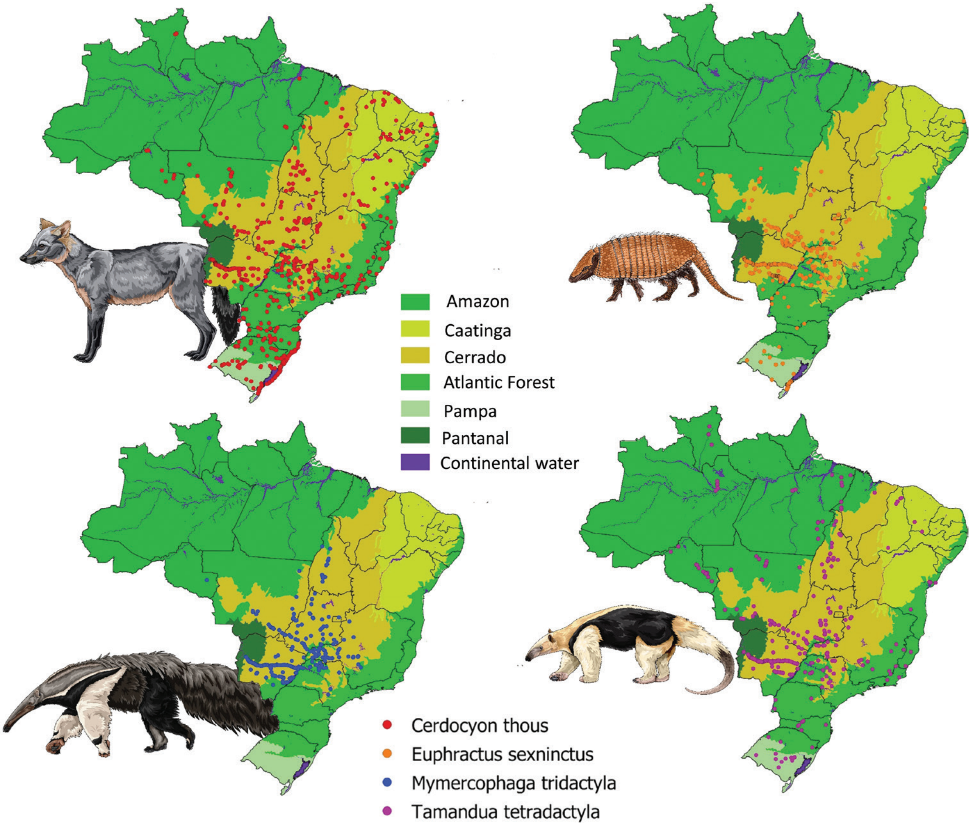

Figure 2. Roadkill samples distribution for the species studied. *Cerdocyon thous* represents the majority of roadkill samples, covering the entire territory. The other three species have samples aggregated in central Brazil, mostly in the Cerrado ecosystem.

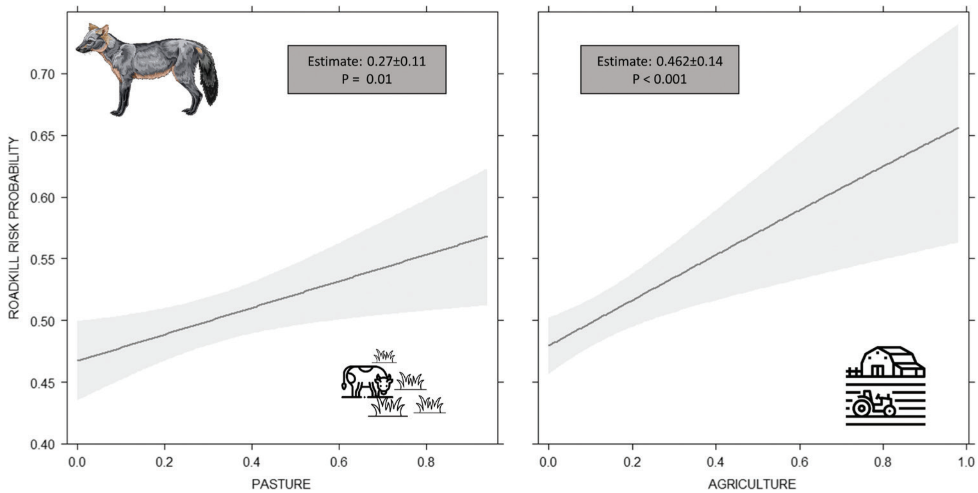

Figure 3. Best model selected by AIC for *C. thous* and its estimated coefficients. A model with two variables responded better to *C. thous* roadkill risk, being pasture and agriculture positively related to roadkill risk.

Table 1. Model selected by species according to Akaike criteria. dAICc represents the AIC distance; df represents degrees of freedom; weight represents how much the model explain de variables related to all other models; evidence is the highest weight model divided by the weight of the focal model. We just considered models with evidence lower or equal to two.

Species	Model	AICc	dAICc	df	Weight	Evidence
Cerdocyon thous	Pasture + Agriculture	3545.9	0.0	3	0.3080	1.00
Euphractus sexcinctus	Farming + Forestry	1612.4	0.0	3	0.3772	1.00
	Pasture + Agriculture	1612.8	0.3	3	0.3173	1.19
Myrmecophaga tridactyla	Forest + Pasture + Forest:Pasture	1170.6	0.0	4	0.2057	1.00
	Forest + Savanna + Forest:Savanna	1171.5	0.9	4	0.1309	1.57
Tamandua tetradactyla	Savanna + Agriculture + Savanna:Agriculture	1111.4	0.0	4	0.8495	1.00

Discussion

Landscape features – habitat, matrix and species dependency

Cerdocyon thous – The roadkill of this species responds positively to two matrix land-uses, pasture, and agriculture in the landscape (Fig. 3). Since it is a generalist species, it can occur in habitat borders, explore vast areas of human-modified landscapes and even use those regions as home ranges (Ferraz et al. 2010; Bueno et al. 2015). The use of those human-modified habitats by *C. thous* serves to show that habitat quality can also be an important factor when predicting roadkill risk. In those modified regions, the resources availability is scarcer and diffuser in the space than in preserved landscapes, making individuals move more in search of them (Regolin et al. 2021), thus increasing the chance of road encounter and, consequently, the roadkill risk.

Besides giving information on the studied animal mortality, roadkill records are also useful for assessing a species occurrence. We found registers of *C. thous* roadkill occurrences out of its original geographical distribution (Lucherini 2015) (Fig. 4). Originally, the crab-eating-fox had its habitat range limited by the dense Amazon forest, but the high-intensity of land use and land cover changes in the region led to the conversion of this forest into open areas, such as pasture and agriculture. That way, *Cerdocyon thous* may have had its geographical distribution expanded by the land use changes and deforestation in the Amazon forest. The growing agribusiness in the region has synergies with road expansion, which leads to several impacts on local ecosystems (Laurance et al. 2002), leading to fish-bone deforestation patterns (Laurance et al. 2002; Pfaff et al. 2007). These might be related to the savannization phenomena of the Amazon Rainforest (Sales et al. 2020). The fish-bones in the landscape resulted from roads being an arrow of habitat loss, and it was exactly in such regions that our data collection found roadkill registers of *Cerdocyon thous* (Fig. 4), as did other works on this species' roadkills (Gumier-Costa and Sperber 2009; Turci and Bernarde 2009).

As a generalist species, *Cerdocyon thous* occurs, and is roadkilled in fragmented human-modified landscapes with agricultural and pasture uses. As reported for *Chrysocyon brachyurus* (Maned-wolf) in the Atlantic Forest (Bereta et al. 2017) and in Amazon Rainforest (Silva-Diogo et al. 2020), the occurrence of carnivores from open

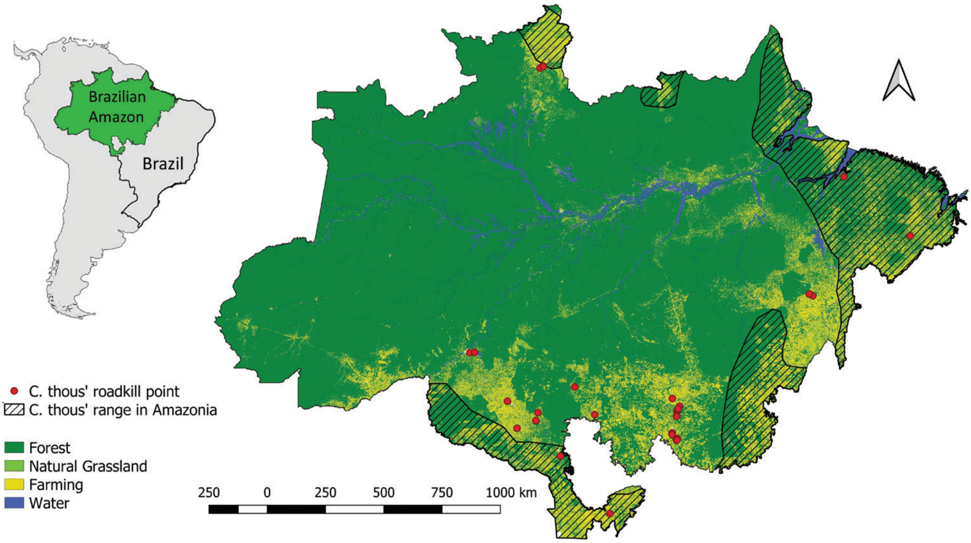

Figure 4. Roadkill records of *C. thous* in Amazon ecosystem. Red dots represent roadkill records of *C. thous* and the hashed area is the original species' range on Amazon. It is possible to notice some registers out of the crab-eating-fox's range according IUCN (Lucherini, 2015), specifically in areas where forests (dark green areas) were converted into farming areas (yellow areas).

environments in forest areas is a result of deforestation, that causes savanna species to expand its occurrence to previously dense forested regions. The creation of those novel ecosystems (Lindenmayer et al. 2008) is related to human-induced modification, and can lead to biotic homogenization (McKinney and Lockwood 1999), when forest dependent species can be replaced for generalist species, compromising the ecosystem functioning. *C. thous* is a generalist species, and its occurrence in Amazon Rainforest can compromise, by competition, populations and the conservation of other niche-equivalent carnivores, like *Atelocynus microtis* (short-eared-dog), a more habitat specialist and forest dependent species (Pitman and Beisiegel 2013).

Euphractus sexcinctus – Like *C. thous*, for this species two land use matrixes are included in the selected model, showing a positive relationship between farming and forestry with roadkill risk (Fig. 5). As all selected models have the same variables (Table 1), we considered, as the most appropriate model, using the one with less complexity to explain the roadkill risk (Table 1, Fig. 5).

This species inhabits a vast number of natural formations, but also human-modified landscapes, such as sugar cane plantations (Dalponte and Tavares-Filho 2004) or even pastures (Anacleto 2007). In the analysis of its threats, the expansion of road network and roadkill is cited as a risk factor (Silva et al. 2015). Since it has generalist habits, its occurrence and roadkill can be associated with commercial tree species in forestry areas, hence its roadkill elevated rates. Forestry regions can be areas of dry soil and low understory coverage, resembling the open dry forests of its original occurrence. The species shows a high density of individuals in the north of São Paulo State, where there is a high landscape coverage of sugar cane, pasture, *Pinus* sp. and *Eucalyptus* sp. cultivation

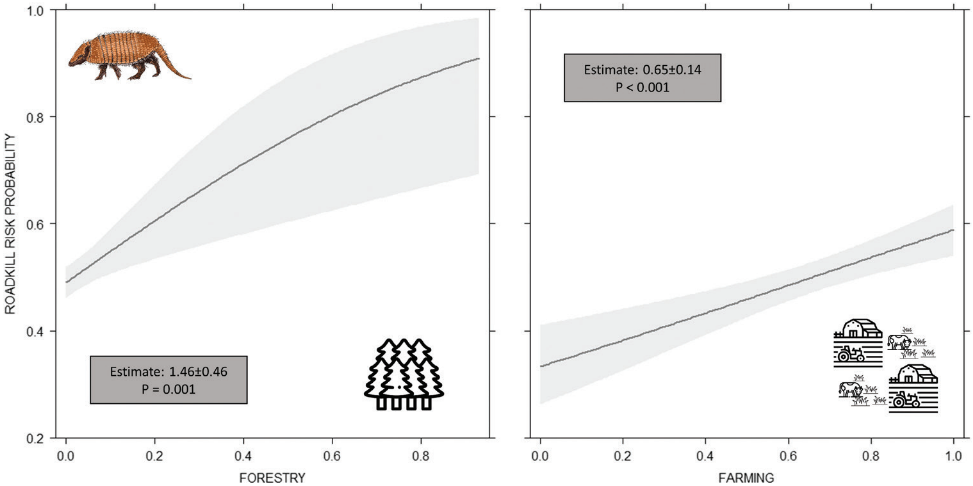

Figure 5. Best model selected by AIC for *E. sexcinctus* and its estimated coefficients. For the six-banded armadillo the best model represents forestry and farming positively related to roadkill risk, showing that the roadkill of this species is related to human modified landscapes.

(Dalponte and Tavares-Filho 2004; Silva et al. 2015), reflecting the areas where these animals are roadkilled. Furthermore, armadillos provide plenty of ecosystem services (Rodrigues et al. 2020), such as soil bioturbation, seed dispersal, and the construction of borrows, which show an important role in sheltering other species for heat control, nesting, and movement (Rodrigues et al. 2020). That indicates the importance of understanding the occurrence and threats to *E. sexcinctus* which can affect other species.

Myrmecophaga tridactyla – the best model to predict the relative risk of roadkill for this species matches with its behavior, including its relationship with pasture, forests and the interaction between these variables (Fig. 6). Among the studied species, this is the only one that is threatened according to national and international sources, considered Vulnerable (VU) in the IUCN red list (Miranda et al. 2014a) and in the national red list of Brazilian threatened fauna (ICMBio 2018). The giant anteater is locally extinct in some Brazilian states, such as Espírito Santo, Santa Catarina and Rio de Janeiro (Bergallo et al. 2000; Passamani and Mendes 2007; FATMA 2011) and it is Critically Endangered (CR) in Rio Grande do Sul (Marques et al. 2002). The main threats to this species are habitat loss and land-conversion to agriculture and pasture (Miranda et al. 2015), as well as the expansion of road network, which causes habitat fragmentation and road mortality. Despite the giant-anteater being frequently associated with savannas, like the Cerrado biome, this animal inhabits a wide range of formation types, such as forests, grass-fields and even pasture and agricultural fields, mainly because its main diet consists of ants and termites, which are very abundant in open areas, but it also has a dependency on shaded areas, like forests and understories (Miranda et al. 2015). Camilo-Alves and Mourão (2006) related this activity to a thermoregulatory behavior (Rodrigues et al. 2008), using open areas in milder temperature during the day and sheltering from the sun in warmer weather (Miranda et al. 2015).

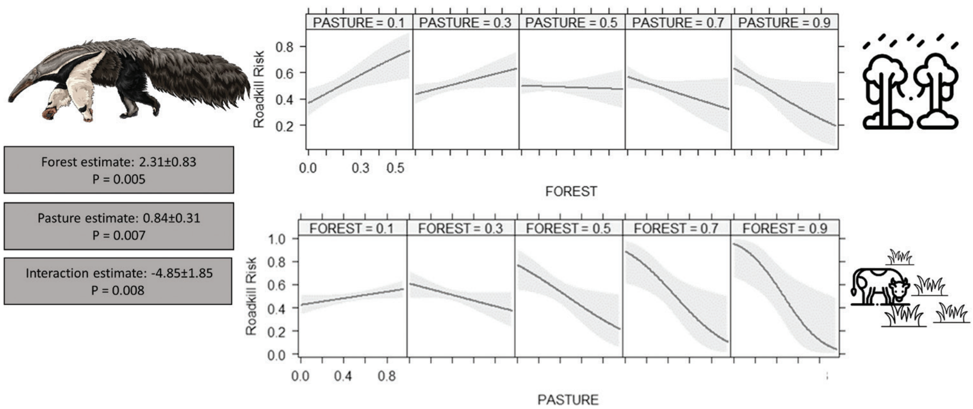

Figure 6. Best model selected by AIC for *M. tridactyla* and its estimated coefficients. The best model shows an interaction between forest and pasture, both variables positively related to roadkill risk, but the size and effect of direction changes according to the proportion of the other variable.

Depending on the amount of matrix in the landscape, the direction of the effect of habitat on roadkill risk changes. In other words, when there are small quantities of forest, the effect of pasture is positive to predict the roadkill, while when there is an increased proportion of forest in the region the effect changes, and the roadkill risk decreases with the increase of pasture areas. This could be related to the species' habits: when the landscape is mostly composed of pastureland, the animals need to move more in search of shaded shelter. This movement decreases in frequency when there are some forested areas in the landscape, allowing the individuals to rest, and therefore, decreasing the chance of encountering a road and consequently being roadkilled. This shows the importance of maintaining habitat patches in the landscape, such as riparian forests or even native vegetation fragments inside private rural property, as established by the Brazilian Forest Code (Metzger 2010). Thereby, we hypothesize that the giant-anteater roadkill risk is associated with larger extensions of monoculture or pasture, without natural formations or habitat patches (Noonan et al. 2021; Versiani et al. 2021).

Tamandua tetradactyla – The roadkill risk of the collared-anteater is strongly related to savanna and agriculture patches, and its interaction (Fig. 7). This species, considered as common in Brazil, is listed as Least Concerned in the IUCN (Miranda et al. 2014b), but in Rio Grande do Sul state it is considered Vulnerable (VU) (Marques et al. 2002). Despite occurring in a wide range of habitats (it can be found in all Brazilian vegetation formations), it has a dependence on areas with tree formation, since it is a semi-arboreal animal that feeds on termites and ants in tree canopies, and finds shelter in hollow trees (Ohana et al. 2015). It is considered a forest dependent species, unlike *C. thous* and *E. sexcinctus*, and is more closely related in terms of habitat needs with *M. tridactyla* (Desbiez and Medri 2010).

This habitat dependence reflects on the best model selected to predict the collared-anteater roadkill risk: the presence of savanna formations modulates the effect of agriculture. When a landscape has no natural formations cover, the effect of agriculture is

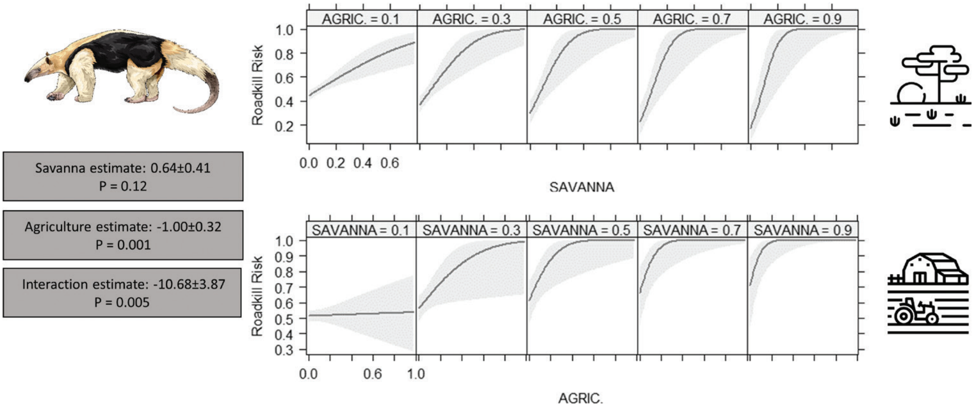

Figure 7. Best model selected by AIC for *T. tetradactyla* and its estimated coefficients. The roadkill risk is negatively related to agriculture. However, the interaction between agriculture and savanna was significant, which changes the effect direction of agriculture in the presence of more savanna areas, increasing the risk of roadkill with the increment of agriculture, in other words, landscapes with savanna and agriculture mosaics are more likely to have collared-anteaters roadkills.

negative, since the species probably do not occur in the area; and with the increment of habitat areas, the roadkill risk increases rapidly, reaching our model's peak when we have at least 40% of savanna and 50% of agriculture.

On the other hand, the roadkill risk when the landscape is entirely comprised of savanna, without agriculture, is very low, and it increases very fast when there is an increase of agricultural coverage. As it is a forest dependent animal, it was unexpected that its roadkill response was better suited to savanna than to dense forests, but that can be explained by this animal's movement pattern. In areas with continuous dense forests the locomotion of individuals occurs mainly through canopies, but in areas with low density of trees, as open areas, savannas and monocultures, it moves by ground. It can also move more often in search for sheltering trees, therefore increasing the chance of being roadkilled.

Limitations and directions for future researches

It is already known that many factors affect the roadkill risk of a species, such as species density and movement patterns (Rytwinski and Fahrig 2013). We also recognize that the home range for each species varies according to each study area, mainly due to differences in habitat quality (Ofstad et al. 2016; Viana et al. 2018). In this research, we aimed to relate roadkill risk with landscape composition in a national scale in a country with continental properties – Brazil, so there is a limitation on the availability of data to better control those factors. We preferred to use the most accurate data we had, which was mean home range for each species, rather than other inaccurate or non-existent data. Others aspects can also affect the roadkill, as nocturnal or diurnal habits; the flux and speed of vehicles in roads; the presence of crossing opportunities, as underpasses and overpasses; the season and weather; and as discussed above, the population density and habitat quality. All those factors can be considered in further research that can compare roads or road segments between themselves, use roadkill rates and model space and time to have more accurate responses. Here, we search for general patterns in large scale considering only space; future research in smaller scales should make an effort to include these variables in the modelling process and analyze how each of them influence the roadkill risk.

Conclusions

For habitat dependent and more sensitive species like anteaters, the effect of the matrix on the roadkill risk depends on habitat availability in the landscape. It changes the strength and direction of the effect according to the proportion of natural areas in the region. As for generalist species, the quantity of human-modified land uses increases the roadkill risk regardless of the habitat availability or natural formations. It also indicates the occurrence of these species in those anthropic areas.

Therefore, the habitat and matrix composition impacts the studied species differently, depending on their demand and habitat dependence. Each species showed different prediction factors regarding their roadkill risk. Overall, all four target species had some dependency on the habitat, but two of them (*Cerdocyon thous* and *Euphractus sexcinctus*) are more tolerant to landscape cover changes, using some human-modified areas as habitat areas. However, the proportion and quality of natural areas should be determinant factors for *Cerdocyon thous* and *Euphractus sexcinctus*' rate of movement, since it influences the chance of crossing a road and dying by roadkill. This movement ecology component needs to be addressed in further studies that relate the type and quality of habitat with species' movement and roadkill rates. Currently, there is not much information regarding those common species with high roadkill rates, especially for *C. thous*, that can potentially cause great amounts of accidents and human injuries on Brazilian roads.

The habitat dependent species have more complex models predicting their roadkill risk, including an interaction component between habitat and matrix. It shows the importance of maintaining the natural coverage of rural properties that, as indicated by Brazilian Forest Code, can potentially decrease the risk of roadkill, connect habitat areas, and increase habitat quality. Given that, areas with vast cover of monoculture and pasture can both decrease the natural populations' size and increase the movement of individuals that can be roadkilled while they are searching for best habitats on the landscape. Since we have shown that not only riparian corridors or continuous habitats are associated with roadkill, but also areas out of protected areas we suggest that more studies investigating the effect of movement in roadkill should be performed. We also highlight the need to consider the landscape as a whole while assessing species protection.

Acknowledgements

We thank FAPESP for the financial support (Process n° 16/12785-0) through DWC research grant, NERF/UFRGS ("Núcleo de Ecologia de Ferrovias e Rodovias" – Universidade Federal do Rio Grande do Sul) and others involved in field data collection, such as Andreas Kindel, Arnaud Desbiez, Janaina Casella and Sidnei Dornelles. We also thank Fernanda Delborgo Abra and ViaFauna for providing the illustrations in this article and contributions to data interpretation; and Guillermo Flórez for statistical contributions. We also thank the MapBiomas initiative, for the land use and land cover mapping and a reward attributed to a preliminary version of this study (CIRINO, 2018).

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Supplementary material 1

Correlation plot and R script for building and selecting best models

Authors: Douglas William Cirino

Data type: R script (text file)

Explanation note: Plot of correlations between predictor variables. The script used for reading variables, building statistical models and selecting the best model by Akaike Information Criteria.

Link: https://doi.org/10.3897/natureconservation.47.73010.suppl1

Nature Conservation 47: 87–104 (2022)
doi: 10.3897/natureconservation.47.73036
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Speed thrills but kills: A case study on seasonal variation in roadkill mortality on National highway 715 (new) in Kaziranga-Karbi Anglong Landscape, Assam, India

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Academic editor: Clara Grilo | Received 14 August 2021 | Accepted 2 December 2021 | Published 25 March 2022

http://zoobank.org/7B181754-48AB-41D1-8243-9A1B8F590AA1

Citation: Sur S, Saikia PK, Saikia MK (2022) Speed thrills but kills: A case study on seasonal variation in roadkill mortality on National Highway 715 (new) in Kaziranga-Karbi Anglong Landscape, Assam, India. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 87–104. https://doi.org/10.3897/natureconservation.47.73036

Abstract

Animal-vehicle collision on the roads is a major cause of mortality of a wide range of animal taxa both within and around protected areas. This study has been conducted in the National Highway 715 (new) covering a continuous stretch of 64 km that passes through Kaziranga National Park (KNP) of Assam (India). The area falls between the boundary of KNP on its north and North Karbi Anglong Wildlife sanctuary on the south. The survey concentrated on the mortality study of four groups of vertebrates viz., amphibians, reptiles, birds, and mammals resulting from collisions with vehicles from October 2016 through September, 2017. A total of 6036 individual roadkills were registered, belonging to 53 species, 23 other taxa and 30 families of vertebrates, with herpetofauna being the most affected group followed by birds and mammals. The study evaluated seasonal variation in the overall roadkill pattern with highest mortality in the monsoon season 38.27% (n = 2310) and with peak casualties starting with the onset of rainfall (February and March) and during monsoons (July and August). The amphibian mortality was also found to be highest during the monsoon with 43.28% (n = 1575) of kills, as compared to the other three groups. NH-715 (new), therefore serves as a challenging passage for the animals, forming a major barrier for the faunal component of the Kaziranga-Karbi Anglong landscape. This study thus tried to reflect the often overlooked issue of roads and highways in terms of direct mortality of animals due to traffic and thereby can be helpful in understanding the seriousness of the situation and identifying prospective measures to be taken for sustainable coexistence of both animals and human.

Keywords
Herpetofauna, Kaziranga National Park, mortality, National Highway, road ecology, vehicular collision

Introduction

India has the second largest road system in the world according to the National Highway Authority of India (NHAI) covering over 5.89 million kilometres with all signs pointing to an explosion of expansion in the upcoming years (Indian Road Industry Report 2020). The state of Assam has a total road length of 47,936 km including 3908.5 km of National Highways, 3134.36 km of State Highways, 413.03 km of major district roads and 37 030 km of rural roads (India Brand Equity Foundation 2019). In India, the total length of roads and the number of automobiles has increased tremendously. The total extent of roads in India has increased more than 11 times during the past six decades from 1951 to 2015 (from 3.99–46.71 lakh kilometre), which was 4.2% in 1950's (ROADS-Statistical Year Book 2018). The number of registered motor vehicles has also been growing at a compound annual growth rate (CAGR) of 10.16% per year over the last five years. Considering this vast network of roads, it is crucial to assess the magnitude of wildlife mortality due to road traffic (Glista et al. 2008).

Roadways are obviously integral to commuting and transportation, but are certainly known to pose some detrimental effects on the flora and fauna surrounding them (Mazumdar and Gogoi 2010). They may affect animal populations in different ways. The most prominent effect of such linear structure is mortality through vehicular collisions (Das et al. 2007; Grilo et al. 2018; Jeganathan et al. 2018). Other more complex consequences identified are habitat modification and fragmentation (Carr and Fahrig 2001), leading to population isolation, changes in animal distribution and movement patterns (Desai and Baskaran 1998), increased inbreeding, decrease in population size and high possibilities of local extinction (Quinn and Hasting 1987). Another corollary effect of road is the volume of space they occupy (Trombulak and Frissell 2000), contamination of roadside habitats due to automobile exhaustions (Beeby and Richmond 1987) and increased avoidance behaviour, thus acting as a barrier to gene flow (Mader 1984). The effect of such infrastructures is felt by mammals (Baskaran and Boominathan 2010), birds (Robertson 1930), reptiles (Das et al. 2007), amphibians (Seshadri et al. 2009) and macro invertebrate fauna (Haskell 2000) as well. Thus, road fragments the habitats, and with the growing demand for more networks, animals are increasingly forced to cross roads to perform their routine necessities and are often killed by vehicles (Hourdequin 2000).

Among the various threats posed to wildlife, collisions with vehicles are becoming a major concern for many species (Bager and Rosa 2011). Road attributes like width, length and condition of the pavement, directly amplify the rate of vehicular collisions. Setting up roads and measures without proper structural designs, leads to an increased rate of vehicular collisions for animals (Oxley et al. 1974). Road density and their constructional works can harm and alter biodiversity at local, regional and landscape scales, the effect of which can sometimes remain unnoticed for decades (Findlay and Houlahan 1997). The International Union for Conservation of Nature (IUCN) also considers roads and railways in their list of threats for various wild animals. Mortality due to vehicular collision for any sustaining population may not exhibit the need of immediate conservation concerns, but it is presumed that small, isolated, declining, threatened populations and species are also affected by road mortality (Mumme et al. 2000). Species-specific behaviour in response to the road environment also guides the risk of vehicular collisions (Erritzoe et al. 2003). Many species use the road for daily activities like foraging, nesting, predation, scavenging, shelter, which can increase their vulnerability to road mortality (Fulton et al. 2008). Road habitats may also act as a habitat sink or ecological trap for birds and small mammals (Mumme et al. 2000).

Factors like roadkill rates, traffic traits and landscape attributes are effective in determining the spatial location of roadkills (Ramp et al 2005), but their temporal distribution for predicting seasonal patterns have been addressed less often. Explanations for seasonal variation in roadkill have been correlated to the breeding and foraging behaviour of the species (Erritzoe et al. 2003). The temporal roadkill patterns of small mammals, birds, and lizards are also linked to their phenology (D'Amico et al. 2015). In Amphibia, seasonal peaks in population sizes (Rosa and Bager 2012) and migration (Langen et al. 2009) have also been related to temporal roadkill patterns. Environmental variations and seasonal life-history traits (D'Amico et al. 2015; McCardle and Fontenot 2016) can also cause temporal or seasonal roadkill peaks.

Our goal in this study was to evaluate the magnitude of mortality due to collisions with vehicles, of vertebrate fauna, specifically amphibians, reptiles, birds, and mammals in the highway stretch that passes through Kaziranga-Karbi Angling landscape complex in North-Eastern India, from October 2016 to September 2017. We also tried to evaluate the seasonal variation and pattern of roadkill distribution among the vertebrate groups in the study area. Similar studies have been carried out in India, but no detailed study for this high diversity hotspot is known yet (Islam and Saikia 2014).

Methods

Study area

The entire study area landscape includes the Kaziranga National Park (KNP, Latitude 26°30'N to 26°50'N and Longitude 92°05'E to 93°41'E), North Karbi Anglong Wildlife Sanctuary, East Karbi Anglong Wildlife Sanctuary (central coordinates: 26°28'0"N, 93°21'29"E), river Brahmaputra and the National Highway (NH) 715 (new) positioned in between KNP and North Karbi Anglong Wildlife Sanctuary, all covering the districts of Golaghat, Nagaon, Sonitpur, and Karbi Anglong.

The studied road site is a continuous 64 km stretch of this NH 715 (new), (Latitude: 26°34'–26°46'N, Longitude: 93°08'–93°36'E) which forms the southern boundary of KNP, connecting Bokakhat to Ghorakati and bisecting the landscape into north and south (Figure 1). In the north lie the low-lying floodplains of KNP and in the south lie the elevated Karbi Anglong hills. This highway is also an Asian Highway No. 1 (AH-1) connecting to Myanmar, and a major communication route to eastern parts of Assam. The NH 715 was formerly known as National Highway 37 (NH 37) and upon revision, now starts from its junction with NH-15 near Tezpur connecting Jakhalabandha, Bokakhat, Jorhat, and terminates at its junction with NH-2 near Jhanji in Sibsagar, Assam for a total length of 197 km.

This paved stretch of highway is 7.5 m wide and crosses a wide array of habitats, including tea gardens, human settlements, agricultural fields, grassland, teak plantations, bamboo plantations, wetlands, open fields, swamps and marshy areas and forest covers at Panbari, Haldibari, Kanchanjuri, and Gorakati areas. The animal movement pattern along the highway can be summarised into two seasonal frames, one during the flooding period (April to September) which includes Pre-monsoon and monsoon season (Borthakur 1986), when flooding in Kaziranga (north side) forces the animals to move southwards to higher elevations to escape flooding. The highway lying between KNP and North Karbi Anglong Wildlife Sanctuary, provides a linear raised ground for the animals to take immediate refuge. The other stride occurs during the non-flooding period (October to March) which includes retreating monsoon and winter season (Borthakur 1986), when animals move to neighbouring linking habitats in search of forage and other natural life necessities.

Quantification of roadkill

We conducted 144 systematic road trips from October 2016 to September 2017, for the entire stretch of the highway (64 kms), starting from Bokakhat to Ghorakati and then returning back to the same start point, accounting for approximately 128 kms for every instance. Data collection was carried out by two observers beginning at 07:00 h during winter and at 05:00 h in summer, depending upon visibility, using a motor vehicle at a steady speed of 25–35 kmph, for three days every week. Survey effort was kept constant throughout the year. This intensive sampling design was incorporated to enhance the detection of smaller carcasses, which could rapidly dissipate due to degradation or scavenging (Glista et al. 2008).

Each encountered carcass was identified to the species level, whenever possible, otherwise to genus or family level. Also, the number of individual carcasses and their status were recorded along with geo-location using a Garmin eTrex 10 GPS. The carcass status was defined as Fresh (carcass found in fresh condition or live killed) or Old (dry carcasses or few remains). All the carcasses were grouped by class as mammal, bird, reptile, and amphibian. The animal carcasses encountered were photographed for identification and were removed from the road to avoid double counting. At certain

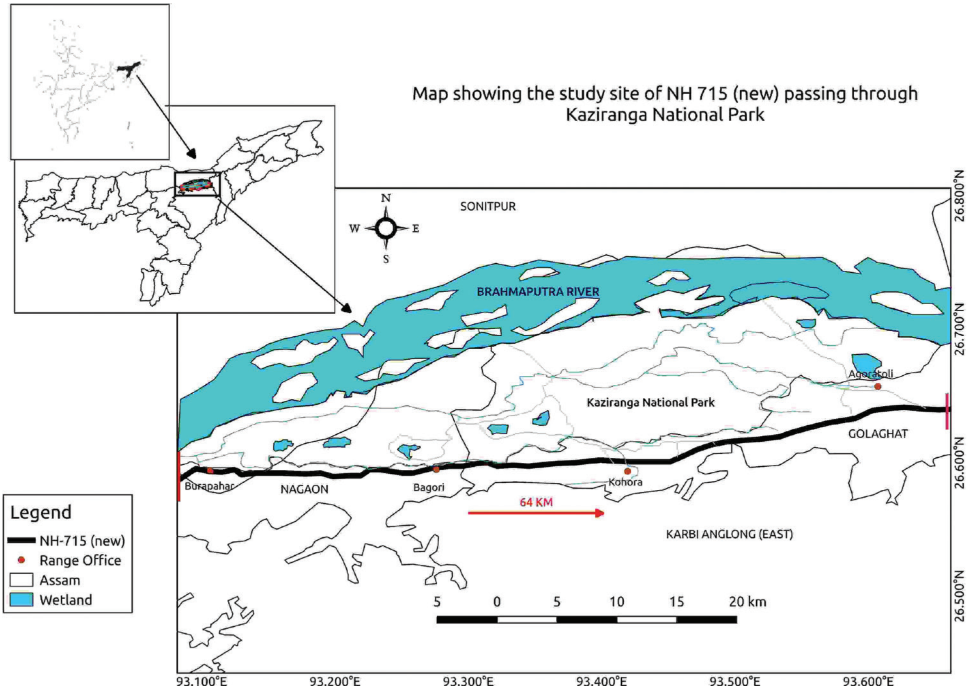

Figure 1. Map showing the study site of NH 715 (new) passing through the KNP.

surveys the amphibian carcasses were so locally abundant that individual counting was not possible. In those situations, an abundance estimate was made at each 10 m-road section. The carcasses were identified using field guides for respective taxa (Dutta 1997; Das 2002; Whitaker and Captain 2004; Grimmett et al. 2011; Menon 2014). Some carcasses found in a severe distorted condition, were grouped as unidentified. Variation in observers can also affect detection rates of dead animals (Kline and Swann 1998).

Animals, specifically reptiles, crossing the road or basking on the road were assisted towards the direction in which they were moving.

Data analysis

We used non-parametric Kruskal-Wallis ANOVA and Mann-Whitney U tests to examine the differences in mean number of roadkill by taxonomic group, month, season, and carcass status. Periods of roadkill occurrences were classified as non-flooding and flooding period. Seasons were defined as winter (December – February), pre-monsoon (March – May), monsoon (June – August) and retreating monsoon (September – November). All the analyses were performed for the total number of roadkills, excluding the unidentified carcasses. All statistical analyses were done using R (R Core Team 2013).

Results

Overall results

We registered altogether 6036 individual roadkills belonging to 53 species (30 families) of four different vertebrate classes during the study period. A total of 121 roadkills (1.92%) remained unidentified because of their bad condition (Table 1). Amphibians were the most affected class, accounting for60.29% of all roadkill (n = 3639) belonging to two families. The reptiles were the second most road-killed class with 21.22% (n = 1281), with eight families. Birds comprised 9.87% of roadkill (n = 596), with 15 families and mammals constituted 8.61% of roadkill (n = 520) with kills in five families (Table 1; Figure 2).

Table 1. List of roadkills recorded in different seasons, at NH-715 (new) from October 2016 to September 2017. PM: Pre-monsoon; M: Monsoon; RM: Retreating monsoon; W: Winter; T: Total number of individuals.

Order	Family	Common name	Scientific name	Roadkill animals				
				PM	M	RM	W	T
			Amphibians					
Anura	Bufonidae	Common Indian Toad	*Duttaphrynus melanostictus*	426	849	50	668	1993
Anura	Dicroglossidae	Indian Bullfrog	*Hoplobatrachus Tigerinus*	60	41	0	31	132
Anura	Dicroglossidae	Fejervarya Spp.	*Fejervarya* Spp.	189	285	6	59	539
Anura	Uncategorised	Toad Spp.	–	156	272	32	206	666
Anura	Uncategorised	Frog Spp.	–	30	22	8	24	84
Unidentified	**Unidentified**	Unidentified	–	63	106	5	51	225
			Reptiles					
Squamata	Typhlopidae	Diard's Worm snake	*Argyrophis diardii*	1	5	0	0	6
Squamata	Typhlopidae	Brahminy Worm Snake	*Rhanphotyphlops brahminus*	2	6	0	0	8
Squamata	Colubridae	Striped Keelback	*Amphiesma stolatum*	33	65	27	17	142
Squamata	Colubridae	Red-necked Keelback	*Rhabdophis subminiatus*	15	13	26	16	70
Squamata	Colubridae	Checkered Keelback	*Xenochrophis piscator*	28	29	25	19	101
Squamata	Colubridae	Common Trinket Snake	*Coelognathus helena Helena*	7	11	0	4	22
Squamata	Colubridae	Copper-headed Trinket snake	*Coelognathus radiatus*	7	8	12	6	33
Squamata	Colubridae	Trinket Snake	*Coelognathus* Spp.	3	4	1	0	8
Squamata	Colubridae	Cat Snake	*Boiga* Spp.	17	18	5	11	51
Squamata	Colubridae	Eastern Cat Snake	*Boiga gokool*	5	9	0	0	14
Squamata	Colubridae	Large-spotted Cat Snake	*Boiga multomaculata*	2	3	0	1	6
Squamata	Colubridae	Eyed Cat Snake	*Boiga siamensis*	1	6	2	6	15
Squamata	Colubridae	Indian Rat Snake	*Ptyas mucosa*	5	8	15	9	37
Squamata	Colubridae	Indo-Chinese Rat Snake	*Ptyas korros*	0	2	0	1	3
Squamata	Colubridae	Ornat Flying Snake	*Chrysopelea ornate*	13	6	8	6	33
Squamata	Colubridae	Painted Bronzeback Tree Snake	*Dendrelaphis pictus*	25	20	21	14	80
Squamata	Colubridae	Bronzeback Tree Snake	*Dendrelaphis* Spp.	7	10	18	16	51
Squamata	Colubridae	Indian Wolf Snake	*Lycodon aulicus*	19	18	7	5	49
Squamata	Colubridae	Yellow-speckled Wolf Snake	*Lycodon jara*	0	6	0	0	6
Squamata	Colubridae	Zaw's Wolf Snake	*Lycodon zawi*	5	3	0	1	9
Squamata	Elapidae	Black Krait	*Bungarus niger*	1	2	0	1	4
Squamata	Elapidae	Banded Krait	*Bungarus fasciatus*	4	8	4	1	17
Squamata	Elapidae	King Cobra	*Ophiophagus hannah*	0	0	0	1	1
Squamata	Elapidae	Krait Spp.	*Bungarus* Spp.	1	1	1	2	5
Squamata	Viperidae	Pit Viper	*Trimeresurus* Spp.	2	7	0	0	9

Order	Family	Common name	Scientific name	Roadkill animals				
				PM	M	RM	W	T
Squamata	Homalopsidae	Common Smooth-scaled Water Snake	*Enhydris enhydris*	2	7	3	3	15
Squamata	Pythonidae	Burmese Python	*Python molurus bivittatus*	9	0	0	0	9
Squamata	Pythonidae	Python Spp.	–	0	1	0	0	1
Squamata	Uncategorised	Snake Spp.	–	36	68	64	53	221
Squamata	Geckoninae	Tokay Gecko	*Gekko gecko*	7	3	0	2	12
Squamata	Geckoninae	Bent-toed Gecko	*Crytodactylus* Spp.	0	1	1	2	4
Squamata	Geckoninae	Lizard Spp.	*Gekko* Spp.	0	2	0	0	2
Squamata	Agamidae	Oriental Garden Lizard	*Calotes versicolor*	61	39	47	66	213
Squamata	Uncategorised	Lizard Spp.	*Calotes* Spp.	0	2	9	7	18
Squamata	Uncategorised	Lizard Spp.	*Unidentified*	0	1	5	5	11
Birds								
Passeriformes	Sturnidae	Common Myna	*Acridotheres tristis*	29	54	32	27	142
Passeriformes	Sturnidae	Asian Pied Starling	*Gracupica contra*	11	12	8	8	39
Passeriformes	Sturnidae	Chestnut Tailed Starling	*Sturnia malabarica*	3	1	1	2	7
Passeriformes	Sturnidae	Jungle Myna	*Acridotheres fuscus*	18	20	8	10	56
Passeriformes	Sturnidae	Common myna/Jungle Myna	*Acridotheres tristis/ Acridotheres fuscus*	5	8	7	9	29
Passeriformes	Cisticolidae	Common Tailorbird	*Orthotomus sutorius*	2	2	0	2	6
Passeriformes	Passeridae	Eurasian Tree Sparrow	*Passer montanus*	6	2	1	1	10
Passeriformes	Passeridae	House Sparrow	*Passer domesticus*	11	5	6	10	32
Passeriformes	Passeridae	Sparrow Spp.	*Passer* Spp.	0	3	0	1	4
Passeriformes	Pycnonotidae	Red-vented Bulbul	*Pycnonotus cafer*	40	32	9	16	97
Passeriformes	Estrildidae	Scaly-breasted Munia	*Lonchura punctulata*	2	1	0	0	3
Passeriformes	Corvidae	House Crow	*Corvus splendens*	4	4	5	3	16
Passeriformes	Aegithinidae	Common Iora	*Aegithina tiphia*	3	3	0	0	6
Passeriformes	Muscicapidae	Oriental Magpie Robin	*Copsychus Saularis*	1	1	1	1	4
Passeriformes	Locustellidae	Striated Grassbird	*Megalurus palustris*	0	0	0	1	1
Falconiformes	Falconidae	Common Kestrel	*Falco tinnunculus*	0	0	1	0	1
Strigiformes	Strigidae	Asian Barred Owlet	*Glaucidium cuculoides*	3	7	0	3	13
Strigiformes	Strigidae	Spotted Owlet	*Athene brama*	2	5	3	0	10
Coraciiformes	Coraciidae	Indian Roller	*Coracius benghalensis*	2	4	0	0	6
Psittaciformes	Psittaculidae	Red-breasted Parakeet	*Psitacula alexandri*	1	1	0	0	2
Psittaciformes	Psittaculidae	Parakeet	*Psittacula* Spp.	0	1	0	0	1
Gruiformes	Rallidae	White-breasted Waterhen	*Amourornis phoenicurus*	10	10	2	7	29
Columbiformes	Columbidae	Yellow-footed Green Pegion	*Treron phoenicoptera*	1	3	0	0	4
Columbiformes	Columbidae	Spotted Dove	*Stigmatopelia chinensis*	9	7	4	6	26
Columbiformes	Columbidae	Ferral Pegion	*Columbia livia* (*ferral*)	7	7	4	5	23
Uncategorised	Uncategorised	Raptor Spp.	–	4	15	1	6	24
Uncategorised	Uncategorised	Owlet Spp.	–	0	1	1	1	3
Mammals								
Chiroptera	–	Bat Spp.	–	10	17	9	10	46
Rodentia	Sciuridae	Hoary-bellied Squirrel	*Callosciurus pygerythrus*	2	1	1	0	4
Rodentia	Sciuridae	Squirrel Spp.	–	3	3	1	2	9
Rodentia	Muridae	House Mouse	*Mus musculus*	8	13	13	10	44
Rodentia	Muridae	Large Bandicoot Rat	*Bandicoota indica*	10	12	10	6	38
Rodentia	–	Rat Spp.	–	53	64	80	96	293
Eulipotyphla	–	Shrew Spp.	–	8	9	7	6	30
Eulipotyphla	–	Mole Spp.	–	19	13	6	8	46
Primates	Cercopithecidae	Rhesus Macaque	*Macaca mulata*	0	0	1	0	1
Primates	Cercopithecidae	Macaque Spp.	–	0	1	0	1	2
Carnivora	Felidae	Indian Leopard	*Panthera pardus fusca*	0	0	0	1	1
Carnivora	Viverridae	Small Indian Civet	*Viverricula indica*	0	2	1	1	4
Carnivora	Viverridae	Civet Spp.	–	0	0	0	1	1
Uncategorised	Uncategorised	Unidentified	Unidentified	10	47	33	31	121

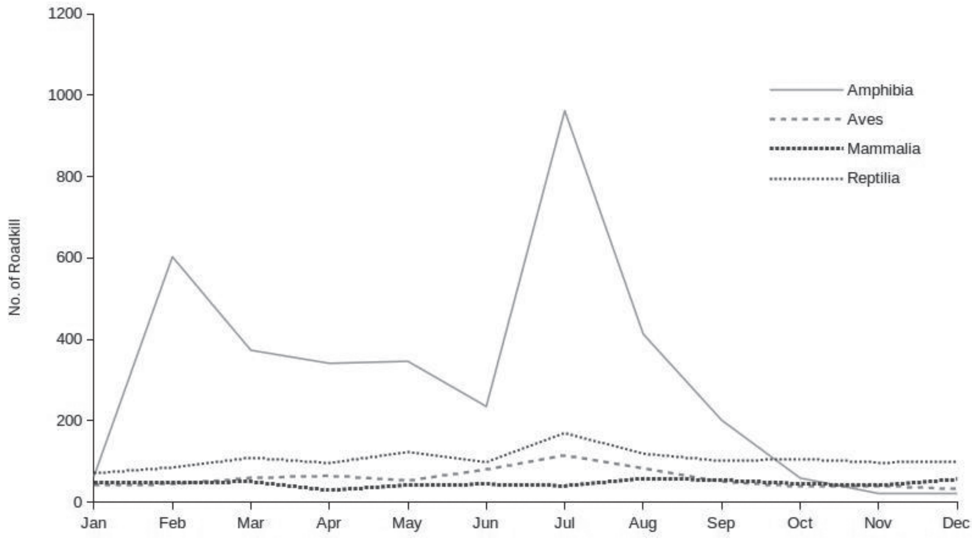

Figure 2. Overall mortality in respective classes.

There were significant differences in the total roadkill numbers by taxonomic groups (χ^2 = 1103.00, P < 0.01, df = 3) and multiple comparisons revealed significant differences between amphibians and the other three groups (P < 0.01; Table 2), showing amphibians with highest casualties, followed by reptiles, birds and mammals. Of the total casualties recorded, 72.53% (n = 4561) of kills, were found to be old kills and 27.46% (n = 1727) were freshly killed (Mann-Whitney U test, Z = -7.165, $P < 0.01$) wild animals. Roadkill rates were 0.05 carcasses/km for mammals, 0.06/km for birds, 0.13/km for reptiles and 0.39/km for amphibians. Overall mortality rate was found to be 0.65/day/km. However, the percentage rank accumulation pattern of roadkills showed stabilization with the number of survey days (n = 144) for both fresh and old category of road-kills (Figure 3).

Herpetofauna were found to be the most affected group with amphibia being the most affected taxa. The Common Indian toad *Duttaphrynus melanostictus* was found to be highest 54.77%, (n = 1993) among two species and three other taxa of amphibians. Similarly, mortality for Oriental Garden Lizard *Calotes versicolor* was 16.63% (n = 213), followed by Buff Striped Keelback *Amphiesma stolatum* 11.09% (n = 142) and Checkered Keelback *Xenochrophis piscator* and 7.88% (n = 101) respectively among 23 species and nine other taxa of reptiles. Among birds, highest mortality was found in Common Myna *Acridotheres tristis* 23.83% (n = 142) among 22 species and four other taxa of birds, and rat spp. (56.34%, n = 293) among six species and seven other taxa of mammals, were dominant road-kills (Table 1). Some rare road-kill encountered include *Boiga multomaculata*, *Lycodon jara*, *Argyrophis diardii*, *Python bivittatus*, *Gekko gecko*, *Crytodactylus* Spp., among snakes and lizards; *Psittacula krameri*, *Falco tinnunculus*, *Aegithina tiphia*, *Megalurus palustris*, *Lonchura punctulata* among birds

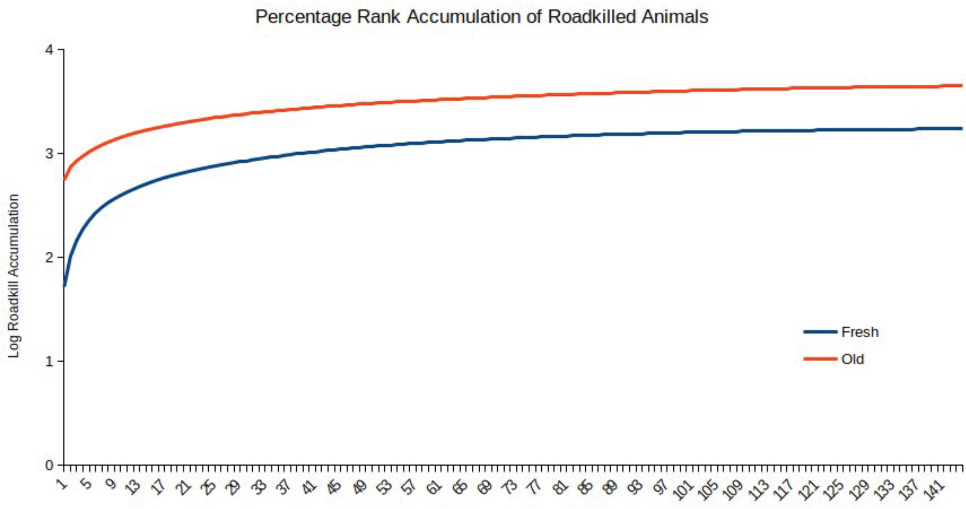

Figure 3. Percentage Rank accumulation of road-killed animals in the study period.

Table 2. Mann-Whitney U Test for total number of roadkills in different seasons and taxonomic group. Win: Winter; PrM: Pre-monsoon; Mon: Monsoon; ReM: Retreating monsoon; Amp: Amphibia; Bir: Birds; Rep: Reptile; Mam: Mammal.

Season	χ^2	Z
	112.30	
Win – PrM	–	3.62**
Win – Mon	–	3.50**
Win – ReM	–	10.82**
PrM – Mon	–	0.13
PrM – ReM	–	8.32**
Mon – ReM	–	8.35**
Taxonomic group	χ^2	**Z**
	1103.00	
Amp – Mam	–	16.37**
Amp – Bir	–	19.24**
Amp – Rep	–	25.90**
Rep – Bir	–	2.65**
Rep – Mam	–	4.93**
Bir – Mam	–	1.98*

‘ ** ’ Significant (P < 0.01); ‘ * ’ Significant (P < 0.05); ‘ ’ Not Significant

and *Panthera pardus*, *Viverricula indica*, *Callosciurus pygerythrus*, *Macaca mullata* were among the mammals.

Among all the road-killed animals found, 96.7% (n = 503) were nocturnal mammals, with species like *Panthera pardus*, *Vivvericula indica*, various unidentified bat, rat mole and shrew species, followed by 14.98% (n = 192) of nocturnal reptiles, belonging to genera *Gekko*, *Boiga*, *Lycodon*, *Bungurus*, and *Trimeresurus* and 4.36% (n = 26) of nocturnal avian species represented by *Athene brama*, *Glaucidium cuculoides* were recorded.

Seasonality of roadkills

Altogether 63.60% (n = 3839) of roadkills occurred during the flooding period: April to September (Pre-monsoon and Monsoon) and 36.40% (n = 2197) of kills occurred in the non-flooding period: October to March (retreating monsoon and winter), with significant differences among them (Kruskal-Wallis, $\chi^2 = 8.56$, $P < 0.01$, df = 1). Thus, we recorded that animal mortality in flooding period was high when compared to mortality in non-flooding period.

This study shows higher mortality in a different season of the year, with maximum kills of 38.37% (n = 2413) in the monsoon season, followed by 25.84% (n = 1625) in winter, 24.84% (n = 1562) in pre-monsoon and 10.94% (n = 688) in retreating monsoon. Thus, the total number of roadkills in each season significantly differs from each other (Kruskal-Wallis test, $\chi^2 = 111.54$, $P < 0.01$, df = 3; Table 2). The Mann Whitney U Test showed significant differences between different seasons ($P < 0.01$) except for pre-monsoon and monsoon (Table 2). The present study also revealed that total amphibian roadkills have significant seasonal variations with the highest mortality in monsoon (2832; $P < 0.01$), followed by pre-monsoon (1689; $P < 0.01$), winter (1661; $P < 0.01$) and retreating monsoon (717; $P < 0.01$), whereas kills in other groups were found to be almost similar throughout the year (Table 2; Figure 4). Moreover, significant differences were found in freshly occurred roadkills in different seasons ($\chi^2 = 47.56$, $P < 0.01$, df = 3) and those found in a decayed state also showed significant differences according to the season ($\chi^2 = 122.41$, $P < 0.01$, df = 3).

The distribution of roadkill records throughout the year was not homogenous, with the highest rates in February, March, July, and August (Table 3). In contrast, November, December, and January showed the lowest roadkill rates. The total casualties in different months revealed significant variations ($\chi^2 = 187.51$, $P < 0.01$, df = 11), with one peak in February-March and a second peak in July-August.

Discussion

The higher incidence of roadkill mortality in the study area is evidence of heavy loss of vertebrate wildlife species in the National highway passing through an important protected area, i.e. KNP of Assam. Similar types of study conducted across the globe also reached comparable findings (Glista et al. 2008; Baskaran and Boominathan 2010; D'Amico et al. 2015). The percentage rank accumulation pattern of roadkill here shows stabilisation with the number of survey days for both fresh and old category of roadkill, thus depicting appropriate survey effort for the concerned study period. However, it is found that only 70 higher roadkill days accounted for 80% of the roadkill statistics in the NH 715 (new) that passes through KNP. This, in turn, signifies the low average number of casualties in most of the survey days (> 70 days), thereby marking the problem to be manageable, if high risk days are identified and proper measures enforced for controlling animal mortality.

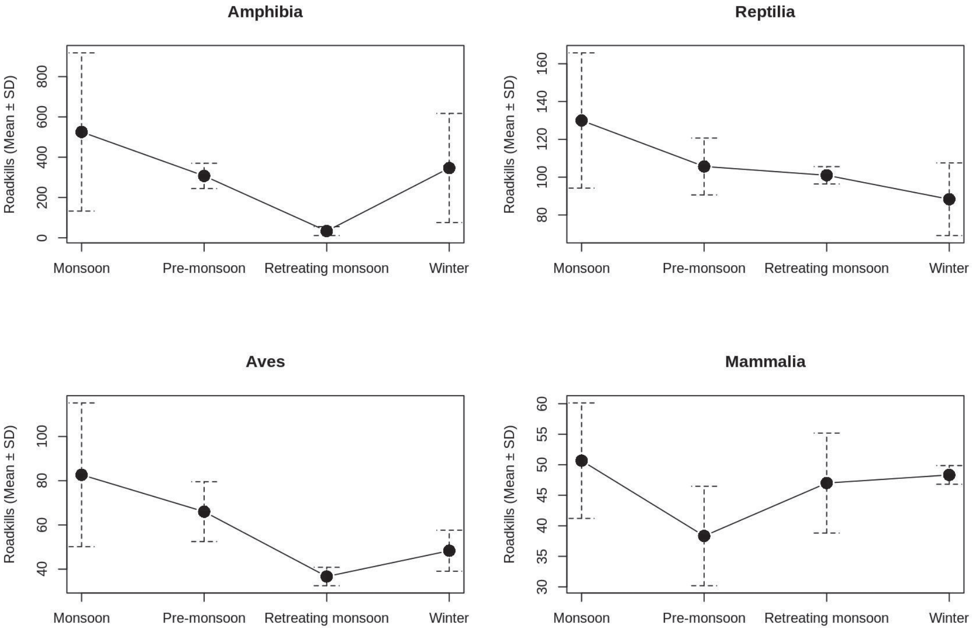

Figure 4. Overall season-wise mean road-kills in different animal groups in the study area.

Table 3. Monthly summary of mortality with percentage kill, mean and standard deviation.

Month	N	Percentage kill (%)	Mean	Standard Deviation
January	217	3.6	1.1	0.41
February	771	12.77	1.9	6.99
March	584	9.68	1.61	1.57
April	515	8.53	1.59	1.6
May	556	9.21	1.43	1.27
June	458	7.59	1.22	0.86
July	1265	20.96	2.7	18.21
August	649	10.75	1.75	2.58
September	396	6.56	1.41	1.32
October	236	3.91	1.08	0.34
November	191	3.16	1.03	0.18
December	198	3.28	1.03	0.16

The present study accounts for the highest number of amphibian roadkills, (60.29%) and thus concurs with the view of Sundar (2004) that amphibians are more vulnerable to collisions with vehicles because they cross roads slowly and are not easily noticeable. Hence drivers tend to disregard them, and this is exacerbated by their activity pattern and population structure (Hels and Buchwald 2001). However, due to lack of existing data on the abundance and ecological structure of amphibia inhabiting the road habitats, in earlier studies in North East India, it hinders us from making any comparative assessment of our work. Hence, we, for the first time are providing quantitative data on roadkill mortalities of amphibia from this region. Also, our findings are in conjunction with that of Vijayakumar et al. (2001) from Anamalai hills, that *Duttaphrynus melanostictus* are dominant among amphibian roadkills. This could be attributed to their high abundance in this area, since they are cosmopolitan in distribution (Dutta 1997) and are known to be abundant in disturbed habitats (Inger et al. 1984). Amphibians gather near street lampposts and vehicle head lights to feast on insects and also show high human commensalism (Daniels 2005), hence could be more prone to roadkills. This study recorded a high number of amphibian mortality during the wet season, marking a sharp increase with the onset of monsoon (February – March) and during monsoon (July – August), but ending with a tremendous decline in the dry season. This bimodal pattern of roadkill observed corresponds to the seasonality of the climate of this region, since this period corresponds to the rainiest season in the study area with rainfall peaks during these months. This could be linked to their breeding pattern and behaviour, as it drives them to aggregate near water bodies (Hels and Buchwald 2001) and thus augments with the findings of Smith and Dodd (2003), in their roadkill study in Florida, where most amphibian roadkills were related to water levels. Therefore, if traffic intensity continues to increase, the increasing roadkill rates may eventually reduce the population to a level where its reproductive output will be too small to reach the carrying capacities of the breeding pools, which in turn may drive the population to a level where demographic stochastic processes become important for the survival of the population (Hels and Buchwald 2001).

There are plenty of reptile roadkill studies from other parts of the country (Seshadri et al. 2009; Baskaran and Boominathan 2010) but focusing on this part of Northeast India only Das et al. (2007) has reflected the gravity of this problem and provided ample evidence of roadkills. Their study recorded 68 individuals of reptiles of which 89.7% were snakes followed by lizards 10.2%, and *Boiga gokool* was the most highly encountered reptile. Whereas, our study revealed a total of 1281 individual reptiles of which 79.70% were snakes and 20.29% were lizards, with *Calotes versicolor* revealed to be the most affected among lizards and *Amphiesma stolatum* among snakes, hence marking an ultimate increase in the number of lizard kills. There are several factors responsible for such a disparity between the studies. For example, changes in traffic velocity, since the study was conducted more than a decade ago, and differences in sampling period and effort. Being, poikilothermic in nature (Porter 1972), reptiles have been consistently reported to be severely affected by road traffic (Trombulak and Frissell 2000) and the present observations on roadkill from NH-715, supports this. Dodd et al. (1989) and Das et al. (2007) postulated that reptiles are more tempted by roads, in order to maintain their body temperature overnight, as the road surface remain warmer than the nearby areas. Also, the movement of reptiles, particularly snakes, is impeded on road surfaces, and hence increases their risk of mortality (Roe et al. 2006). The current findings of very high numbers of lizard (*Calotes versicolor*) compared to snakes, could be attributed to the higher number of canopy gaps between both sides of the road, thus enhancing their activity near the road. In addition, most lizard kills were observed in locations with high canopy gaps. However, this finding remains in disparity with the findings of Dodd et al. (1989) and Das et al. (2007).

Bernardino and Dalrymphe (1992) found a substantial increase in the number of snake mortalities during the dry season (37% of total kills) as compared to mortalities in the wet season but our study reflects a more or less equal distribution of snake mortality throughout the year. This could be because of the high breeding activity of most of the snakes during the summer and the rainy season (Chittaragi and Hosetti 2014), and mortality during the dry season could have occurred because of increased vehicular influx of visitors to the park, since increase in traffic volume in conjunction with movement rates, makes the animals more prone to roadkill (Chittaragi and Hosetti 2014). Also, unlike mammals, water does not act as a limiting factor for reptile movement during the floods.

Birds are attracted to roads as a location of resource availability, notably food. (Rytwinski and Fahrig 2012). The road attracts predator populations towards particular small mammals and carrion, insects and worms washed out on to roads, and snakes that are attracted to the heat (Erritzoe et al. 2003). Other resources found near or on the roads are grit and salt (Erritzoe et al. 2003), puddles that serve as a water source (Hodson 1962), telephone and power lines that serve as perches (Robertson 1930) and road fencing that offer breeding sites and shelter (Mead 1997). Hence an enormous number of birds fall victims to vehicular collision, while they concentrate on these resources available along roads. A study in Mudumalai Tiger reserve by Bhaskaran and Boominathan (2010) found that birds were least affected by traffic and comprised 7% of the total kills. Also, it was augmented that birds are less susceptible to vehicular hits because of their ability to fly away quickly. However, the present study recorded 9.87% (n = 596) of avian mortality and found them to be highly susceptible to roadkill due to combination of a variety of factors. Birds thus, mostly succumb to ecological traps, since they descend on the road to feed on carcasses of other road killed animals, small insects, grains spread on the road by fringe farmers, grits and small sand particles, specifically by some species (S. S. personal observation) and to prey on amphibians and reptiles available on the paved road. It was also observed that nocturnal birds like owlets were vulnerable to roadkill, colliding frequently with fast-moving vehicles in this area of study because of their low-level flight and predatory behaviour (Boves 2007). Here, at certain areas where there has been higher bird mortality, both the sides of the highway are at a much lower elevation, and birds, when flying from the lowlands, get hit by vehicles while crossing the highway. The fact that birds were more affected during the wet season than the dry season could be because of the increase in herpetofaunal movement on the road, depicting the high availability of prey and also the increase in carcass availability.

This study recorded the mortality of an endangered carnivore, one Indian Leopard *Panthera pardus* and three Small Indian Civet *Viverricula indica*. These figures seem to be very small compared to other taxa, but such loss is intolerable considering their low population density. Several similar studies across India have reported a high roadkill of large cats (Gruisen 1998a; Bhaskaran and Boominathan 2010). Various studies in mammal roadkill in India conducted in many protected areas have also documented the deaths of many species of conservation concern (Rajvanshi et al. 2001). This study also records the roadkill of a primate Rhesus Macaque *macaca mullata*. Although the mortality rate is lower, the number is still significant. Rhesus macaques were observed crossing the highway almost daily at certain locations, but mostly nearer to human settlements. Although they are very intelligent and highly adaptive primates, they still fall victim to roadkill. Most of the mammal roadkills recorded in this study are nocturnal (Bandicoot Rat, Indian Leopard, Small Indian Civet, House Mouse, and various unidentified Rat and Bat Sp.) species that could have been killed while crossing the roads, as they get blinded by the vehicle's headlights (Bhaskaran and Boominathan 2010). Also rat and mouse mortality seemed to be higher in areas near agricultural patches and at the time of rearing of paddy (S. S. personal observation).

Also, a substantial majority of the animal carcasses, 1.92% (n = 121) remained unidentified and categorised as "uncategorised", since they could only be identified up to order, due to their extreme decomposed state. This, in turn, opens up the scope for further detailed studies regarding more precise identification of roadkills.

Conclusion

In conclusion, it could be said that mortality due to collisions with vehicles has been identified as a major conservation issue, but one that is very challenging to address. Ecologists have been trying to diarize the estimation of road-kills for a long time (Stoner 1925), but their impacts are difficult to quantify and requires systematic studies (Smith and Dodd 2003). However due to a variety of factors like searcher efficiency (Kline and Swann 1998), scavenger bias (Boves 2007) or actual cause of death (Kerlinger and Lein 1988), these figures may remain underestimated. Likewise, the figures can also be over-estimated, considering only carcasses are being studied (Hernandez 1988). Therefore, a more detailed study of the same is vital. . This study is prefatory in nature, and further detailed survey of roadkills in relation to species occupancy, their abundance and behaviour will help in understanding the problem at a broader level. Nevertheless, our work clearly indicates the perilous concerns of this issue, revealing a very high number of annual roadkills.. The major factor contributing to these roadkills is the high speed of the vehicles. Thus, reduction of speed should be managed along with proper mitigation designs for the safe movement and existence of all the animals.

Linear infrastructures are an integral part of our daily system and are a major root of developmental activities. But development must always run in parallel with our naturally functioning ecosystem, since our sustenance depends upon the sustenance of nature. Hence, we need not put a stop to development but rather incorporate proper and eco-friendly designs and innovations in tandem with it, in order to reduce vehicular collisions in intrusions within any protected area. It is thereby, important to quantify the magnitude and the effect of vehicular traffic on faunal groups, which would help conserve them, as various infrastructure projects, including roads and highways, are being planned to cater to the country's growing needs.

Acknowledgements

We extend our sincere thanks to the Department of Zoology, Gauhati University, Guwahati, for their help and support. We also acknowledge the Forest Department Kaziranga National Park and PCCF Wildlife & CWLW Assam (WL/FG.31/Pt/2017) for granting us permission to carry out our work. We thank all our field assistants and resource persons, without whose help this work would not have been completed.

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Supplementary material 1

Figures S1–S5

Authors: Somoyita Sur, Prasanta Kumar Saikia, Malabika Kakati Saikia

Data type: zip archive

Explanation note: Road-killed Amphibians, snakes, lizards, birds, mammals.

Link: https://doi.org/10.3897/natureconservation.47.73036.suppl1

Nature Conservation 47: 105–119 (2022)
doi: 10.3897/natureconservation.47.71348
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Exploring 15 years of brown bear (*Ursus arctos*)-vehicle collisions in northwestern Greece

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Academic editor: Clara Grilo | Received 9 July 2021 | Accepted 15 September 2021 | Published 25 March 2022

http://zoobank.org/D41113EF-1827-4D18-B27C-D9DFD54A4B02

Citation: Psaralexi M, Lazarina M, Mertzanis Y, Michaelidou D-E, Sgardelis S (2022) Exploring 15 years of brown bear (*Ursus arctos*)-vehicle collisions in northwestern Greece. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 105–119. https://doi.org/10.3897/natureconservation.47.71348

Abstract

Road networks provide several benefits to human societies; however, they are also one of the major drivers of fragmentation and habitat degradation. Their negative effects include wildlife-vehicle collisions which are associated with increased barrier effects, restricted gene flow, and increased local extinction risk. Large carnivores, such as the brown bear (*Ursus arctos*), are vulnerable to road mortality while they also put human safety at risk in every collision. We recorded approximately 100 bear-vehicle collisions during the last 15 years (2005–2020) in northwestern Greece and identified common aspects for collisions, i.e., spatial, or temporal segregation of collision events, road features, and age or sex of the involved animals. We recorded collisions in both the core distribution area of brown bears, as well as at the periphery, where few individuals, mostly males, disperse. According to our findings, there are four collision hotspots which include ca. 60% of total collisions. Bear-vehicle collisions occurred mostly in periods of increased animal mobility, under poor light conditions and low visibility. In most cases, we deem that a collision was unavoidable at the time of animal detection, because the driver could not have reacted in time to avoid it. Appropriate fencing, in combination with the retention of safe passages for the animals, can minimize collisions. Therefore, such mitigation measures, wildlife warning signs and other collision prevention systems, such as animal detection systems, should be adopted to decrease the number of bear-vehicle collisions and improve road safety.

Keywords

Collision patterns, *Ursus arctos*, wildlife-vehicle collisions

Introduction

Globally, road networks are expanding at an unprecedented rate (Alamgir et al. 2017). The total length of roads already exceeds 64 million km (van der Ree et al. 2015) and by 2050, at least 25 million km of additional roads are expected to be built (Laurance et al. 2014). Transportation infrastructure promotes economic growth and human welfare (Kati et al. 2020), thus the majority of new roads (ca. 90%) will be constructed in developing nations (Alamgir et al. 2017). On the other hand, roads are also one of the most important drivers of landscape fragmentation, habitat degradation and biodiversity loss (van der Ree et al. 2011; Ceia-Hasse et al. 2018). Road effects include edge and barrier effects (Trombulak and Frissell 2000), as well as extensive wildlife mortality due to collisions with vehicles (Barbosa et al. 2020).

Wildlife–vehicle collisions are among the most important road effects to wildlife as their impact reaches far beyond the kill (Ascensão et al. 2013). They are the most pronounced and well documented road effect (Grilo et al. 2009; Ascensão et al. 2017) and a significant threat for several species; in some cases, roadkill is the main cause of human-related mortality (Forman and Alexander 1998), e.g., the case of the barn owl (*Tyto alba*) (Fajardo 2001), and the Iberian lynx (*Lynx pardinus*) in Doñana, Spain (Ferreras et al. 1992). The needs of large carnivores for broad, relatively undisturbed areas and their low reproductive rates render them vulnerable to road effects, and especially to road-related mortality (Rytwinski and Fahrig 2011). As such, the brown bear (*Ursus arctos*) population is negatively affected in a much larger range than the road segment where collisions occur (Kaczensky et al. 2003). Wildlife-vehicle collisions can reduce effective population sizes and gene flow, influence local population dynamics, and increase demographic structure (Ramp and Ben-Ami 2006; Balkenhol and Waits 2009). High traffic volumes restrict animal movement (Northrup et al. 2012; Skuban et al. 2017), while road mortality also entails a barrier effect and decreased landscape connectivity and thus, may lead to loss of genetic variation through genetic drift (Jackson and Fahrig 2011). These effects may lead to populations bottlenecks (Straka et al. 2012) and decrease the probability of a population's long-term survival, with local populations being prone to extinction due to stochastic events (Balkenhol and Waits 2009; Ascensão et al. 2013).

The brown bear is an emblematic species and strictly protected large carnivore species in most European countries and is listed in Annex II and IV of the EU Habitats Directive (92/43/EEC). In Greece, brown bears reach their southern-most distribution in Europe (Karamanlidis et al. 2018). The species is found in two disjunct subpopulations: the eastern population nucleus in the Rhodope complex and the western population nucleus in the Pindos – Peristeri mountain ranges (Mertzanis 1994; Mertzanis et al. 2008). The two subpopulations have cross-border connections with the Eastern Balkans and the Dinaric-Pindus populations respectively (Chapron et al. 2014; Boitani et al. 2015). The species is protected under both national and international legislation. Consistent with the large carnivore population recovery in Europe (Chapron et al. 2014), brown bears exhibited a remarkable demographic and range recovery in Greece and the species now counts approximately 500 individuals (Karamanlidis et al. 2015; Pylidis et al. 2021). Yet, threats and pressures remain, and specific measures must be adopted to guarantee the species' long-term survival (Mertzanis et al. 2009; Karamanlidis et al. 2021). Bear-vehicle collisions (BVCs) have often made the news over the past few years, raising both conservation and road safety issues (Kaczensky et al. 2003). In this study, we explored the spatial and temporal patterns of BVCs in Greece. We used BVC data that occurred during a 15-year period (2005–2020) and attempted to detect collision hotspots and factors that increase collision risk. In this context, we mapped seasonal and daily peaks, and their relation to the age and sex of involved individuals, as well as to the different ecological seasons of bears. Furthermore, we explored the characteristics of the road network and BVC location such as spatial extent, speed limit, and viewshed to identify conditions that might be linked to increased BVC risk, and calculated an average vehicle's stopping distance in an attempt to discern between high and low risk locations.

Methods

Study area

The study area coincides with the species' range in Greece (distribution area: 24,500.3 km^2, Fig. 1a). The landscape exhibits great heterogeneity, varying from natural and semi-natural areas to human dominated landscapes. Thus, a mosaic of different habitats, such as broadleaf and coniferous forests, shrublands and grasslands, agricultural and artificial lands, characterizes the study area.

Data collection and analysis

We collected data on BVCs for the past 15 years (2005–2020), with the Bear Emergency Team being the main source of information. The Bear Emergency Team deals with human-bear interference incidents and operates under the official "Bear-human proximity and interference Management Protocol" operational manual with the endorsement of the state. However, there are several cases of BVCs that remain unrecorded as they were not reported to the authorities, usually because property damage was minor, and the injured animal fled. We included a handful of such incidents in our database, recorded after coincidental personal communication with the people involved.

For every BVC, event-level information (location, date, and time of incidence) and individual-level information (sex and age of the animal, and number of injured animal) were recorded. We explored the spatial distribution of BVCs and spotted areas of high BVC density, by applying the kernel density method and visualizing density by a heatmap with the function 'heatmap' of ArcGIS Pro (ArcGIS Software by ESRI). For every area that showed high BVC density, we calculated the length of roads where BVCs have occurred, the convex hull area, and road density (road length/convex hull area). Furthermore, we explored how the incidences are distributed across the biologically meaningful seasons for brown bear activities, as described by de Gabriel Hernando et al. (2020): "emergence" (1 March–21 April), "mating" (22 April–21 June), "post-mating" (22 June–7 August), "early hyperphagia" (8 August–7 October) and "late hyperphagia" (8 October–15 December) season. For each BVC location, we obtained weather data (Visual Crossing Corporation 2021) and also sunrise and sunset times (Hoffmann 2021) to identify conditions (e.g., rainy conditions or night) favoring BVC.

We explored how characteristics of road network and location are linked to BVCs. We also derived road network vector data in our study area (Geofabrik GmbH and OpenStreetMap Contributors 2020) and recorded, per case, the speed limit imposed by the national Highway Code or by local signage. Then, we calculated per case an average vehicle's stopping distance following the guidelines of the "American Association of State Highway and Transportation Officials" and taking into account weather conditions to detect road surface wetness. Viewshed per BVC location was also estimated within a 1 km buffer zone using the digital surface model produced in the framework of the Reference Data Access (RDA) Action of the EU GMES/Copernicus program (Copernicus Land Monitoring Services 2020). Based on the estimated viewshed at both sides of the BVC location, we calculated the mean distance where a driver could have spotted the animal on the road (sight distance) and juxtaposed it to stopping distance, as estimated per incident, to identify cases where a BVC might have been avoided (low risk locations). Accordingly, we consider high risk the locations where vehicles are not able to stop in time and avoid the BVC as the sight distance is shorter than the stopping distance. Lastly, we calculated the visibility index (visible length/total length of the road segment) within the 1 km buffer zone. All the calculations were performed with the ArcMap 10.7 and ArcGIS Pro (ArcGIS Software by ESRI).

Results

A total of 101 BVCs were recorded between 2005 and 2020, with all incidences occurring in the western bear population nucleus in the Pindos – Peristeri mountain ranges. Annual BVC-attributable mortality corresponds to approximately 1.2% of the total population with the mean annual number of BVCs being 6.3 ± 4 (min = 1 in 2006, max = 16 in 2012). Among the involved individuals, 30 were female and 38 male bears, while in 33 individuals the sex was not identified. Ages of the bears varied from 4 months old up to ca. 25 years of age. Specifically, 39 individuals were adults (>4 years old), 17 subadults (1.5–4 years old), 17 cubs (<1.5 years old) and 28 were bears whose age has not been recorded. In only one case two animals, an adult female with a cub, were involved in a single collision.

We identified four areas with high BVC density (Fig. 1b): a) between the Vernon and Gramos mountains, at the outskirts of Kastoria and between the neighboring villages (location H1), b) at the western foothills of mount Askio (location H2), c) south

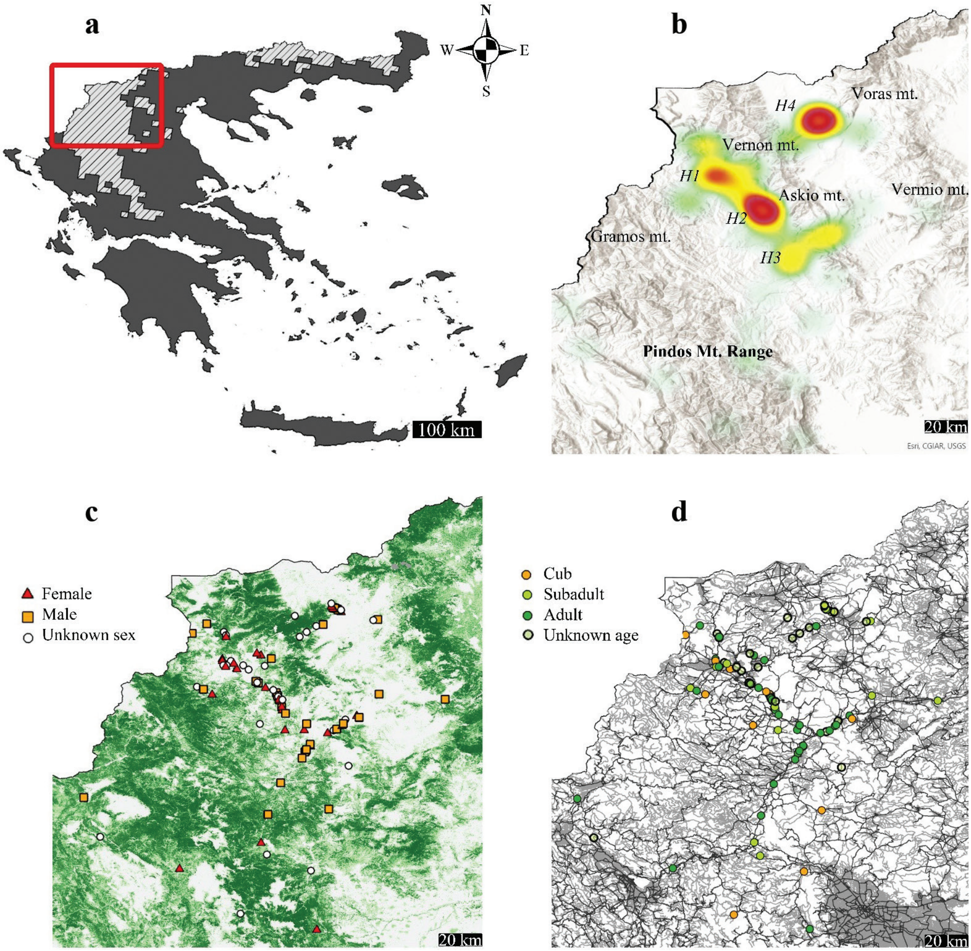

Figure 1. a Brown bear distribution in Greece is presented with a hatch pattern against a dark background **b** BVC heatmap and the main mountains in northwestern Greece **c** BVCs by sex with a tree cover density basemap (Copernicus Land Monitoring Services 2020 **d** BVCs by age class with a road network basemap (Geofabrik GmbH and OpenStreetMap Contributors 2020)

of mount Askio (location H3) and, d) between the Vernon and Voras mountains (location H4) (Table 1). Significantly, there have been some BVCs at the periphery of bear core habitat and distribution where mostly male bears were hit by vehicles, e.g., BVC at the southern foothills of mount Vermio. By contrast, in core habitat areas and areas characterized by increased human presence, i.e., proximity to towns and/or in more densely populated areas, we found that mostly females and young bears were hit by vehicles (Fig. 1c, d). For instance, at location H1 which exhibits the highest road density (Table 1) and is covered by discontinuous urban fabric, six female bears and five bears of unknown sex were involved in BVCs, out of which three were cubs, three subadults, two adult and three bears of unknown age. Finally, in location H4, at least 16 BVCs

Table 1. Details on the four high bear-vehicle collision (BVC) density locations (H1–H4) in northwestern Greece, in terms of BVC number and the area's road network (description of the BVC related road segments, total length of road segments where BVCs occurred, convex hull area, road density).

Location	Number of BVCs	Description of the BVC related road segments	Total length of road segments where BVCs occurred (km)	Convex hull area (km²)	Road density (km/km²)
H1	11	Secondary road complex	40.7	16.8	6.8
H2	18	A 15 km motorway segment & adjacent old national network segments	22.4	16.5	2.6
H3	14	A 32 km motorway segment & an adjacent secondary road segment	39.8	57.8	1.9
H4	16	A 4 km national road segment & 1 km of the adjacent old network	5	2.9	1

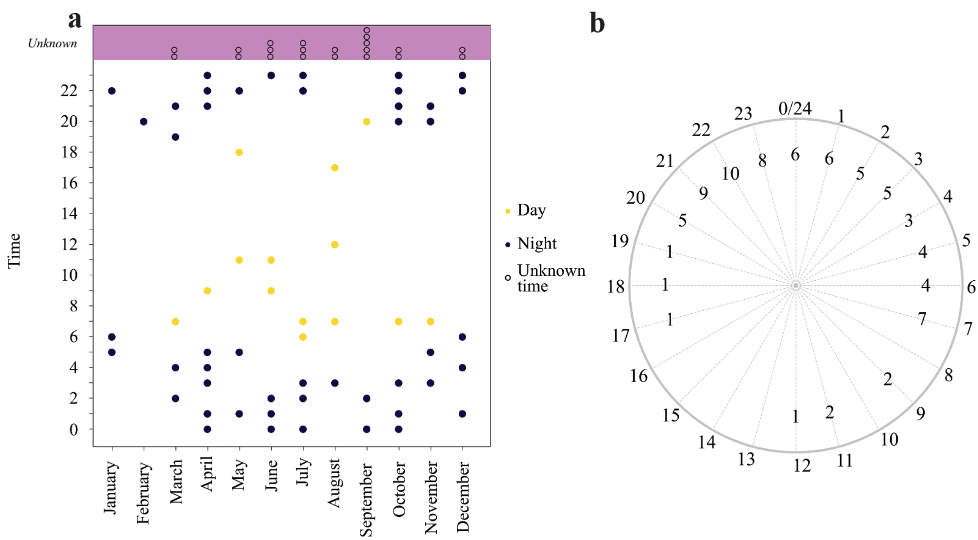

Figure 2. a BVCs across month of the year and time of day. Yellow indicates BVCs that occurred during daytime and dark blue the ones that occurred during the night, considering sunrise and sunset time by location. BVCs whose time of occurrence has not been recorded, are presented in the purple bar at the top of the figure **b** a clocklike figure where inner values indicate count of BVCs per time of day.

occurred during the past 15 years, which comprise of four collisions with females, seven with males and five with bears of unknown sex. In terms of age, they involved three cubs, five subadults, three adults and five bears of unknown age.

The 77% of BVCs occurred during the night (Fig. 2) and ca. 38% was associated to rainy weather. Most BVCs occurred in autumn (35%), followed by summer (28%), spring (26%) and lastly, winter (10%). The maximum number of BVCs took place in October (16 BVCs) (Fig. 2a).

When analyzed across the biologically defined seasons for bears, BVCs peak during late hyperphagia (n = 19) and mating (n = 18) and reach a minimum count of 6 during denning season. More males than females were involved in BVCs (23 males out of 35

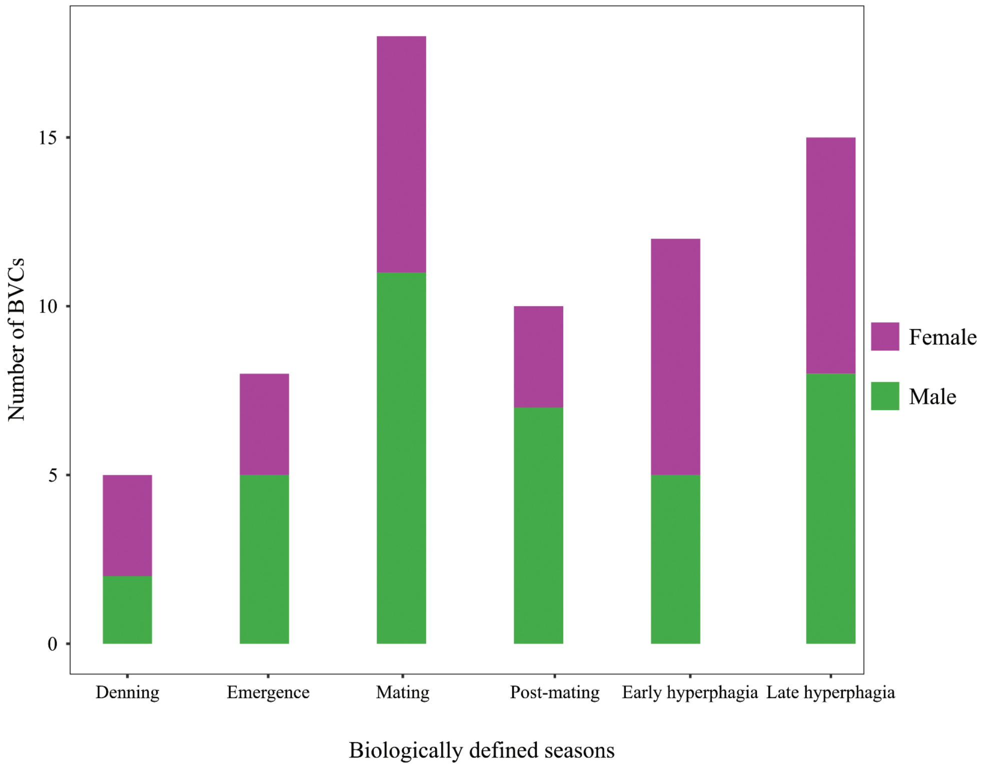

Figure 3. Number of BVCs per sex, across biologically defined seasons.

Table 2. Descriptive statistics for the estimated stopping distance, sight distance (estimated using the viewshed per location) and visibility index (calculated as visible length/total length of the road segment) for the 101 bear-vehicle collisions recorded.

	Mean	Minimum	Maximum
Stopping distance (m)	131.0 ± 76.1	25.7	304.9
Sight distance (m)	198.5 ± 159.8	2.4	865.7
Visibility index	0.3 ± 0.2	0.01	1

collisions) during emergence, mating, and post-mating seasons, whereas more females were involved during early and late hyperphagia (15 females out of 27 collisions) (Fig. 3).

Regarding the road characteristics at the collision point, the estimated mean stopping distance was smaller than the mean sight distance, i.e., the driver could potentially see the bear, react in time, and avoid the collision (Table 2). However, considering each case individually, we found larger stopping distances in 68% of the incidents, rendering those BVCs unavoidable for the drivers and the road segment as a high-risk location (Fig. 4). Furthermore, the visibility index at the locations where BVCs have occurred was generally low, and only 30% of the segment on average was visible due to the terrain.

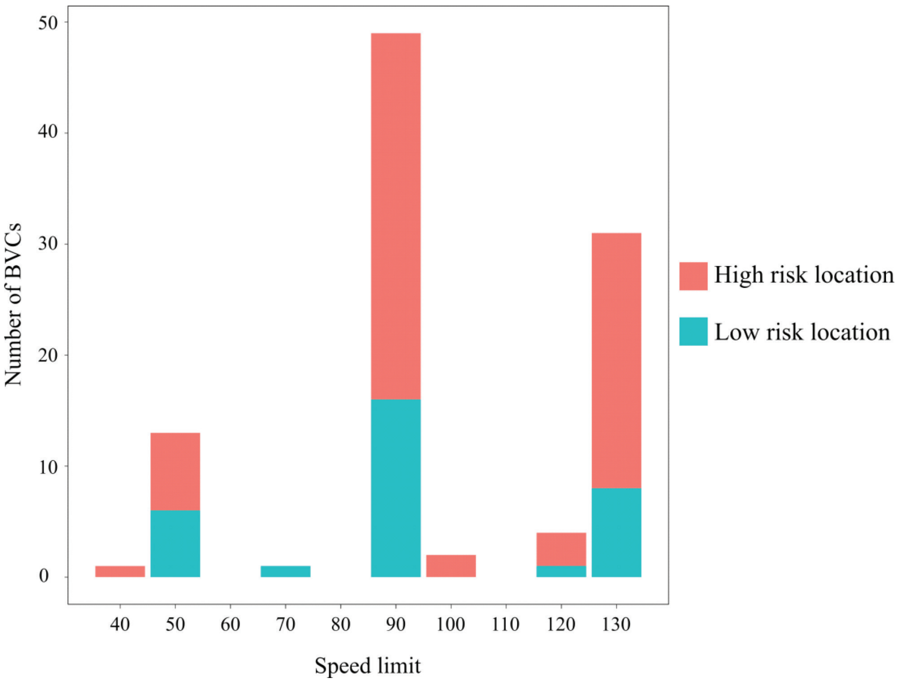

Figure 4. BVC counts across legal speed limits. Red indicates BVC counts in high-risk locations, where the collisions may have been unavoidable according to the sight distance set against the stopping distance, whereas blue marks BVC counts in low risk locations.

Discussion

Our results showed that at least 100 brown bears have been involved in BVCs over the last 15 years. We detected four collision "hotspots" in the western nucleus of bear population of Greece, located in the Pindos – Peristeri mountain ranges. Each of these areas is unique in terms of extent, road types and density, as well as the profile BVC victims. Furthermore, we found distinct temporal patterns pervading the collisions, which are linked to both driving conditions and the species' seasonal and circadian activity. Hence, we found that drivers are more likely to be involved in BVCs during late spring and fall when mating and hyperphagia take place. BVCs also seem to be linked to low visibility conditions which relate to both the terrain characteristics and low light conditions. Lastly, our results suggest that in most cases, it may not have been possible for the driver to react in time and thus, the collision was unavoidable.

Brown bear daily activity patterns have been well documented and in southern Europe the species demonstrates mainly a crepuscular and nocturnal activity pattern (Roth and Huber 1986; Clevenger et al. 1990; Kaczensky et al. 2006; de Gabriel Hernando et al. 2020), with human activity having a strong effect on circadian habitat use (Naves et al. 2001). The increased BVC risk during the night found here was possibly due to the species' nocturnal activity coupled with low light driving, when visibility is limited, and reaction times are longer (Eloholma et al. 2006).

BVC seasonal patterns were consistent to the species' life-history phenology and, like other carnivores, increased collisions were linked with higher mobility periods (Grilo et al. 2009). Both bear circannual activity and BVC number peaked in late spring and fall, i.e., mating and hyperphagia (Clevenger et al. 1990; Mertzanis 1994; García-Rodríguez et al. 2020) ecological seasons (de Gabriel Hernando et al. 2020). Bears exhibit a roam-to-mate behavior (Steyaert et al. 2012), thus both sexes increase their home ranges, and consequently road crossings during mating. Home ranges decrease during post-mating for both male and females without cubs (Dahle and Swenson 2003) and re-increase during hyperphagia (de Gabriel Hernando et al. 2020), when individuals become again more mobile in order to locate suitable resources, store fat and ultimately prepare for denning and reproduction (Ordiz et al. 2016; Sergiel et al. 2020). However, the two sexes do not cross roads equally (Sawaya et al. 2014) and crossing intensity changes seasonally (Guthrie 2012). Males cross roads more intensively during mating while searching for mates, whereas females increase road crossings during hyperphagia (Guthrie 2012) and as a result, BVCs also follow this pattern (Fig. 3).

The overlap of wildlife road crossing activity with other conditions increasing collision risk, such as poor light and road surface conditions can be considered the recipe for collision hotspots (Neumann et al. 2012). The majority of BVCs occurred under low conspicuity conditions (77%), and at locations where the average vehicle's stopping distance was larger than the sight distance (ca. 70%). Yet, considering that most drivers feel safe surpassing the legal speed limit (Mannering 2009), it is safe to assume that more than 70% of BVCs were already unavoidable when the driver detected the animal on the road. Such speed limit compliance issues render speed limit reduction a collision prevention measure of mixed effectiveness (Huijser and McGowen 2010).

We identified four BVC hotspots which include 58% of the total collisions. At location H1, which is dominated by humans and is characterized by high road density, we found mainly female and young bears in BVCs. Young bears and females with dependent offspring often select areas close to human settlements to avoid infanticide by males (Steyaert et al. 2013; Elfström et al. 2014). This type of mortality is critical for local population demography and overall conservation efforts (Palomero et al. 2007). Location H4, at which 50% (eight out of 16) of the involved bears were of young age, plays a major role in conservation efforts. Furthermore, the number of males denotes dispersal behavior, as dispersal in bears is sex-biased (Zedrosser et al. 2007) and location H4 is considered to be the main corridor connecting the Vernon and Voras mountains; with the former hosting part of the source population and the latter being an area of population recovery during the past decades. Wildlife-vehicle collisions are common in H4 as the landscape topography funnels wildlife there. However, BVCs eliminate would-be-crossers, reduce abundance and connectivity (Jackson and Fahrig 2011) and hence, they jeopardize the successful recovery of the species in Voras and the adjacent mountains (e.g., Pinovo and Tzena).

Wildlife-vehicle collision prevention measures include fencing combined with crossing opportunities, animal detection systems and seasonal wildlife warning signs (Huijser et al. 2009; Huijser and McGowen 2010). In Greece, a bear-proof fence (2.2 m high, 0.8 m overhang with a negative angle, 1.5 m horizontal mesh), has been installed on both sides of motorway A29 and along the south-western segment of A2.

This fence in combination with the retention of safe passages for the animals (e.g., overpasses and underpasses) has substantially decreased BVCs in location H2. Specifically, approximately 20 BVCs occurred on motorway A29 from its operation (2009) until the complete fence installation in 2014; since then, only one BVC occurred on the motorway (2015). Similarly, the motorway in location H3 has also been fenced and not a single BVC has been recorded since then. Yet, collision hotspots do not always indicate the optimal location to install mitigation measures (Zimmermann-Teixeira et al. 2017), and while placement of mitigation measures is vital in predicting effectiveness, preserving road permeability and habitat connectivity are also important aspects for planners to consider (Glista et al. 2009); especially since locations with high wildlife crossing rates do not always overlap with collision hotspots (Find'o et al. 2019).

Fencing is an effective mitigation measure in decreasing wildlife-vehicle collisions that when implemented appropriately can eliminate barrier effects and collision clustering at fence ends (Clevenger et al. 2001; Huijser and McGowen 2010). However, for areas like locations H1 and H4, fencing does not seem to be the best choice. Location H4 lacks the wildlife safe passage opportunities, and a fence would create an unsurpassable obstacle, which would hinder animal movement in the corridor connecting the Vernon and Voras mountains. Other collision countermeasures, such as animal detection and animal warning systems should be evaluated and considered in location H4 to minimize collisions. Location H1 poses an even greater challenge though. As BVCs occur on several roads in this peri-urban landscape, fencing is not a realistic option, whereas animal warning systems may only transfer the problem from one road to another. Adoption of animal detection systems, driver warning signs and speed reduction measures can contribute to decreasing BVCs in the area. Still, local driver awareness raising will be key in encouraging and ensuring slower and more careful driving in the area, and ultimately achieving the reduction of wildlife vehicle collisions.

Wildlife-vehicle collisions are the product of various factors such as road surface and environmental characteristics, as well as, road traffic, wildlife abundance and driving conditions (Seiler 2005; Neumann et al. 2012). In the present study, we found that most BVCs occur in hotspot locations when bear mobility increases and other BVC-favorable conditions are met, i.e. poor light conditions and low visibility. Wildlife-vehicle collision prevention solutions are necessary to minimize BVCs and enhance road safety for both wildlife and humans.

Acknowledgements

We thank the Bear Emergency Team, as well as all parties and/or individuals who provided information on bear-vehicle collisions.

This research is co-financed by Greece and the European Union (European Social Fund – ESF) through the Operational Programme "Human Resources Development, Education and Lifelong Learning" in the context of the project "Strengthening Human Resources Research Potential via Doctorate Research" (MIS-5000432), implemented by the State Scholarships Foundation (IKV).

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Nature Conservation 47: 121–153 (2022)
doi: 10.3897/natureconservation.47.72970
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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'Animals under wheels': Wildlife roadkill data collection by citizen scientists as a part of their nature recording activities

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Academic editor: Sara Santos | Received 13 August 2021 | Accepted 27 December 2021 | Published 25 March 2022

http://zoobank.org/55B9F61D-9889-47ED-8D39-B7B4B76C2E45

Citation: Swinnen KRR, Jacobs A, Claus K, Ruyts S, Vercayie D, Lambrechts J, Herremans M (2022) 'Animals under wheels': Wildlife roadkill data collection by citizen scientists as a part of their nature recording activities. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 121–153. https://doi.org/10.3897/natureconservation.47.72970

Abstract

'Animals under wheels' is a citizen science driven project that has collected almost 90,000 roadkill records from Flanders, Belgium, mainly between 2008 and 2020. However, until now, the platform and results have never been presented comprehensively to the scientific community and we highlight strengths and challenges of this system. Data collection occurred using the subsite www.dierenonderdewielen.be ('animals under wheels') or the multi-purpose biodiversity platform observation.org and the apps, allowing the registration of roadkill and living organisms alike. We recorded 4,314 citizen scientists who contributed with at least a single roadkill record (207-1,314 active users per year). Non-roadkill records were registered by 85% of these users and the median time between registration of the first and last record was over 6 years, indicating a very high volunteer retention. Based on photographs presented with the roadkill records (n = 7,687), volunteer users correctly identified 98.2% of the species. Vertebrates represent 99% of all roadkill records. Over 145,000 km of transects were monitored, resulting in 1,726 mammal and 2,041 bird victims. Carcass encounter rates and composition of the top 10 detected species list was dependent on monitoring speed. Roadkill data collected during transects only represented 6% of all roadkill data available in the dataset. The remaining 60,478 bird and mammal roadkill records were opportunistically collected. The top species list, based on the opportunistically collected roadkill data, is clearly biased towards larger, enigmatic species. Although indirect evidence showed an increase in search effort for roadkill from 2010-2020, the number of roadkill records did not increase, indicating that roadkills are diminishing. Mitigation measures preventing roadkill could have had an effect on this, but decrease in population densities was likely to (partially) influence this result. As a case study, the mammal roadkill data were explored. We used linear regressions for the 17 most registered mammal species, determining per species if the relative proportion per year changed significantly between 2010 and 2020 (1 significant decrease, 7 significant increases). We investigated the seasonal patterns in roadkill for the 17 mammal species, and patterns per species were consistent over the years, although restrictions on human movement, due to COVID-19, influenced the seasonal pattern for some species in 2020. In conclusion, citizen scientists are a very valuable asset in investigating wildlife roadkill. While we present the results from Flanders, the platform and apps are freely available for projects anywhere in the world.

Keywords
Citizen science, data quality, mammals, presence only data, relative trends, roadkill, structured monitoring, seasonal patterns

Introduction

Roads directly impact populations and species due to vehicle induced mortality. An estimated 29 million mammals and 194 million birds are killed annually on European roads (Grilo et al. 2020). Worldwide, all mortality sources considered, natural or human, vehicle induced mortality was 7% for adult mammals and 1% for adult birds (Hill et al. 2019).

Apart from direct mortality by wildlife vehicle collisions, roads and traffic do have multiple effects on ecosystems and wildlife populations including habitat loss and habitat fragmentation (Taylor and Goldingay 2010; Whittington et al. 2019). Roads can have genetic effects by acting as a barrier and decreasing genetic diversity (Coffin 2007;Holderegger and Di Giulio 2010). Furthermore, the presence of roads, and the intensity of their use, can result in behavioural changes of individuals and species (Mumme et al. 2000; Kerley et al. 2002; Whittington et al. 2019).

Monitoring of wildlife roadkill can, apart from the collection of the numbers being killed, facilitate monitoring of population trends, species distribution and invasions, animal behaviour and contaminants and disease (Schwartz et al. 2020). Volunteer citizen scientists can collect and/or process data as part of a scientific inquiry (Silvertown 2009) and they play an important role in the data collection of roadkill records in projects which have been initiated worldwide http://globalroadkill.net (Shilling et al. 2015). Globally, there are dozens of web based systems to register wildlife vehicle collision casualties or roadkill (Shilling et al. 2015). Citizen science data on roadkill has proven to be a valuable data source for the identification of potential roadkill hotspots (Shilling and Waetjen 2015; Périquet et al. 2018; Englefield et al. 2020), temporal patterns in roadkill (Raymond et al. 2021) and species range maps (Tiedeman et al. 2019). Long term motivation of volunteers, support for the identification of roadkill and feedback to volunteers are of critical importance in sustaining roadkill citizen science projects (Bil et al. 2020). The Flemish project 'Animals under wheels' (Dieren onder de wielen) is one of the largest citizen science driven roadkill databases worldwide (Waetjen and Shilling 2017). However, until now, the platform and results have never been presented comprehensively to the scientific community. We highlight strengths and challenges of this system, which is easily and freely available to be deployed anywhere in the world for roadkill monitoring (and general biodiversity monitoring as well).

Methods

We describe and analyse the roadkill data submitted to the online biodiversity database https://waarnemingen.be, the local Flemish version of the international platform https://observation.org. This platform allows for the registration of observations of all plants, fungi and animals. Since the launch in 2008 until 2020, this resulted in more than 26,200 species and 31,5 million observations for the 13,522 km^2 of Flanders, generating one of the densest biodiversity datasets in the world. Flanders is the northern region of Belgium, situated in Western Europe. It has a very high human density of 487 inhabitants/km^2 (Statbel 2020) and 5.08 km of roads/km^2, one of the densest road systems in the whole of Europe (Vercayie and Herremans 2015). Flanders has 883 km of motorways, 6,040 km of regional roads and 64,080 km of local roads (FPS Mobility and Transport 2011). We show the 2019 traffic data since this is the last year without a COVID-19 impact. Daily, over 70 million vehicle kilometres are driven on Flemish motorways (Hoornaert 2019) and the monitoring of 880 motorway segments indicated an average daily traffic volume of 37,592 vehicles per segment per day (median = 32,067, min = 4,440 and max = 131,508) (Vlaams Verkeerscentrum 2021). On regional roads, the monitoring of 127 segments showed an average daily traffic volume of 17,583 vehicles per segment per day (median = 16,666, min = 2,381 and max = 36,649). For local roads, the authors are not aware of available data. The most recent available data from 2017 indicate the Flemish registered vehicles drive 61.1 billion kilometre per year (Kwanten 2018).

Roadkill data in the waarnemingen.be database can be submitted using: (a) the online platform https://waarnemingen.be, (b) the subsite www.dierenonderdewielen.be ('animals under wheels') or (c) the apps ObsMapp for Android, iObs for iPhone and recently ObsIdentify for all devices. On the online platform, the location of the observation must be pinpointed on the map, date/time selected and species and additional observation information 'roadkill' label must be selected using controlled vocabulary (Waetjen and Shilling 2017). In the apps, location and time are derived from the smartphone. Species and 'roadkill' must be selected using controlled vocabulary in the appropriate data fields. Photographs and additional information can be added to an observation but are not mandatory. The apps do also function in a voice recognition mode to register observations, which is always useful, but essential when monitoring during driving (Vercayie and Herremans 2015).

We analyse the number of users registering roadkill records, the active users per year and the number of new users per year (recruitment) to show the long-term viability of the project. We investigate the number of roadkill records per user and the distribution between users including the corresponding Gini coefficient, a measure of unevenness (0: totally equal, 1: a single person is responsible for all records) (Sauermann and Franzoni 2015). We calculate the retention time per user, defined as the time between the registration of the first and the last roadkill per user. For all roadkill registering citizen scientists, we examine if they also registered observations of plants, fungi or living wildlife within the waarnemingen.be database.

Data quality

Quality control of the data is an important step in all scientific processes, and also very important for citizen science projects (Wiggins et al. 2011). The data validation procedure in the 'waarnemingen.be'-database combines species specialists (experienced volunteers) assigning a validation status to observations and an algorithm automatically evaluating observations. This multi-step process depends on the proof presented (not mandatory but possible), species status (common vs rare), location and time (was there already a proven record of presence within a species group dependent defined range of space and time) of the observation (Swinnen et al. 2018). Species specialists can assign a validation status to an observation: (a) 'Approved (based on evidence)', evidence can be a picture or sound, (b) 'Approved (based on expert judgement)', the additional information or the knowledge of the observer makes it highly likely this is a correct observation, (c) 'Under review', temporary status, no decision has been taken yet, (d) 'Cannot be assessed', proof or explanation does not allow for a decision to be made, (e) 'Rejected', observation was wrong and user does not correct it. The algorithm can also assign a validation status: (f) 'Automatic validation', for a record to be automatically validated, there need to be a number of earlier observations of the species supported by proof (at least one or two), within a certain radius (ranging from 100 m to 10 km) within a specified time range (60–3000 days). Remaining observations are classified (g) 'unverified'. The validation process is an interactive process where users can be contacted for additional information or suggested to change the species name or other details in case of an error. We investigate the possible error ratio by calculating the percentage of approved observations (based on photographic evidence) which was initially wrong but corrected by the user after interaction with a validator.

Methodology of data collection

To allow standardised data collection and a quantifiable measure of search effort, two options for data registration are offered to users. In 2013, the option to gather standardised transect data was added to the website. Users were asked to choose a specific route, draw it online and check it at least once every two weeks, but not more than once a day. They were asked to fill in the survey, even if no roadkill was detected. These type of transects are called fixed transects in this manuscript. Since 2018, smartphone users can allow their app to register their transect while observing nature and registering observations. When finished, users indicate per species group if their transect can be used as a roadkill monitoring transect. Since there are no requirements for transects to be identical, or to be repeated over time, we call them variable transects.

For the fixed transects, users register the transport modus (on foot, by bike, by car). For the variable transects, the transect is recorded by the smartphone and we derived the speed from the track length and duration, and classified transects as 0–7 km/h as on foot, 7–25 km/h by bike and >25 km/h by car (although another motorised vehicle is also possible). This distinction according to speed is important because speed affects detection probability and it is known that searching on foot is more effective than counting while driving (Slater 2002). Data collected during standardised monitoring contains more information but it is also more demanding for volunteers resulting in a smaller number of participants (Bonney et al. 2009).

Waarnemingen.be is mainly used as a personal notebook by naturalists to register and document their sightings. Although some users are aware of the additional scientific advantages standardised data collection offers, the majority of all observations in waarnemingen.be are presence only records (also known as roving records) (Vercayie and Herremans 2015). Given the correct identification of the species, presence is confirmed but search effort is unknown. The absence of a record can have multiple causes: no roadkill present, no observer present or both present but not registered by the observer. We show a summary of the transect data including transect characteristics and top 10 of recorded bird and mammal species and calculate the average distance that needs to be covered to encounter a roadkill. For the presence only data, a top 20 for bird and mammal casualties is presented and we compare the results with the data collected during transect counts. While herpetofauna is also an important species group, e.g. because of their worldwide threatened status (Heigl et al. 2017), we do not discuss them here since they are only recorded at lower driving speeds, and a larger (roadkill) database, separate from waarnemingen.be is available, calling for a specific analysis.

Case study: mammal roadkill records

The number of new observations (of all organisms) submitted to waarnemingen.be continues to increase year after year, from 400,000 in 2008 to over 6,000,000 in 2020 (and over 8.7 million in 2021). For 2010–2020 we investigate by means of a linear regression (R Core Team 2016): (a) is there an increase in mammal roadkill observations? (b) is there an increase in mammal observations (excluding all automated observations by camera traps and bat-detectors since they do not represent human search effort)? (c) are both correlated?

The large majority of roadkill data is collected as presence only data. Since search effort is unknown, absolute roadkill trends per species cannot be calculated. However, relative trends can be calculated and give an indication of the increase or decrease of roadkill abundance of a specific species compared to the other species killed on the road. For this analysis all mammal roadkill records were combined (presence only and transect data), excluding observations where observers indicated they were uncertain of species determination (1.5% of observations), and only species with a minimum of 50 roadkill individuals were withheld, resulting in 17 species (only species level records were considered). Per species, the percentual abundance per year from these 17 species was calculated. By using a linear regression, we determine per species if the relative proportion per year changed significantly between 2010 and 2020. Graphs were made using ggplot 2 (R Core Team 2016; Wickham 2016). Based on unstructured, presence only, citizen science data on roadkill, we propose the relative change in proportion of roadkill victims as a means to gain insight in relative population changes as roadkill numbers are expected to be strongly and positively associated with the local abundance of living animals (Baker et al. 2004; George et al. 2011; Pettett et al. 2018; Schwartz et al. 2020).

Apart from the local abundance, timing within the year does influence the number of victims found. Animals are sensitive to wildlife vehicle collisions during movement. This can be daily movement while foraging or patrolling home ranges, or seasonality in mating, juvenile dispersal or migration (Taylor and Goldingay 2010; Garriga et al. 2017; Schwartz et al. 2020). For all roadkill data combined (presence only and transect data) we plot species specific density functions using ggplot 2 (R Core Team 2016; Wickham 2016). For this, the number of records was used, and not the number of individuals. Overall, 98.7% of records comprises a single individual, but more than one individual is also sometimes reported. This can reflect reality, multiple individuals killed at once or, sometimes, users combine a number of observations from a timespan from the same location and add a single observation to the database. Analysing these 'combination records' as if all individuals were killed at the same time would introduce errors in this seasonal pattern and to avoid this, the number of observations was used. For species with more than 1,000 records, we show the annual seasonal pattern in roadkill data. When fewer data are available, a single density plot combining the data from 2010–2020 is shown.

Results

Within Flanders, 89,276 roadkill records were registered from 1960–2020 (Fig. 1). Mammals (52,847), birds (23,346) and herpetofauna (11,762) represent 99% of roadkill observations. Coleoptera (n = 499) is the invertebrate group with the most roadkill records. One record can contain multiple individuals. Most records (93%) date from 2008 onwards, the launch of waarnemingen.be. The majority of 'historical' records (79%) were added by a single account (Regional Mammal Workgroup).

A total of 4,314 citizen scientists submitted at least one roadkill record from Flanders (Fig. 2). Male roadkill registering volunteers (1,547) are three times as abundant compared to females (457). For 2,310 citizen scientists the sex is unknown. On average 881 users were active per year (range 207–1,314) and this number shows a steady increase. Per year, on average 332 (range 207–465) 'new' users register their first roadkill victim with an increase of 20% in 2020 compared to the second best year (2009).

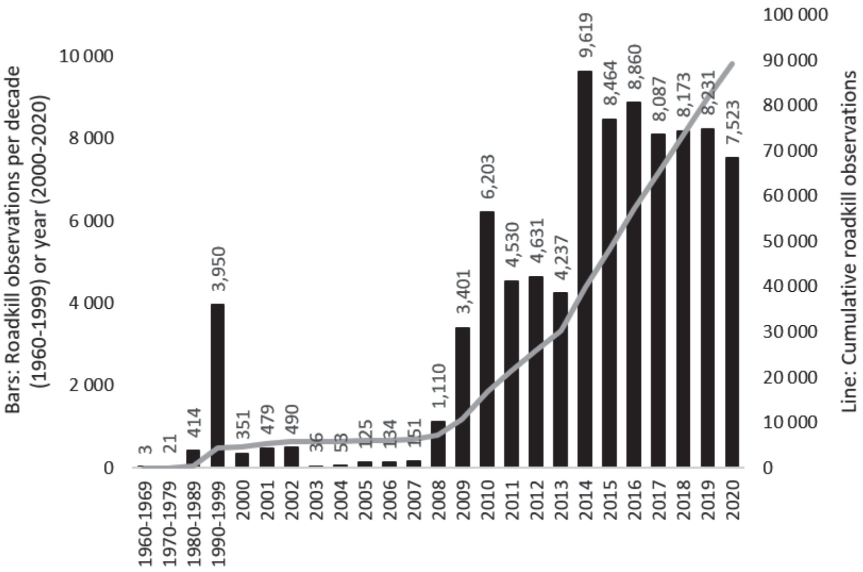

Figure 1. Roadkill observations per decade (1960-1999) or per year (2000-2020) and cumulative number of roadkill observations in Flanders, Belgium.

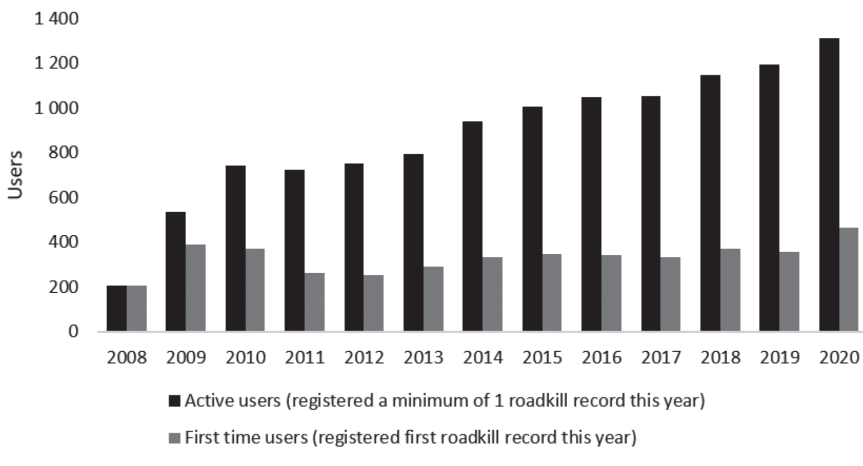

Figure 2. the number of active roadkill registering users per year in Flanders and the number of first time roadkill registering users per year in Flanders since 2008, the launch of https://waarnemingen.be until 2020.

Contributions of users are unequal with 44.4% of users only registering a single roadkill record (see Table 1). The median number of roadkill records per user is 2 (average 21, range 1–4,931). The Gini coefficient of inequality between users is 0.87.

When including all roadkill registering users, volunteer retention time, i.e. the median time between registration of first and last roadkill record, is 7 days. For users

Table 1. The amount of roadkill observations in 8 classes and the number of users in each class, including the percentage of users per class.

Roadkill observations	Users	% of users
1	1,914	44.4%
2-5	1,254	29.1%
6-10	368	8.5%
11-20	267	6.2%
21-50	258	6.0%
51-100	114	2.6%
101-500	109	2.5%
501-5000	30	0.7%

with only a single roadkill record, we consider this single record as the first and the last record and the time between records was 0 days. When excluding the users with only a single roadkill record, the median volunteer retention time increases to over 4 year (1,501 days).

The majority of roadkill recorders (85%) did also submit non-roadkill observations to the biodiversity database and together they are responsible for 25.9 million non-roadkill observations (on a total of 31.5 million non-roadkill records by 49,447 users registered in 2008–2020 in Flanders). This indicates that for most users, the registration of roadkill is a natural part of their registration of nature observations, but the focus is rarely on roadkill alone. When calculating the median volunteer retention time of citizen scientists which registered at least a single roadkill record, based on all of their observations, roadkill and living organisms together, this exceeds 6 years (2,318 days, range 0–5,243 days).

Data quality

In total, 38.9% of records were approved based on different procedures (Table 2). For all observations approved based on the presented photographic evidence, only 139 out of 7,687 recordings needed to be corrected by the validator. This results in an error rate of 1.8%. In only a very small percentage of cases, users do not respond to suggestions to change the species and the observation is then rejected.

All observations which were rejected, under review or which cannot be assessed are removed in the following analyses.

Table 2. Validation status of the roadkill recordings in Flanders (1960-2020).

Validation status	Number of observations (%)
Approved (based on evidence)	7,687 (8.61%)
Approved (based on expert judgement)	10,951 (12.27%)
Approved (automatic procedure)	16,062 (17.99%)
Under review	16 (0.02%)
Rejected	42 (0.05%)
Cannot be assessed	288 (0.32%)
Unverified	54,230 (60.74%)

Methodology of data collection

Transect data

We registered 309 fixed transects online since the start in 2013 until 2020. A little under half (148) were registered online but never monitored by the user. The remaining 161 transects were monitored at least once, resulting in 2,521 records of bird and mammal roadkill during 59,256 km of monitoring. In Table 3 we show the fixed transect characteristics and results grouped per transport mode.

We registered 4,778 variable transects for bird and mammal roadkill since 2018, the year when the smartphone applications (ObsMapp and iObs) allowed it, until the end of 2020. Each transect is considered unique since small variations in the registration of the transect are present, resulting in no repeated counts per transect. This resulted in 1,246 bird and mammal roadkill registrations while monitoring 86,235 km. In contrast with the fixed transects, it is possible the user only monitors a single species group. Therefore, mammal and bird transects are shown separately in Table 4.

When combining both transect types 3,767 roadkill records were registered. For birds, carcass encounter rates vary from 1 carcass per 75.7 km on foot, 1 carcass per 59.3 km by car to 1 carcass per 34.6 km by bike. For mammal, carcass encounter rates are similar, 1 carcass per 74.7 km on foot, 1 carcass per 70.7 km by car and 1 carcass per 43.5 km by bike. We show the top 10 of most frequently recorded (wild) roadkill species for birds and mammals while monitoring transects by car (Table 5) and bike (Table 6). We include observations not identified to species level, but they are unranked.

Table 3. Fixed transect characteristics and results grouped per transport mode (2013-2020). * A single transect can be monitored on foot, by bike and by car. That's why the sum of the different transects differs from 161.

	Distance (km)	Different transect*	# counts	Median # counts per transect	Average # counts per transect (range)	Roadkill Birds found	Roadkill Mammals found
By car	32,673	103	2,722	8	26 (1-484)	581	497
By bike	26,063	92	4,815	16.5	52 (1-1,204)	782	636
On foot	520	31	299	1	10 (1-70)	15	10

Table 4. Variable transect characteristics and results grouped per transport mode (2018-2020).

		Distance (km)	Different transects	Roadkill victims
By car	Birds	36,999	1,570	593
By car	Mammals	39,910	1,723	529
By bike	Birds	2,943	262	57
By bike	Mammals	3,137	285	35
On foot	Birds	1,600	461	13
On foot	Mammals	1,646	477	19

Table 5. Top 10 of birds and mammal roadkill victims encountered the most frequently by car during transect monitoring. Observations not identified to species level are shown but not ranked.

Birds	Scientific name	Common name	# ind.
1	*Columba palumbus*	Common wood pigeon	329
	Aves unknown	Bird unknown	286
2	*Turdus merula*	Common blackbird	172
3	*Phasianus colchicus*	Common pheasant	74
4	*Anas platyrhynchos*	Mallard	37
5	*Corvus corone*	Carrion crow	30
6	*Buteo buteo*	Common buzzard	20
7	*Pica pica*	Eurasian magpie	18
8	*Coloeus monedula*	Western jackdaw	17
9	*Gallinula chloropus*	Common moorhen	17
10	*Strix aluco*	Tawny owl	16
Mammals	**Scientific name**	**Common name**	**# ind.**
	Mammalia unknown	Mammal unknown	270
1	*Erinaceus europaeus*	Hedgehog	223
2	*Lepus europaeus*	European hare	97
3	*Rattus norvegicus*	Brown rat	79
4	*Oryctolagus cuniculus*	European rabbit	70
5	*Martes foina*	Beech marten	67
6	*Sciurus vulgaris*	Red squirrel	39
6	*Vulpes vulpes*	Red fox	39
8	*Mustela putorius*	European polecat	18
	Rattus unknown	Rat unknown	7
9	*Capreolus capreolus*	Roe deer	5
	Mustelidae unknown	Marten unknown	5
10	*Talpa europaea*	European mole	3

Table 6. Top 10 of birds and mammal roadkill victims encountered the most frequently by bike during transect monitoring. Observations not identified to species level are shown but not ranked.

Birds	Scientific name	Common name	# ind.
1	*Turdus merula*	Common blackbird	256
2	*Columba palumbus*	Common woodpigeon	169
	Aves unknown	Bird unknown	58
3	*Phasianus colchicus*	Common pheasant	46
4	*Anas platyrhynchos*	Mallard	28
5	*Coloeus monedula*	Western jackdaw	28
6	*Gallinula chloropus*	Common moorhen	24
7	*Passer domesticus*	House sparrow	24
8	*Erithacus rubecula*	European robin	23
9	*Streptopelia decaocto*	Eurasian collared dove	22
10	*Parus major*	Great tit	20
Mammals	**Scientific name**	**Common name**	**# ind.**
1	*Erinaceus europaeus*	Hedgehog	182
2	*Rattus norvegicus*	Brown rat	144
3	*Oryctolagus cuniculus*	European rabbit	71
4	*Lepus europaeus*	European hare	52
5	*Sciurus vulgaris*	Red squirrel	29
	Mammalia unknown	Mammal unknown	22
6	*Apodemus sylvaticus*	Wood mouse	14
6	*Martes foina*	Beech marten	14
	Muridae unknown	Mouse/rat unknown	12
	Soricidae unknown	Shrew unknown	12
8	*Talpa europaea*	European mole	11
	Rattus unknown	Rat unknown	10
	Rodentia unknown	Rodent unknown	10
	Microtidae unknown	Vole unknown	8
9	*Vulpes vulpes*	Red fox	6
10	*Crocidura russula*	Greater white-toothed shrew	5

Presence only data

A total of 20,638 bird victims and 39,849 mammal victims were registered in waarnemingen.be from 2010–2020. Consequently, 94% of all roadkill records from 2010–2020 are presence only data. We show the top 20 in Table 7.

Table 7. Top 20 of most registered bird and mammal roadkill victims which are collected as presence only records. Observations not identified to species level are shown but not ranked.

Birds	Scientific name	Common name	# ind.
1	*Turdus merula*	Common blackbird	3,686
2	*Columba palumbus*	Common woodpigeon	3,624
3	*Anas platyrhynchos*	Mallard	1,411
4	*Phasianus colchicus*	Common pheasant	1,294
5	*Tyto alba*	Western barn owl	926
6	*Strix aluco*	Tawny owl	817
	Aves unknown	Bird unknown	766
7	*Gallinula chloropus*	Common moorhen	761
8	*Buteo buteo*	Common buzzard	728
9	*Pica pica*	Eurasian magpie	504
10	*Passer domesticus*	House sparrow	404
11	*Coloeus monedula*	Western jackdaw	402
12	*Athene noctua*	Little owl	333
13	*Corvus corone*	Carrion crow	267
14	*Streptopelia decaocto*	Eurasian collared dove	248
15	*Asio otus*	Long-eared owl	234
16	*Erithacus rubecula*	European robin	213
17	*Garrulus glandarius*	Eurasian jay	212
18	*Falco tinnunculus*	Common kestrel	194
19	*Larus argentatus*	European herring gull	193
20	*Turdus philomelos*	Song thrush	175
Mammals	**Scientific name**	**Common name**	**# ind.**
1	*Erinaceus europaeus*	Hedgehog	12,147
2	*Vulpes vulpes*	Red fox	5,353
3	*Sciurus vulgaris*	Red squirrel	3,779
4	*Martes foina*	Beech marten	3,619
5	*Mustela putorius*	Western polecat	2,591
6	*Oryctolagus cuniculus*	European rabbit	2,569
7	*Lepus europaeus*	European hare	2,148
8	*Rattus norvegicus*	Brown rat	2,108
9	*Capreolus capreolus*	Roe deer	855
	Mammalia unknown	Mammal unknown	488
10	*Talpa europaea*	European mole	317
	Mustelidae unknown	Marten unknown	287
11	*Meles meles*	Eurasian badger	283
12	*Mustela nivalis*	Least weasel	232
13	*Mustela erminea*	Stoat	186
	Martes foina/martes	Beech/Pine marten	171
14	*Sus scrofa*	Wild boar	137
	Rattus unkown	Rat unknown	74
15	*Castor fiber*	Eurasian beaver	67
16	*Martes martes*	Pine marten	65
17	*Apodemus sylvaticus*	Wood mouse	63
18	*Crocidura russula*	Greater white-toothed shrew	59
19	*Pipistrellus pipistrellus*	Common pipistrelle	46
20	*Mus musculus*	House mouse	40

Mammal case study

We compare the number of non-roadkill mammal observations (one observation can contain multiple individuals) with the number of mammal roadkill observations (transect and present only data combined) annually from 2010–2020 in Flanders, Belgium (Table 8).

Over the years, there is a significant increase in non-roadkill mammal observations (slope = 9106, t = 4.49, p-value = 0.00150**) but no significant increase in roadkill registrations (slope = 118, t = 1.88, p-value = 0.09). There is also no significant correlation between non-roadkill and roadkill mammal observations (slope = 0.008, t = 1.379, p-value = 0.201).

Table 9 shows the 17 mammal species with more than 50 roadkill individuals, the outcomes from the linear regression between year (2010–2020) and the percentual abundance per year.

Table 8. Mammalian roadkill and non-roadkill observations per year and the percentage of roadkill compared to all mammal observations from 2010-2020 in Flanders. Obs.= observations.

Year	Mammal roadkill obs.	Non-roadkill mammal obs.	Mammal roadkill as % of total mammal obs.
2010	3,338	20,201	14.2%
2011	2,740	21,100	11.5%
2012	2,884	30,009	8.8%
2013	2,639	27,211	8.8%
2014	4,836	46,033	9.5%
2015	4,212	35,815	10.5%
2016	4,408	51,417	7.9%
2017	3,866	108,415	3.4%
2018	4,040	123,193	3.2%
2019	4,312	73,858	5.5%
2020	3,580	88,850	3.9%

Table 9. Outcome of the linear regression for the 17 most registered mammal species in Flanders from 2010-2020. Significant codes in the p-value column: <0.1 . >0.05, <0.05 * > 0.01, <0.01 ** > 0.001, <0.001 *** For common names, see Table 7.

Rank	Species	N	slope	Std. error	t-value	p-value
1	*Erinaceus europaeus*	12,262	-0.051	0.325	-0.158	0.878
2	*Vulpes vulpes*	5,193	-0.467	0.230	-2.029	0.073 .
3	*Sciurus vulgaris*	3,769	0.047	0.131	0.358	0.728
4	*Martes foina*	3,566	0.425	0.121	3.526	0.006 **
5	*Oryctolagus cuniculus*	2,578	-0.339	0.170	-1.994	0.077 .
6	*Mustela putorius*	2,514	-0.450	0.129	-3.500	0.007 **
7	*Rattus norvegicus*	2,268	0.141	0.159	0.884	0.400
8	*Lepus europaeus*	2,252	0.269	0.089	3.013	0.015 *
9	*Capreolus capreolus*	798	0.147	0.046	3.165	0.012 *
10	*Talpa europaea*	328	0.023	0.024	0.961	0.362
11	*Meles meles*	275	0.119	0.035	3.431	0.007 **
12	*Mustela nivalis*	226	-0.004	0.012	-0.342	0.740
13	*Mustela erminea*	185	-0.004	0.013	-0.306	0.767
14	*Sus scrofa*	103	0.057	0.009	6.007	0.0002 ***
15	*Apodemus sylvaticus*	74	0.020	0.004	5.389	0.0004 ***
16	*Castor fiber*	60	0.041	0.010	3.797	0.004 **
17	*Martes martes*	57	0.028	0.014	1.995	0.077 .

Graphs showing percentual abundance per year per species are shown in Appendix A. *Mustela putorius* is the only species with a significant decreasing relative trend from 2010–2020. There are seven species with an increasing relative trend, ordered here from steepest to gentlest slope: *Martes foina*, *Lepus europeaus*, *Capreolus capreolus*, *Meles meles*, *Sus scrofa*, *Castor fiber* and *Apodemus sylvaticus*. Graphs showing seasonal patterns in relative density per species for each year (2010–2020) are added to Appendix B. Seasonal patterns in roadkill recordings differ clearly from species to species with most species showing a bi- or unimodal pattern. When comparing the pattern from a single species over multiple years, the consistency within the patterns is (very) good. Also the species with fewer observations show mostly a clear seasonal pattern.

Discussion

The detected and registered roadkill observations are only the tip of the iceberg. Even a structured daily roadkill census underestimates the death rate (of smaller victims) with a factor 12–16 (Slater 2002). Apart from the effect that roadkill has on wildlife (populations) there is also an economic cost. There are no numbers available for Flanders, or the whole of Europe, but wildlife-vehicle collisions in Spain cost 105 million € yearly (Sáenz-de-Santa-María and Tellería 2015) while the animal-vehicle accidents with ungulates in Sweden resulted in a cost of 275 million € in 2015 (Gren and Jägerbrand 2019).

For Flanders, *Capreolus capreolus*, *Sus scrofa*, *Canis lupus* and *Castor fiber* are among the heaviest wild mammals, but injury or even death of drivers or passengers can also occur when crashing into, or trying to avoid, smaller animals (Langbein 2007). A better understanding of roadkill is therefore in the best interest of wildlife and humans.

The amount of roadkill records increased heavily since the launch of https://waarnemingen.be in 2008 and together, over 4,300 citizen scientists collected almost 90,000 roadkill records. Similar to crowd science user contribution patterns, a small number of users contributed most of the recordings and the Gini coefficient of 0.87 is very similar to the average crowd science Gini coefficient of 0.85 Sauermann and Franzoni (2015) calculated for 7 crowd science projects. The registration of roadkill seems to be an integrated part of the nature observation and registration, for most volunteers, since 85% of users did also register non-roadkill observations. The use of a multi-purpose biodiversity platform has a positive effect on the retention time, which is over 6 years for roadkill recorders in waarnemingen.be. This long volunteer retention time indicates that allowing the registration of all species groups, roadkill or not, using the tools the users are already familiar with, is a successful alternative, and possibly even preferable to a single purpose data platform focussing on roadkill alone.

Some scientists may be sceptical about the data quality of records collected by citizen scientists, although they have the potential to produce data with an accuracy at least equal to professionals (Kosmala et al. 2016). We report a species identification accuracy of roadkill recordings with photographs of 98% (n = 7,687) which is nearly identical to the 97% presented by Waetjen and Shilling (2017). This high proportion of correct species identification is an indication of the quality of the database. However, we suspect species identification accuracy to be lower for records without photographs since many of these identifications are from driving vehicles. Although more than 60% of observations are unverified, the majority of these observations are 'common' species, which are mainly registered by a limited group of experienced nature observers, and there is no reason to assume 'a priori' that these records contain more errors. Depending on the purpose of the analysis, different data selections can be made but the increase in data quality by eliminating all possible errors does not always compensate for the loss in data quantity (Van Eupen et al. 2021). Continuous communication on the importance of photographs when registering roadkill aims to increase the amount of verifiable records in the future.

Differences in the most registered species depending on data collection method

In order to determine which species is killed the most in traffic, standardised monitoring is necessary. Our results indicate that for birds and mammal species, searching at an intermediate speed from 7 to 25 km/h results in the highest number of carcasses found. This is somewhat unexpected given that a slower speed should increase detection rates (Slater 2002). We suggest that the searching for roadkill carcasses was fitted into the routine of a number of people in the past years and that biking happens more frequently next to busy roads, where more carcasses are present compared to walking, which is more likely along calmer roads. Driving by car resulted in roughly the same encounter rates of birds and mammals carcasses compared to walking, however due to the higher speed, corpses not identified to species level are more numerous. Stopping safely to identify the species is often not possible in Belgium and stopping on motorways is forbidden (and dangerous) (minimum speed 70 km/h, maximum speed 120 km/h). At this speed, identification at species level is frequently impossible.

The quality of transect data (with a standard protocol) is higher but it is more difficult to find volunteers to collect them (Bonney et al. 2009; Vercayie and Herremans 2015). As a consequence, they only represent 6% of all available roadkill data from Flanders. Although informative for local situations, currently, this is too sparse for region-wide analysis. The variable transects are promising in this respect because they can be monitored anywhere and anytime, but they are currently not yet widely enough adopted by the user community. It is also too early for a detailed analysis since they were only launched in 2018. Additional promotion and awareness in the user community of the applicability could boost the popularity of these variable transects.

There is a clear difference between the rank list of most observed species during transects and the rank list of most observed species in the opportunistic data. When comparing data collected by car and bike, it is clear that only larger species are registered from cars and a higher proportion was not identified on species level. For the mammal data, all rank lists of most observed species are led by Hedgehogs (with the exception of unidentified mammals which outrank them in species lists collected from cars). Hedgehogs are frequently reported as traffic victims in Western Europe (Huijser and Bergers 2000; Pettett et al. 2018) and road mortality of Hedgehogs is expected to be an important factor in their decline (Wright et al. 2020). Common blackbirds are ranked third by monitoring from the car, but first in the other lists. This is not unexpected since they had the highest predicted roadkill rate, 12 individuals/km/year, in the model of Grilo et al. (2020) and are among the most frequently killed bird species in Western Europe (Erritzoe et al. 2003). Even transect data must be interpreted with care. Carcass persistence times and detection depend on size, with smaller animals being removed faster by scavengers (Santos et al. 2011; Teixeira et al. 2013; Ratton et al. 2014). Detection probability of larger mammals can also be influenced since they are more likely to be removed by maintenance workers or during police intervention at the site of an accident. Data collected by these services can be an important addition to the data collected by citizen scientists. Although proven to be a valuable data source (Grilo et al. 2009) additional steps need to be taken in Flanders to collect and centralise this data.

As expected, the ranking of victims collected as presence only data differs from the rankings in the transect data: presence only data show a clear bias to larger species, but possibly also species which are perceived as more interesting. Number two in the presence only data ranking is Red fox, which ranks only 6th in transects by car, and 9th in transects by bike. Foxes are infrequently seen alive, so, an encounter with a dead fox is for many people special enough to report. The number three, Red squirrel ranked 6th in transects by car and 5th in transects by bike. The Brown rat, the species encountered most frequently as roadkill (with exception from the Hedgehog) in transects by bike was only ranked 8th in the presence only data list. This indicates that due to reporting bias the presence only data should not be used to determine which species are killed the most in traffic.

Mammal case study

From 2010–2020 there is a strong increase in the number of non-roadkill mammal observations registered on waarnemingen.be but no significant increase in registered roadkill mammal observations. It is known that retention of volunteers can be challenging (Pocock et al. 2014; Shilling et al. 2015, 2020) but the number of observers registering roadkill has never been higher than the past 3 years (see Fig. 2) and their retention time on the waarnemingen.be platform exceeds 6 year. Volunteer participation depends also on repeated communication about the project. Over the last 3 years, our own communication channels mentioned the project 'animals under wheels' in 23 newsletters, we provided 15 contributions to written magazines, made 2 promotion videos and contributed to 10 national symposiums. Mainstream media wrote 47 articles about the project, and we gave 20 radio and 3 TV interviews (overview in Jacobs et al. (2021)) on the subject. This indicates that the absence in increase in registered roadkill mammals is not due to a reduction in observers/search effort but we believe that this is a strong indication that the number of roadkill is diminishing. Additional standardised collected data could confirm/refute this hypothesis. If this reduction is caused by effective road mitigation such as fencing, when possibly combined with crossing structures or animal detection systems (Rytwinski et al. 2016) this reduction does not reflect a decrease in population but a decrease in wildlife victims due to the mitigation measures. However, it might also reflect a reduction in abundance of (a number of) mammal species in Flanders that are most prone to being killed by vehicles.

Our species specific linear regression models indicate that 8 out of 17 mammal species have a significant change in proportion of roadkill victims through time. The number of reported roadkill victims of *Mustela putorius*, the Western polecat, declines, with the steepest significant slope of all species (slope = -0.450). The polecat is suspected to be in decline in Belgium, and also in most neighbouring countries (Croose et al. 2018) and there are indications this decline was already present from 1998–2010 (Van Den Berge and Gouwy 2012).

The proportion of victims of the seven other species are increasing over the years. Two species are (recently) recolonising (parts of) Flanders after a period of absence: Eurasian beaver (Swinnen et al. 2017) and Wild boar (Rutten et al. 2019). Roe deer has increased in range and numbers significantly since the 70's (Casaer and Huysentruyt 2016), Beech marten, is doing the same the last decades (Van Den Berge 2016) and more recently, Badgers are also expanding from their last stronghold (Van Den Berge et al. 2017). Although the increase in population density is not quantified, we assume that this translates in higher relative roadkill numbers. The increase of the Eurasian hare was unexpected since the species was recently added as vulnerable to the red list of the Netherlands (bordering Flanders) (van Norren et al. 2020). However, for Flanders no monitoring scheme is in place. For Wood mouse we have no knowledge of population monitoring. This is a small-bodied species resulting in low carcass retention times (Santos et al. 2011; Ratton et al. 2014) and they were recorded relatively infrequently indicating that these results have to be interpreted cautiously. Remarkable is that the number of reported European hedgehog roadkill remains stable from 2010–2020. Until 2018, a strong decrease was occurring, but in 2019 and 2020 the proportion abruptly increased and was again at the 2010 level. This increase is currently unexplained but a fast recovery of the populations seems unlikely. There are reports of an unknown disease the last few years in Hedgehogs, possibly this also influences behaviour and making Hedgehogs more sensitive to being killed by cars.

Species distribution maps can be consulted at www.waarnemingen.be and additional info in Verkem et al. (2003). Linear regression models were also performed for the period of 2010–2019 since the global pandemic of the coronavirus disease (COVID-19) in 2020 resulted also in Flanders in confinement measures which are expected to have affected the search effort and the number of animals killed (Bíl et al. 2021; Driessen 2021). All trends remained similar, with the exception of the European hare, where the increase became non-significant.

Although the seasonal patterns are based on the rough data, without any correction for search effort within or between years, patterns of the same species are (highly) consistent. We expect that the large amount of data smoothens smaller inter- and within-year variation in search effort of individual observers. However, major events are detectable. In Flanders, there was a strict ban on non-necessary (car)travel from the 18th of March 2020 to the 8th of June 2020 due to the COVID-19 pandemic. Apart from the lives of wildlife this would have saved (Bíl et al. 2021; Driessen 2021), also very few observers were on the road to quantify this effect. Determining which of both factors was the most important is not possible using presence only data. For species in which the peak period of kills overlaps with the confinement measures, such as Western polecat, the seasonal pattern of 2020 is clearly affected. Knowing the roadkill patterns can help to protect specific species of interest by using specific warning signs, and (temporal) road closure can even increase habitat quality (Whittington et al. 2019). Although no age or sex of the individuals was recorded in most cases, most peaks in roadkill density are presumed to be linked to increased movement because of mating or juvenile movements and dispersal (Carvalho et al. 2018; Raymond et al. 2021).

We show that roadkill monitoring using citizen scientists can generate informative results. However, this is not the endpoint. Data collected during the 'animals under wheels' project also contributed to the mitigation of local mortality hotspots. Furthermore, the data can be consulted by policy makers and a number of questions were asked in the Flemish Parliament concerning wildlife roadkill, indicating that the problem is acknowledged at the political level.

Conclusion

Large quantities of roadkill records are collected by citizen scientists in Flanders, Belgium. Volunteers remain engaged for a long period of time, probably due to the use of a multi-purpose platform which also allows the registration of living organisms. Species identification accuracy is high. Data collected using a standardised protocol is present, however, data quantities are currently too low for nation-wide analysis. Currently, 94% of all roadkill data are presence only records. Our results indicate that the amount of mammal roadkill is diminishing in Flanders, possibly due to mitigation measures or due to reduced population densities. We show that the citizen science data can be used to detect trends in percentual abundance of roadkill per species per year and to show seasonal patterns in relative roadkill density. Additional research to identify and consequently mitigate roadkill hotspots, minimise and correct for biases and the comparison between roadkill and population trends remains to be done. An increased effort to convince observers to collect standardised transect data and photographs of roadkill will increase the value of the dataset even further. We conclude that citizen scientists are playing an important role in roadkill research and will continue to do so in the future.

Acknowledgements

The authors like to thank all citizen scientists for their records and the species experts for the validation. Without your contributions, roadkill in Flanders would be a black box. We thank Dominique Verbelen for his work on the bird species names. We thank the IENE 2020 conference organising committee for the possibility to publish in the Special issue: Linear Infrastructure Networks with Ecological Solutions. We thank the editor and the anonymous referee for their contribution in significantly improving the manuscript.

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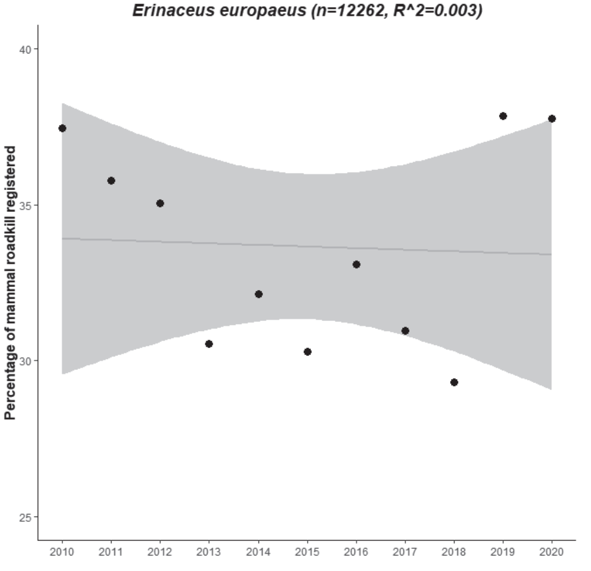
Appendix A

For the 17 mammal species with more than 50 roadkill individuals, we show the linear regression figures between year (2010–2020) and the percentual abundance per year. Significant regressions are shown with a black line, non-significant with a grey line.



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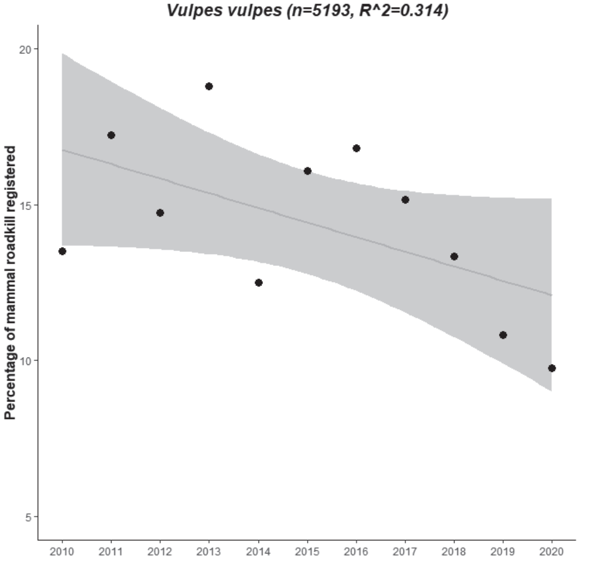

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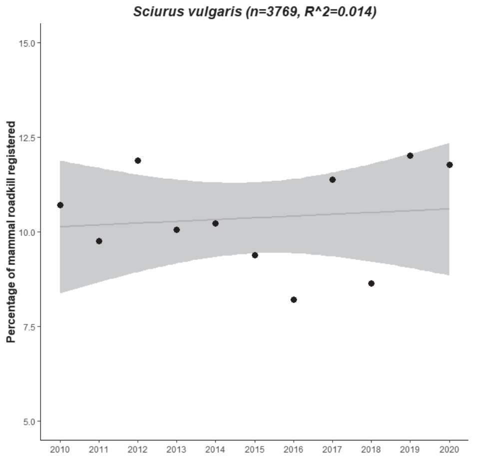

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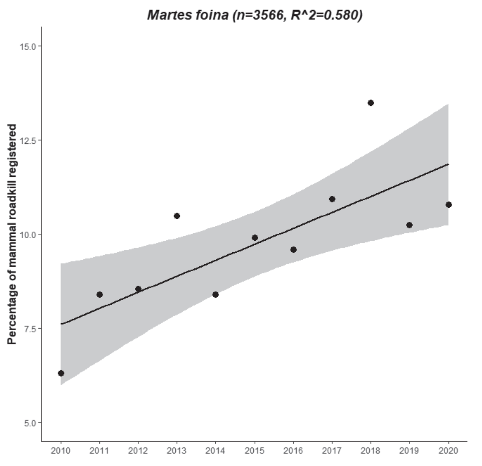

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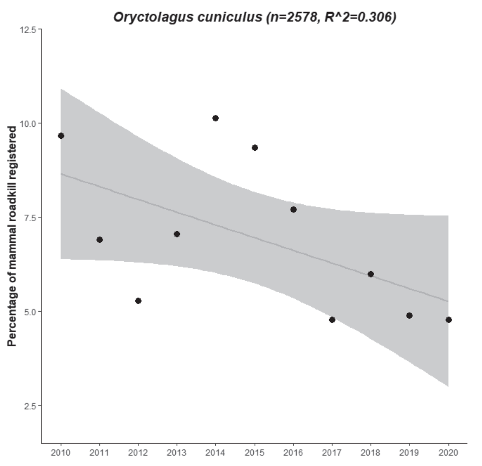

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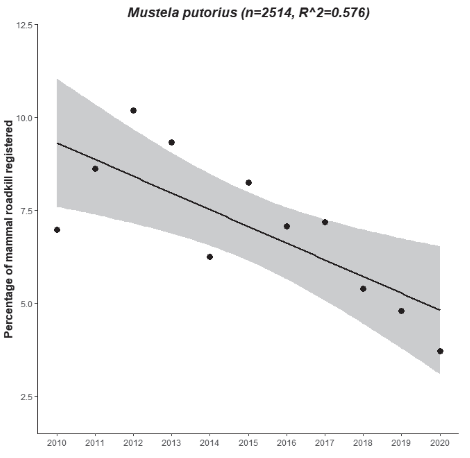

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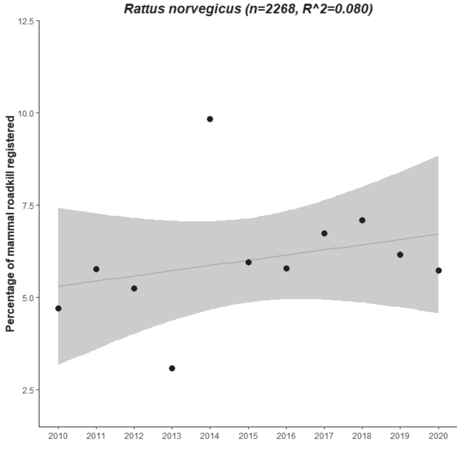

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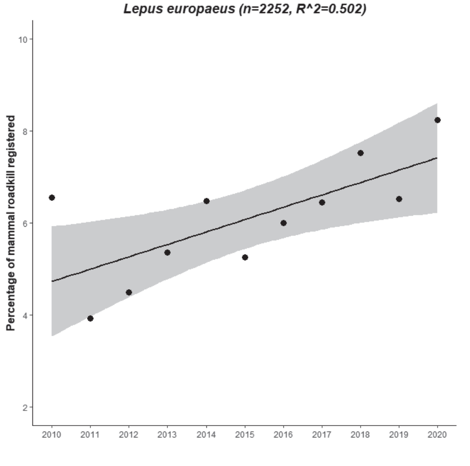

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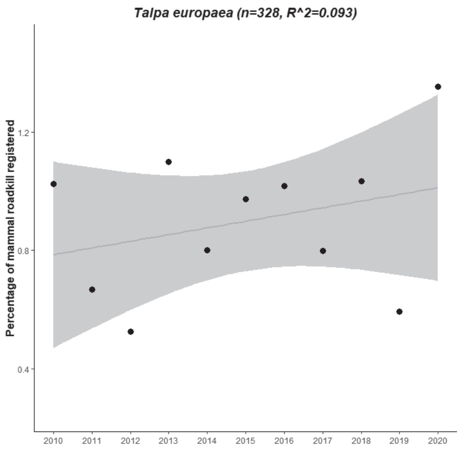

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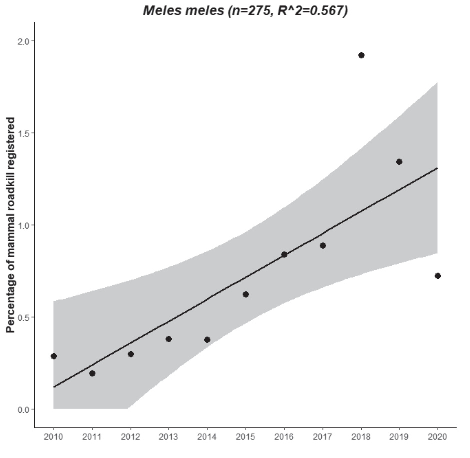

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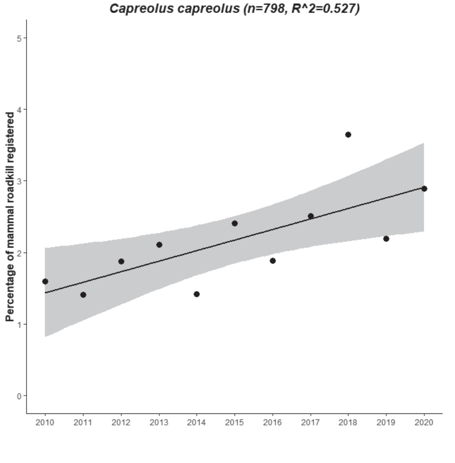

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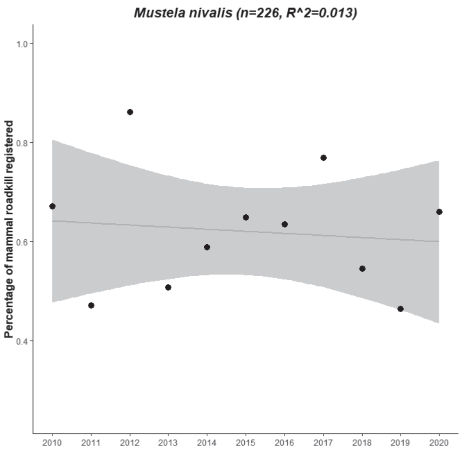

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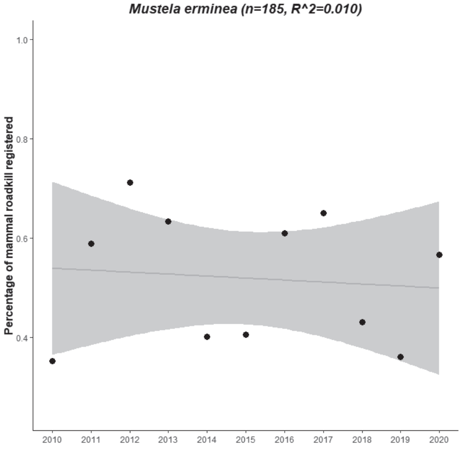

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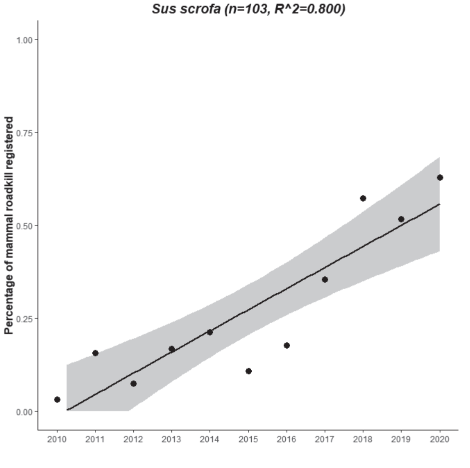

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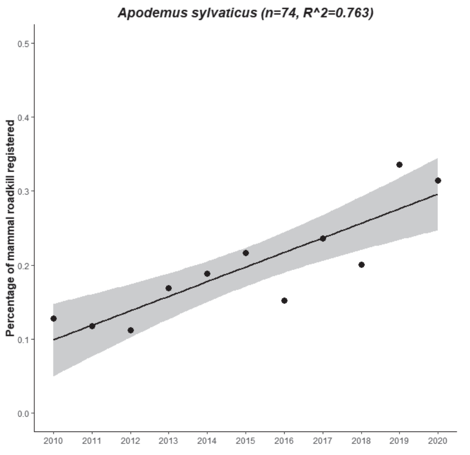

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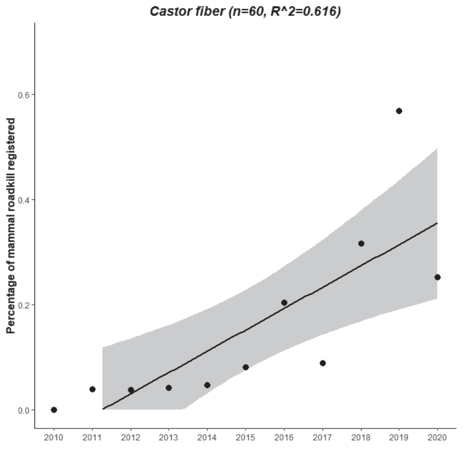

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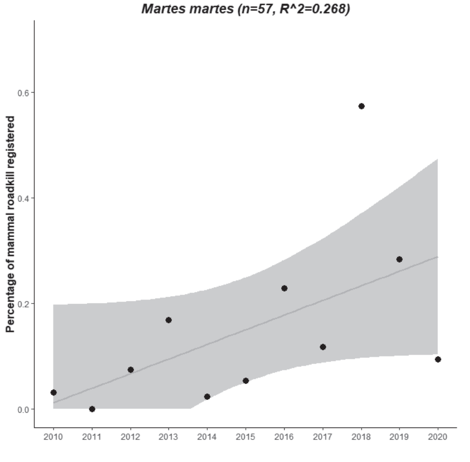
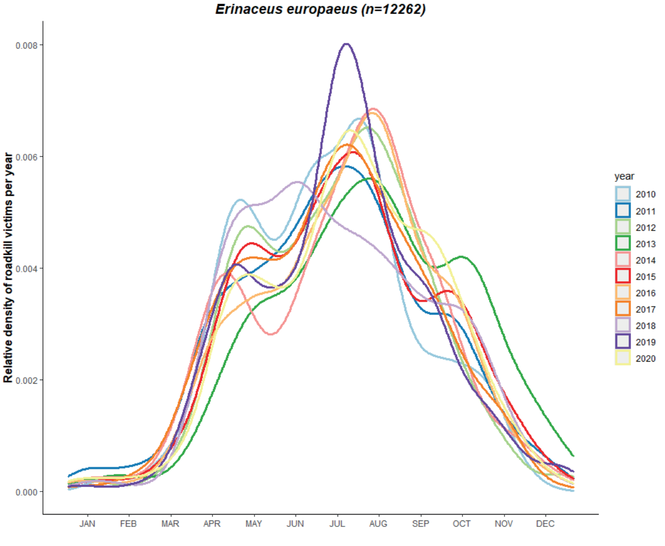


Figure A17.

Appendix B

For the 17 most recorded mammal species we show the variation in the roadkill pattern within Flanders. For species with more than 1000 recordings, we show the pattern of each individual year (2010-2020). For species with fewer than 1000 recordings all data are combined to generate a general pattern.



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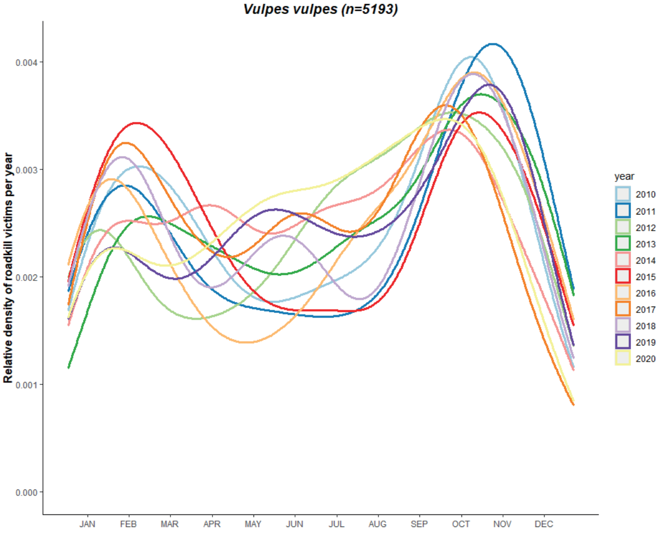

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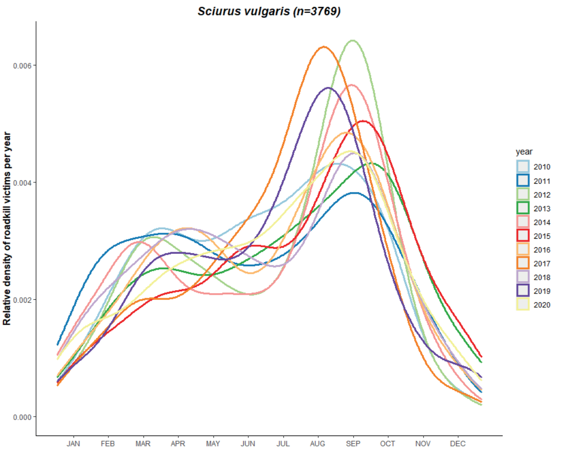

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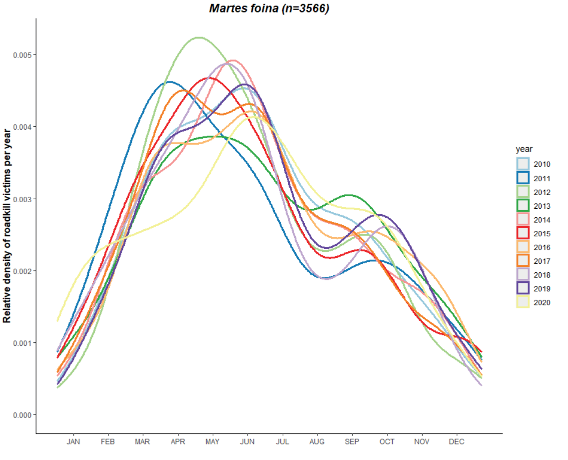

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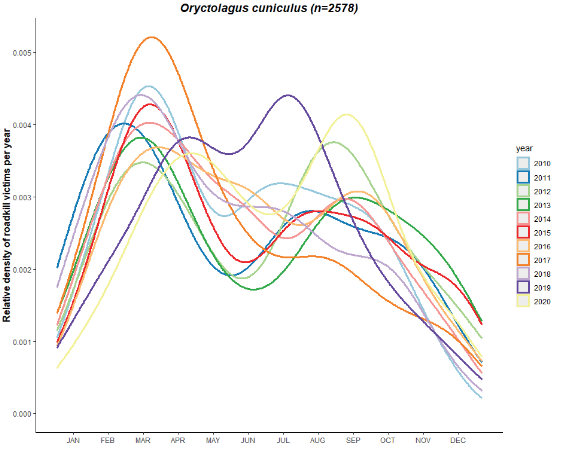

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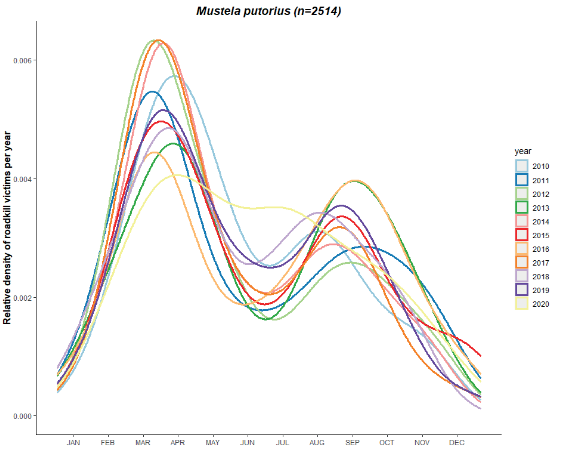

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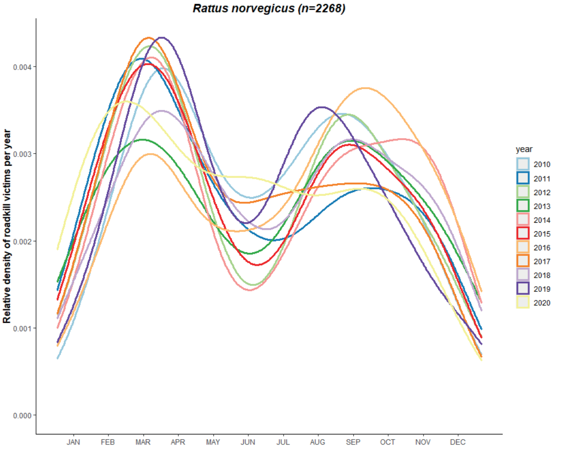

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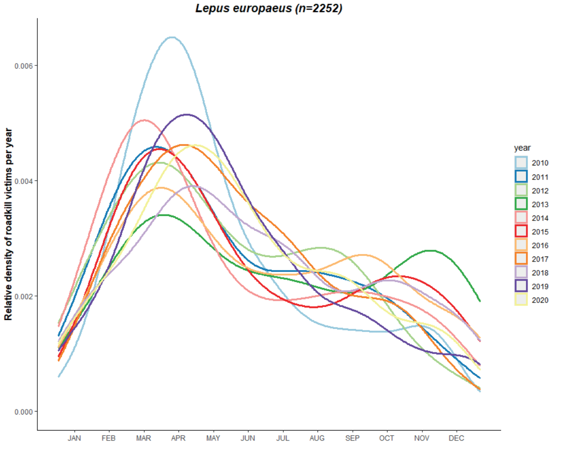

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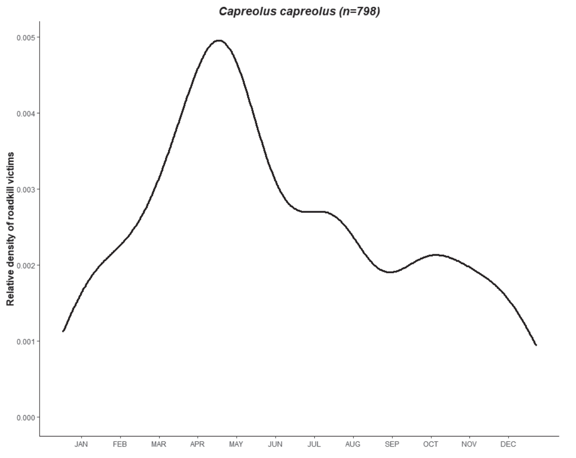

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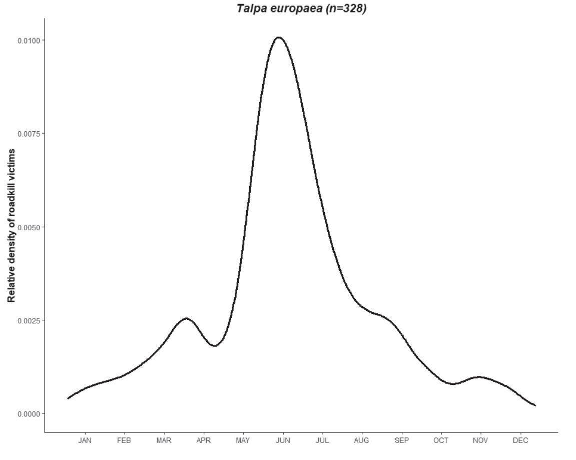

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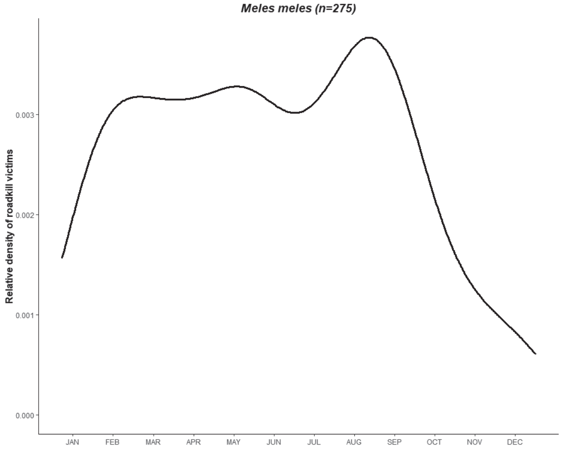

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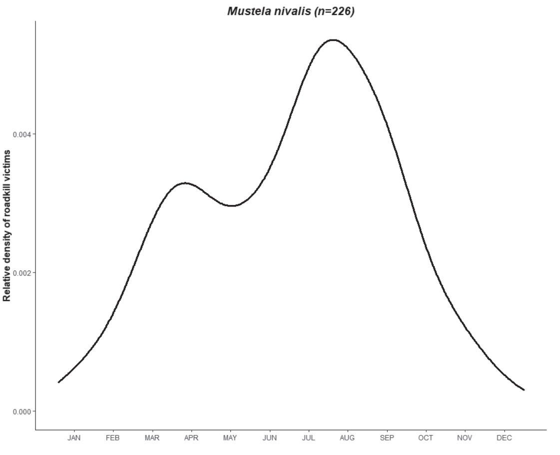

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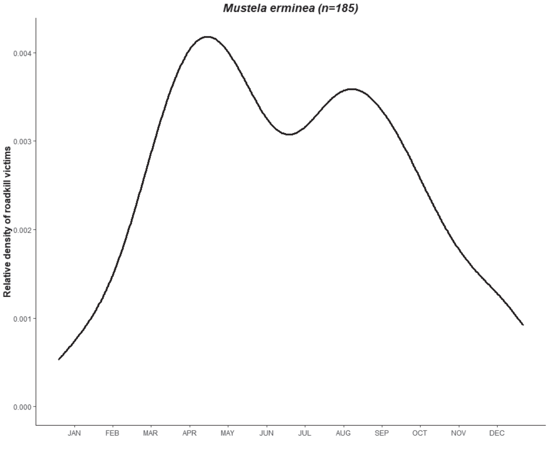

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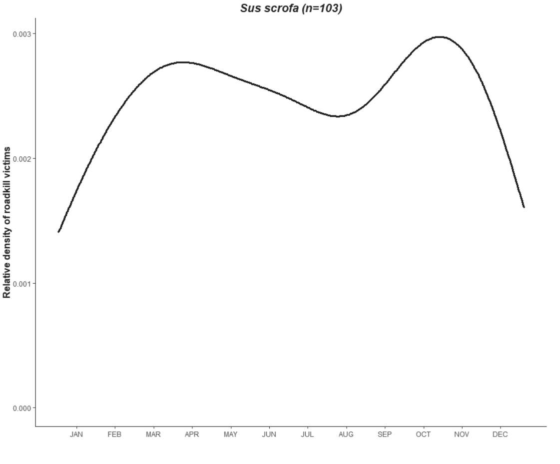

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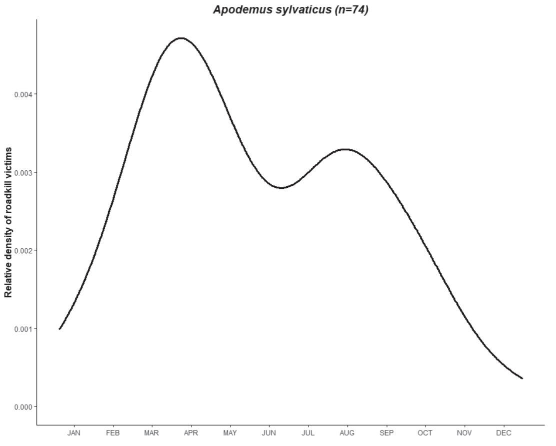

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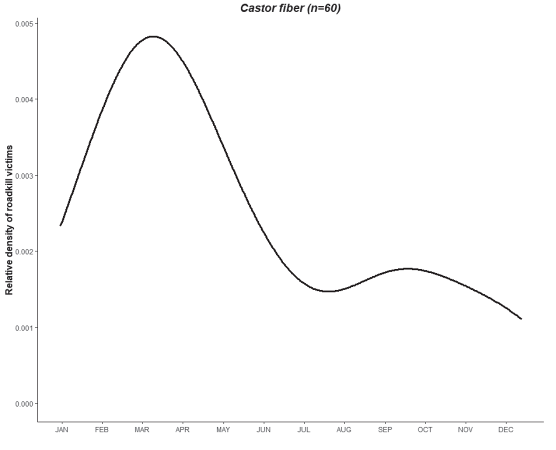

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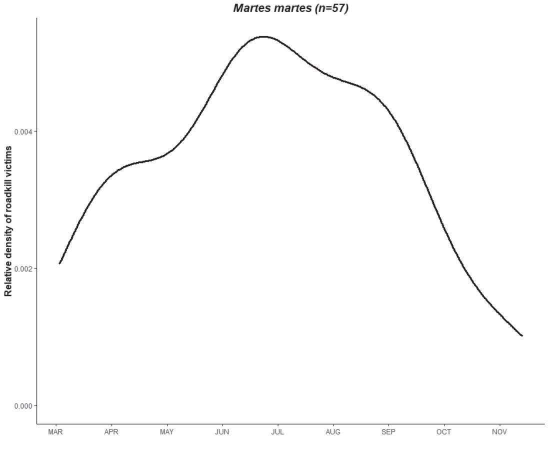

Figure B17.

Nature Conservation 47: 155–175 (2022)
doi: 10.3897/natureconservation.47.72781
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Assessing behaviour states of a forest carnivore in a road-dominated landscape using Hidden Markov Models

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Academic editor: Manisha Bhardwaj | Received 9 August 2021 | Accepted 31 January 2022 | Published 25 March 2022

http://zoobank.org/75B2DD98-8088-4F9C-931A-F37139891403

Citation: Ferreira EM, Valerio F, Medinas D, Fernandes N, Craveiro J, Costa P, Silva JP, Carrapato C, Mira A, Santos SM (2022) Assessing behaviour states of a forest carnivore in a road-dominated landscape using Hidden Markov Models. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 155–175. https://doi.org/10.3897/natureconservation.47.72781

Abstract

Anthropogenic infrastructures and land-use changes are major threats to animal movements across heterogeneous landscapes. Yet, the behavioural consequences of such constraints remain poorly understood. We investigated the relationship between the behaviour of the Common genet (*Genetta genetta*) and road proximity, within a dominant mixed forest-agricultural landscape in southern Portugal, fragmented by roads. Specifically, we aimed to: (i) identify and characterise the behavioural states displayed by genets and related movement patterns; and (ii) understand how behavioural states are influenced by proximity to main paved roads and landscape features. We used a multivariate Hidden Markov Model (HMM) to characterise the fine-scale movements (10-min fixes GPS) of seven genets tracked during 187 nights (mean 27 days per individual) during the period 2016–2019, using distance to major paved roads and landscape features as predictors. Our findings indicated that genet's movement patterns were composed

* These authors contributed equally to this work.

of three basic behavioural states, classified as "*resting*" (short step-lengths [mean = 10.6 m] and highly tortuous), "*foraging*" (intermediate step-lengths [mean = 46.1 m] and with a wide range in turning angle) and "*travelling*" (longer step-lengths [mean = 113.7 m] and mainly linear movements). Within the genet's main activity-period (17.00 h-08.00 h), the movement model predicts that genets spend 36.7% of their time travelling, 35.4% foraging and 28.0% resting. The probability of genets displaying the travelling state was highest in areas far away from roads (> 500 m), whereas foraging and resting states were more likely in areas relatively close to roads (up to 500 m). Landscape features also had a pronounced effect on behaviour state occurrence. More specifically, travelling was most likely to occur in areas with lower forest edge density and close to riparian habitats, while foraging was more likely to occur in areas with higher forest edge density and far away from riparian habitats. The results suggest that, although roads represent a behavioural barrier to the movement of genets, they also take advantage of road proximity as foraging areas. Our study demonstrates that the HMM approach is useful for disentangling movement behaviour and understanding how animals respond to roadsides and fragmented habitats. We emphasise that road-engaged stakeholders need to consider movement behaviour of genets when targeting management practices to maximise road permeability for wildlife.

Keywords
Behavioural barrier, foraging, Genetta genetta, habitat fragmentation, movement behaviour, movement ecology, road proximity

Introduction

Movement behaviour is a key characteristic of animal species, dictating how, when and why individuals move through landscape in order to access resources, mates and seek safety from predators and disturbance, along with other activities (e.g. migration) at various spatio-temporal scales (Nathan et al. 2008; Wittemyer et al. 2019). Movement underpins variation in individual fitness, affecting populations' dynamics (e.g. species interactions and distribution) and is essential for long-term population persistence (e.g. gene flow; Morales et al. 2010). As such, the survival and persistence of animal species depend on the success of their movements across landscapes, especially anthropogenic landscapes (Tucker et al. 2018). Human activities (e.g. agriculture and urbanisation) are the main drivers of landscape fragmentation and habitat loss worldwide (Venter et al. 2016), thus impacting animal movement. High quality habitats are frequently dissected into small patches, surrounded by unsuitable habitat and anthropogenic features, such as roads (e.g. van der Ree et al. 2015). As a result, species are forced to move between isolated patches of suitable habitat within an often inhospitable matrix, posing constraints on their movement decisions and, ultimately, on their survival chances (e.g. roadkill; McCall et al. 2010; Basille et al. 2013).

Roads are one of the most important causes of habitat fragmentation worldwide. Roads have multiple negative impacts on terrestrial wildlife populations (Barrientos et al. 2021), namely through increased wildlife mortality (Ascensão et al. 2014; Grilo et al. 2018), hampering ecological connectivity (Carvalho et al. 2016; Chen and Koprowski 2016; Ascensão et al. 2017) or affecting species activity and individual behaviour (e.g. Kociolek et al. 2011; Medinas et al. 2019). Some traits make certain species more vulnerable to road impacts than others (Rytwinski and Fahrig 2012). Given their wide-reaching home ranges and dispersal needs, medium and large-sized carnivores are more likely to encounter a road on their daily movements and, consequently, have higher probability of being road-killed (Rytwinski and Fahrig 2012; Tucker et al. 2018). On the other hand, if they avoid the road, gene flow between populations on both sides of the road may be reduced in the long term, leading to an increased extinction risk (e.g. Holderegger and Di Giulio 2010). Whereas the impacts on mortality and connectivity have been examined in literature (Rytwinski and Fahrig 2013; Teixeira et al. 2020), the consequences on wildlife behaviour from the presence/proximity of roads are scarcely addressed. Road-dominated environments can prompt different behavioural responses, wherein species may exhibit different movement patterns, depending on their sex, age, life-history and landscape context (e.g. Ascensão et al. 2016; Carvalho et al. 2018). Certain species, for example, tend to avoid or move faster in poor habitat quality areas and in proximity of roads (Carvalho et al. 2016; Gaston et al. 2016). On the other hand, roads can promote foraging areas that are highly attractive to a variety of predator species (Barrientos and Bolonio 2008; Silva et al. 2019). Thus, it is critical for road mitigation planning to understand how road proximity and landscape conditions affect behaviour patterns of mammal carnivores, as these can influence the effectiveness of mitigation outcomes (e.g. Scrafford et al. 2018; Zeller et al. 2019).

Despite the evident role of behaviour on animal movement (Nathan et al. 2008), movement analyses that consider the effects of behaviour are still uncommon and remain a key challenge in ecology (Zeller et al. 2012; McClintock et al. 2020). Traditionally, animal movement responses to roads and landscape context have been quantified by analysing telemetry-based data as a function of extrinsic factors (e.g. habitat composition, daily period), while disregarding behaviour effects. Nevertheless, animal movement paths are composed of a mixture of underlying behavioural states, characterised by specific and unique signatures (Nathan et al. 2008; Wittemyer et al. 2019). These behavioural states are adopted by animals in response to environmental gradients and biological needs, dictating observed movement patterns (van Beest et al. 2019; Farhadinia et al. 2020). Due to recent advances in analyses, it is now possible to describe the mechanisms underlying animal movement, allowing for a more explicit assessment of the influence of animal behaviour on movement patterns (e.g. Gardiner et al. 2019). One flexible tool is the Hidden Markov Model (**HMM**), which allows the interpretation and classification of behavioural states from movement data, depending on the specific characteristics of individual movement paths (Patterson et al. 2017; McClintock et al. 2020).

Here, we studied the relationship between the movement behaviour of a Mediterranean forest carnivore, the common genet (*Genetta genetta*) and road proximity within an open dominant forest landscape in southern Portugal, included in an area fragmented by roads. We used a multivariate Hidden Markov Model (HMM) applied on fine-scale GPS data. Specifically, we aimed to: (i) identify and characterise the behavioural states displayed by genets; and (ii) understand how behavioural states are affected by proximity to roads and landscape predictors. The genet was selected as a model species because, as a carnivore, its low population density and large home range make it vulnerable to the effects of road and habitat fragmentation (Rytwinski and

Fahrig 2012; Ceia-Hasse et al. 2017). Genets are widespread through Mediterranean areas, are semi-arboreal and move preferentially within forest patches with dense shrub vegetation cover and close to riparian habitats (Camps and Alldredge 2013; Carvalho et al. 2016; Grilo et al. 2016). In addition, previous studies have shown that this carnivore is often road-killed (Grilo et al. 2009; Carvalho et al. 2018) and that movements and space use are constrained by roads (Galantinho and Mira 2009; Carvalho et al. 2016; Carvalho et al. 2018). However, information is scarce on their behavioural patterns at fine scale when close to roads, this information being fundamental when planning road mitigation measures.

Methods

Study area

Our study was carried out in the Alentejo Region, southern Portugal (38°37'24.33"N, 8°06'26.44"W; Fig. 1). We focused on the linear infrastructure corridor linking Montemor-o-Novo to Évora, which is comprised of a medium-high traffic national road (EN114; nocturnal traffic varies from 882 to 1683 vehicles/night; EP 2005), with high mortality values of genets (mean mortality rate of 12.8 individuals/100 km/year; Carvalho et al. 2018). It also includes a section of the A6 motorway running parallel to the EN114, along with other low-traffic regional roads scattered throughout the area. The landscape is dominated by cork (*Quercus suber*) and holm oak (*Quercus rotundifolia*) stands, an agroforestry system with varying tree density, while also comprising pastures and crops. Other less representative land-cover types include olive groves, some plantations of *Pinus* spp. and *Eucalyptus* spp. and urban areas, which are scarce. The result is a fragmented landscape bisected by roads, with forest patches of varying size that are interspersed with agricultural fields and linear natural elements, such as riparian habitats. The topography is generally flat or undulating and ranges from 150 to 400 m a.s.l. The climate is Mediterranean, with mild, wet winters (average daily temperature ranging from 5.8 to 12.8 °C in January) and hot, dry summers (average daily temperature ranging from 16.3 to 30.2 °C in July). The average annual precipitation is 609.4 mm (IPMA 2020).

Genets trapping and handling

Genets were live-captured in forest patches adjacent to the EN114 road in three different sessions (December 2016, January 2018 and January 2019), each one being carried out for 2–3 weeks. We used 10–12 wire cages (Tomahawk Deluxe Single door live traps) baited with sardines and eggs, deployed in suitable genet habitats (e.g. forest with riparian or shrub areas). The traps were placed approximately 500 m apart and within 1 km from paved roads. This design of trap spacing was based on the average radius (~ 1 km) of genet home range (3.3 km^2; Santos-Reis et al. 2004), to maximise animal capture.

Each captured animal was immediately transported to the Veterinary Hospital (University of Évora) where a veterinarian conducted sedation and handling of genets. Sedation was performed with a mixture of ketamine hydrochloride (100 mg ml^{-1}) (Imalgene 1000, Lyon, France) and medetomidine hydrochloride (1 mg ml^{-1}) (Domitor, Pfizer, New York, USA) (ratio 2:1 by volume) using a dosage of 0.12 ml kg^{-1} (Carvalho et al. 2014). After being weighed, sexed and observed, genets were tagged for individual identification with Passive integrated transponders (PIT; model HPT9, Biomark, Boise, USA). Genets were equipped with GPS collars: Litetrack RF-40 VHF DL (45 g), Biotrack, Dorset, UK; and low-cost GPS/GSM collars (~ 50 g), Movetech Telemetry. Only adult and/or subadult animals were collared as long as the equipment weighed less than 3.5% of the animal's body weight and if the individuals were in good health (Ossi et al. 2019). Animals were released at the point of capture in the same day after fully recovering from anaesthesia. Capture and handling procedures were in conformity with Portuguese legal regulations (658/2016/CAPT; 659/2016/CAPT; 37/2018/CAPT; 38/2018/CAPT; 136/2019/CAPT).

Collection and processing of movement data

GPS collars were set to obtain spatial locations every 10 minutes during the period of main activity of genets (17.00 h–08.00 h). Data from the first five hours after animal collaring were discarded to ensure the lowest possible behavioural bias. In addition, we removed all spatial locations that: (1) had a dilution of precision (DOP) > 3, following Biotrack GPS collar specifications and (2) locations with DOP < 3, but potentially erroneous (e.g. within a dam or too far away within consecutive locations), considering the average positional error associated with the spatial locations (mean = 8 m; SD = 10). We also regularised the time of spatial locations to fulfil HMM assumptions – negligible measurement error and regular sampling (Michelot et al. 2016).

A night of tracking (without more than two consecutive missed locations; > 30 min) was defined as the sampling unit, thus constituting a time series of successive locations (e.g. animal path) (e.g. Gardiner et al. 2019). Isolated missing locations (NAs) were linearly interpolated in paths containing a maximum of 15% of NAs, corresponding to a maximum of one missing location per hour (23% of NAs in 49% of paths). Time regularisation and spatial interpolation of locations were performed with the R package "adehabitatLT" (Calenge 2006).

Movement data were obtained for seven genets (one female and six males) successfully tracked during 187 nights (mean 27 days per individual) between 30 November 2016 and 29 March 2019, temporally spanning the species breeding season (Carvalho et al. 2018).

Road and landscape predictors

We calculated a set of important explanatory predictors for genet movement in the same landscape (Carvalho et al. 2016). Thus, six predictors reflecting road proximity, land cover, forest configuration and habitat productivity were considered (Table 1). The Euclidean distance of the genet locations to the nearest major paved road ("Road") was

Table 1. Description and source of the environmental predictors used for HMM models.

Code	Description	Predictor type	Median (min – max)
Road	Distance to the nearest main paved road (m)	Anthropogenic features	461.0 (0.0–1978.0)
DForest	Distance to the nearest forest patch (m)	Landscape features	6.3 (0.0–690.9)
ForestED	Density of forest edges (m/ha) in a buffer of 100 m	Landscape features	229.0 (0.0–627.1)
ForestPS	Mean patch size of forest habitats in a buffer of 100 m (ha)	Landscape features	2.0 (0.0–3.3)
Riparian	Distance to the nearest riparian habitat (m)	Landscape features	176.6 (0.0–1290.0)
Product	Habitat productivity measured in a 100 m pixel	Landscape features	0.4 (0.1–0.7)

calculated from the OpenStreetMap geospatial data repository (OpenStreetMap 2020). Agroforestry land-use classes (Level 1) were extracted from the Portuguese land-cover "Carta de Ocupação do Solo" product (COS 2018), on which the forest configuration variables, "DForest", "ForestED" and "ForestPS" were calculated. "DForest" was calculated from the Euclidian distance to forests, while the latter two predictors were calculated using the metrics of edge density ("ForestED") and patch size ("ForestPS"), from FRAGSTATS v.2.0 software (McGarigal et al. 2012). Distance to riparian habitats ("Riparian") was obtained after the intersection of the stream layer with the tree density layer from the EU-Hydro and Tree Cover Density products, respectively, both retrieved from the Copernicus Land Monitoring Service (Copernicus 2020). Moreover, we also calculated an additional predictor, habitat productivity ("Product"), following Oeser et al. (2019), a proxy of resource availability for genets, as similarly explored in other studies for other mammals (Carter et al. 2019; Beumer et al. 2020). Habitat productivity was derived from Landsat-8 Operational Land Imager (OLI) using the Level-1 collection of atmospherically-corrected imageries through the Google Earth Engine cloud platform (Gorelick et al. 2017). This remote sensing predictor was calculated to reflect the habitat productivity at the time the movement was sampled, thus reflecting high temporal and spatial precision of habitat conditions. For this purpose, we derived the Tasseled Cap greenness metric by transforming the Landsat multispectral bands (Crist and Cicone 1984; Oeser et al. 2019). We further applied the median and a normalisation procedure to the calculated time-series metrics. Such procedure temporally reflected the exact period when each individual genet was sampled, from December to January (see above) (Grilo et al. 2009; Carvalho et al. 2018).

The predictors, not based on distances, were upscaled to 100 m (Carvalho et al. 2016; Valerio et al. 2019). We appended the raster values of all predictors to the genet spatial locations using the R package "raster" in R (Hijmans and van Etten 2012).

Data analysis

Behavioural states of the genets were inferred using HMM from movement data. We developed HMMs by modelling step length with a gamma distribution and turning angles using a von Mises distribution – a circular analogue of the normal distribution (Michelot et al. 2016). We considered HMMs with three behavioural states, since 3-state models are usually statistically well-supported and biologically meaningful in studies involving terrestrial mammals (e.g. Gardiner et al. 2019; Farhadinia et al. 2020). Furthermore, to ensure optimisation of Maximum Likelihood (numerical stability), we ran 50 HMMs trials with different sets of randomly chosen starting values within a range of plausible values (Michelot and Langrock 2019), determined by inspecting histograms of step length and turning angles (Michelot et al. 2019). We found that model output was robust to different sets of starting values, reflecting a converging value of Maximum Likelihood. We therefore used the average values applied in the trials to construct the null model, still confirming that it led to the same convergence value of Maximum Likelihood.

To assess the influence of roads and landscape features on behavioural state occupancy, we used explanatory predictors in the transition probabilities of the state process (Farhadinia et al. 2020). The predictors were standardised before fitting the models to ensure numerical stability and were previously tested for collinearity ($r < 0.7$) for all pairs of predictors, so no collinearity was found. We first applied univariate models, testing one predictor at a time through Akaike Information Criterion (AIC; Akaike 1973), then comparing the AIC values with the AIC of the null model (e.g. van Beest et al. 2019; Gardiner et al. 2019). Only predictors whose univariate models showed an AIC improvement higher than five over the null model were retained for further analysis. After this screening, a forward selection procedure was used to assess the influence of the retained predictors. We again used AIC for multivariate analysis to select the best ranked and most parsimonious model from the candidate models (Burnham and Anderson 2002). To validate the best model, we examined the goodness-of-fit using the pseudo-residuals (Michelot et al. 2019). Finally, we applied the "Viterbi" algorithm to predict the most likely sequence of states (e.g. van Beest et al. 2019), hence assigning a state to each observation in the input dataset and calculating the probabilities of genets occupying the different behavioural states as a function of each predictor. Additionally, for the predictors included in the best model, we calculated the median values of all GPS locations to obtain a reference value of each predictor. Owing to the small sample size for females (one tracked animal), the two sexes were merged into HMM models. The movement models were fitted with the R package "moveHMM" (Michelot et al. 2016).

Results

Overall results

The average number of tracking days ranged from 7 to 66 days per individual (mean = 27 days), with an average number of 1058 locations per individual (Table 2).

We fitted five 3-state HMMs with different predictor dependencies on transition probabilities. The predictor "DForest" was excluded in the initial screening procedure. The forward selection procedure indicated that the HMM with five predictors produced the best model (the lowest AIC value; Table 3). Inspection of the model pseudo-residuals revealed that the goodness-of-fit was good both for step length and turning angle, with no significant evidence of lack of fit or autocorrelation problems (Suppl. material 1: Fig. S1). Thus, we focused on the movement patterns, state-allocation and predictor effects derived from this full model.

Table 2. Details of seven genets tracked in southern Portugal (Évora). For each individual, we provide detailed information about sex, age class, body weight, capture year, beginning and end date of tracking, the number of tracking days and number of GPS locations.

ID animal	Sex	Age	Weight (g)	Year	Tracking start	Tracking end	Tracking days	GPS locations
C	M	Adult	1500	2016	30/11/2016	09/12/2016	10	548
E	M	Adult	1800	2018	08/01/2018	16/01/2018	9	179
F	M	Adult	1500	2018	03/01/2018	10/01/2018	8	236
H	M	Sub-adult	1300	2019	15/01/2019	05/03/2019	50	1444
I	M	Sub-adult	1250	2019	19/01/2019	25/01/2019	7	175
J	F	Adult	1700	2019	23/01/2019	29/03/2019	66	3058
L	M	Sub-adult	1160	2019	31/01/2019	08/03/2019	37	1765
mean			1459				27	1058
sd			237				24	1091

Table 3. Summary of the log-likelihood, AIC and ΔAIC values for the tested HMM. The ΔAIC is the difference of Akaike Information Criterion between each model and the best model, indicated in bold.

Model	Log-likelihood	AIC	ΔAIC
ForestED + Riparian + Road + Product + ForestPS	-39209.41	**78518.81**	0.00
ForestED + Riparian + Road + Product	-39225.78	78539.57	20.76
ForestED + Riparian + Road	-39239.44	78554.88	36.07
ForestED + Riparian	-39256.19	78576.39	57.58
ForestED	-39273.62	78599.24	80.43
Null model (no predictors)	-39303.05	78646.10	127.29

Behaviour state-allocation

The best HMM indicated that genets' movement patterns were composed of three behavioural states (Fig. 2): state 1 with short step-lengths (mean = 10.56 m) and high turning angles (undirected movement; mean = -3.13); state 2 having medium step-lengths (mean = 46.09 m) and a wide range in turning angle (mean = 0.09), though smaller than state 1 and with low concentration, indicating a mix of tortuous movements with forward movements; state 3 included larger step-lengths (mean = 113.74 m) and turning angles highly concentrated around zero (mean = -0.01), indicating mainly fast and linear movements. The three behavioural states (1, 2 and 3) are consistent with "*resting*", "*foraging*" and "*travelling*", respectively. Within the main activity-period (17.00 h-08.00 h), the movement model predicts that genets spend 36.7% of their time travelling (range: 6.9–61.5%), 35.4% foraging (range: 20.4–54.3%) and 28.0% resting (range: 14.5–40.3%; Suppl. material 1: Fig. S2). Genets are, thus, actively moving 72% of their night-time, either foraging or travelling.

State occupancy in relation to predictors

The occurrence of the three behavioural states was best explained by "ForestED", "Riparian", "Road", "Product" and "ForestPS", outperforming all other models which presented ΔAIC values > 20 (Table 3). "Road" was found to be the third most

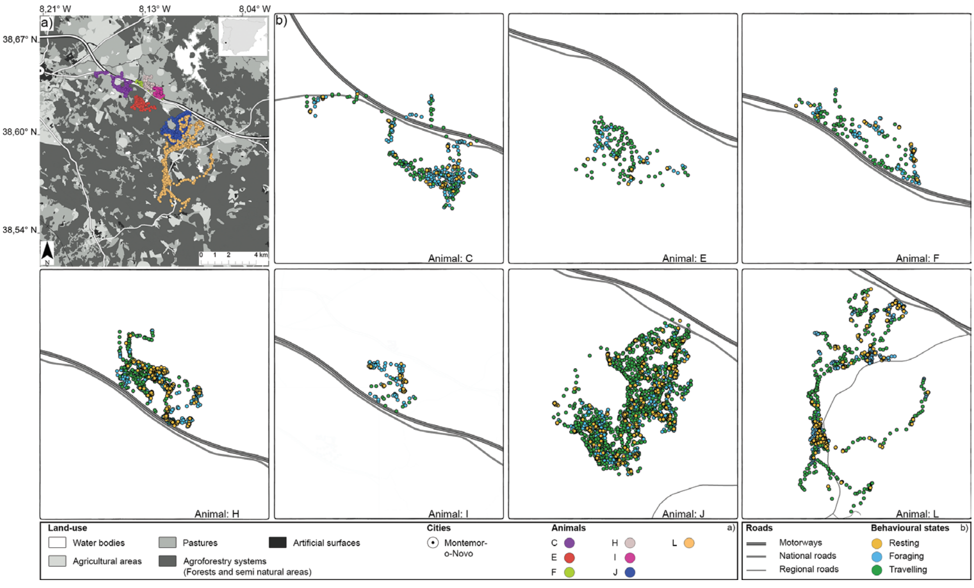

Figure 1. Location of the study area, showing all genet's locations (**a**) and locations of each radio-tracked individual, colour coded by their corresponding state (**b**). Yellow is resting (state 1), blue is foraging (state 2) and green is travelling (state 3).

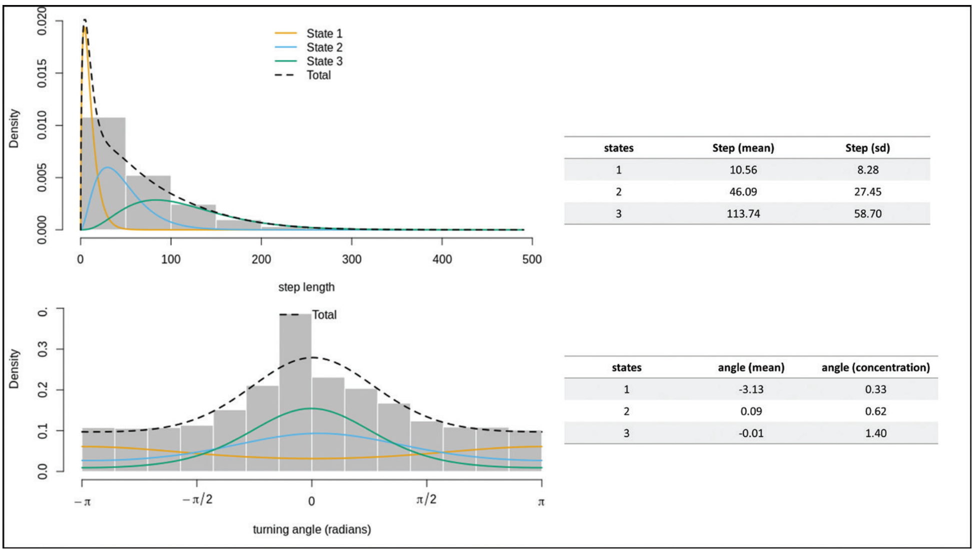

Figure 2. Histograms of observed step lengths (upper plot) and turnings angles (lower plot) with fitted distributions derived from a three-state model for all tracked genets. The coloured lines represent the estimated densities in each state, while the dashed black line is their sum. Tables included in the panels provide estimates of mean step length and standard deviation (sd) and mean turning angle and angle concentration, for observed step lengths (upper table) and turnings angles (lower table). States are: 1 = resting, 2 = foraging, 3 = travelling.

important predictor on the state probability (ΔAIC = 25.66; Table 4). The probability of genets exhibiting the "*travelling*" state was highest in areas far away from roads, whereas "*foraging*" and "*resting*" states were more likely in areas close to roads (Fig. 3). Accordingly, considering the median distance of all GPS locations to roads (461 m), when genets moved beyond that threshold, the "*travelling*" state is predicted for 46.6% of the time, becoming the dominant behavioural state (Suppl. material 1: Fig. S2). In contrast, when moving within 461 m from roads, the "*resting*" or "*foraging*" state are predicted for most of the time (42% and 31% for "*foraging*" and "*resting*", respectively). Landscape predictors also had a pronounced effect on behaviour state occurrence, particularly "ForestED" and "Riparian" and, to a lesser extent, "Product" (Tables 3, 4). "ForestPS" contributed to the final model, but its effect was less clear (Fig. 3). Furthermore, "*travelling*" had highest probability to occur in areas with lower forest

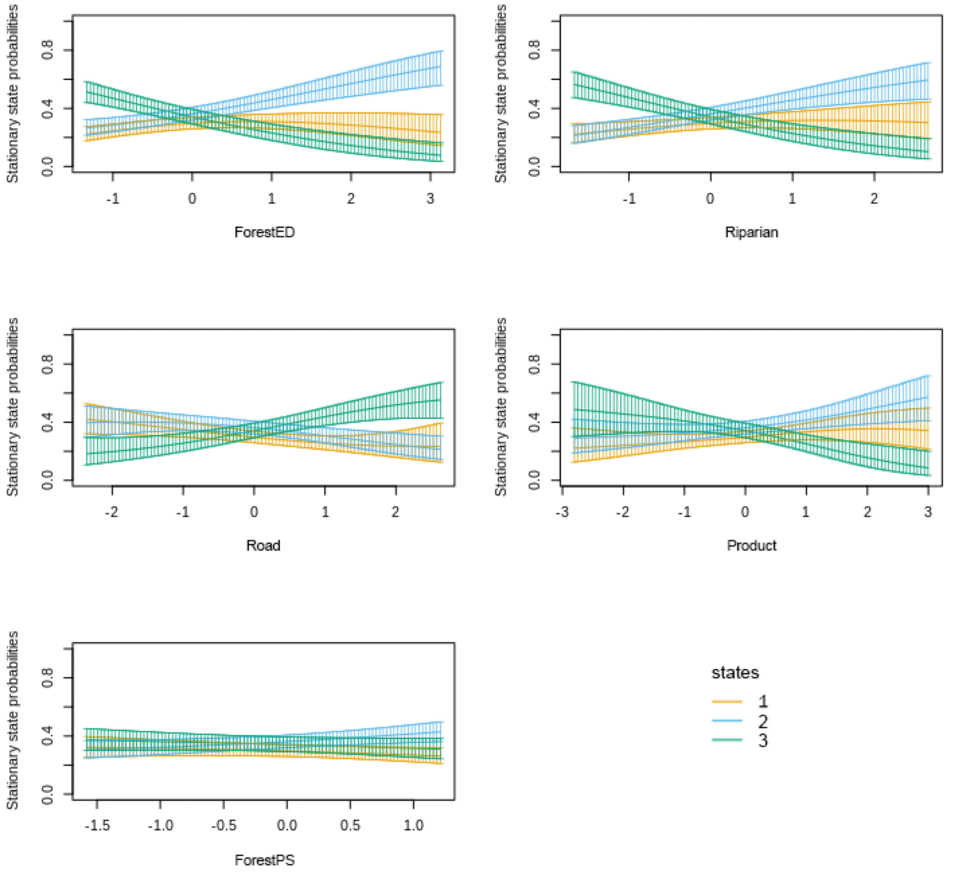

Figure 3. Stationary state probabilities (with 95% confidence intervals) as a function of each predictor considered in the best HMM model (from upper left to the right: ForestED, Riparian, Road, Product and ForestPS). States are: 1 = resting, 2 = foraging, 3 = travelling.

Table 4. Summary of the log-likelihood, AIC and ΔAIC values for the full model and for the set of models that included all, except one predictor, testing the relative importance of each predictor in the full model (the higher the ΔAIC, the higher relative importance of the predictor in explaining genet behaviour states).

Model	Log-likelihood	AIC	ΔAIC
Full model	-39209.41	**78518.81**	0.00
- ForestED	-39237.30	78562.61	43.80
- Riparian	-39233.79	78555.58	36.77
- Road	-39228.24	78544.47	25.66
- Product	-39225.91	78539.82	21.01
- ForestPS	-39225.78	78539.57	20.76

edge density (lower than 229 m/ha) and close to riparian habitats (less than 176 m), while "*foraging*" was most likely to occur in areas with higher forest edge density, while far away from riparian habitats and in more productive areas (Fig. 3). The "*resting*" state also had the highest probability of occurrence in areas with high forest edge density and far away from riparian habitats, although it was less frequent than the "*foraging*" state (Fig. 3). The overlap of areas for state probabilities as a function of "ForestPS" (and, to a lesser degree, "Product") suggests that, although contributing to the final model, these predictors have a minor influence on the occurrence of genet behavioural states (Fig. 3).

Discussion

Hidden Markov Models are used in our study to distinguish the behaviours of a small forest carnivore in an area crossed by a main road and highway corridors. We were able to infer three behavioural states (resting, foraging and travelling) using data from movement paths collected at fine spatiotemporal scales. Changes between states were influenced by distance to roads, but forest edge density and distance to riparian habitats also had a stronger effect, while the productivity habitat metric played a role as well.

Overall, our findings shed light on how genets make decisions about roads and landscape features, specifically their perception of road vicinities. To our best knowledge, this is a novel approach to road ecology applied to carnivores. We discuss the behavioural states identified, as well as the insights gained for road mitigation planning.

Are roads a behavioural barrier to genets or a resource provider?

Roads can be very attractive to carnivores because they offer food resources and easier travel routes (Bateman and Fleming 2012; Zimmermann et al. 2014; Dickie et al. 2016; Andersen et al. 2017). Road verges, in particular, can attract prey by providing them with vegetation cover, very often unavailable in surrounding areas (Ascensão et al. 2012; Silva et al. 2019; Galantinho et al. 2020; Valerio et al. 2020).

Our fine-scale results indicate that, in areas close to roads, the dominant types of behaviour by genets are foraging and resting, while in areas further away from roads, the travelling behaviour is more frequent. This suggests that animals use road verges and adjacent areas (< 500 m) for feeding, but not as travel routes. The resting state includes true resting sites (see Carvalho et al. 2014), but may also include short-term pauses in foraging periods, a slowdown in movement when approaching prey or a perception of a danger (e.g. road noise and light). The association of foraging behaviour with road proximity might be explained by the higher and denser vegetation in verges when compared to adjacent farmland which is commonly explored for cattle grazing, removing the refuge given by the shrub layer (Ascensão et al. 2012; Silva et al. 2019; Galantinho et al. 2020). Thus, the maintenance of shrub strata in road verges provides some benefits for certain prey species (Ascensão et al. 2015), which then attracts genets to search for food in road verges and edge habitats. This is in line with recent data suggesting that predators are attracted to road verges due to the higher prey abundance (Barrientos and Bolonio 2008), particularly small mammals (Ascensão et al. 2015; Silva et al. 2019). Indeed, genets, beyond berry tree fruits, prey mainly on small vertebrates, frequently the wood mouse (Virgós et al. 1999; Rosalino and Santos-Reis 2002; Barrientos and Virgós 2006) which is abundant in road verges even when these are embedded in forested areas (Galantinho et al. 2020).

Furthermore, our results also highlight that night-time resting behaviour is more likely in areas close to roads. This finding conflicts with other studies that, although based on gravel roads, refer other carnivores, such as African wild dogs and wolves, to avoid using road proximities when resting (Zimmermann et al. 2014; Abrahms et al. 2016). In addition, our results concern the time period when genets are most active (night-time) and our resting state should be viewed differently, as it also includes movement pauses of short time duration (less than an hour). In our study, it is likely that active foraging states alternate with movement pauses, including ambushing behaviour before catching prey. Nevertheless, the resting state also includes the typical resting behaviour in trees, commonly used in the study area (at an average height of 3 m; Carvalho et al. 2014). It is, thus, possible that the disturbance caused by the proximity of roads might be compensated by the shelter provided by the tree height from human activities and predators (Carvalho et al. 2014).

Previous results, based on telemetry, have shown that the space use and movements of genets are constrained by the presence of roads, with home ranges bordered by them (Carvalho et al. 2018). This suggests the existence of a behavioural avoidance towards roads, although the local genet population does not present genetic structuring (Carvalho et al. 2018). Our results support these conclusions (a barrier effect associated with roads), as the radio-tracked individuals in our study concentrated their movements on one side of the road corridor (national road and highway) and rarely crossed it. From the radio-tracked animals in the present study, only one adult male (animal C) crossed both the national road and the parallel highway, quickly returning to the regularly used side of the road. When exploring the other side of the highway, only foraging and travelling states were predicted. Thus, our results suggest that, although roads represent a behavioural barrier to the movement of genets, they also take advantage of the proximity of roads as foraging areas.

Interestingly, our results also show that the travelling state occurred less frequently near roads. This is a novel finding, as some studies, yet focusing on gravel roads, found that roads are selected for travelling of African wild dogs (Abrahms et al. 2016), Norwegian wolves (Zimmermann et al. 2014) and red foxes (Bischof et al. 2019). If roads are themselves a territory boundary, with infrequent visits of neighbouring conspecifics from the opposite side, then it should be more advantageous for genets, from a competition standpoint, to patrol their territory (or explore neighbourhood) in areas far away from roads. When these areas have high quality habitat, they are more likely to be attractive to other individuals and should be secured by the territory owner. Moreover, when travelling at such a distance from the road, they avoid road disturbance and reduce the roadkill risk.

Landscape influence on behaviour

Genets are known to preferentially use forest areas and riparian habitats (Matos et al. 2009; Pereira and Rodríguez 2010). Our results are in line with these findings and go even further by identifying the different types of behaviour associated with different habitat characteristics. In our study, foraging behaviour was more likely at forest edges, far away from riparian habitats and in higher productivity habitats. Forest edges may offer foraging opportunities, in more open areas, given the higher habitat suitability for small mammals, as previously mentioned for road verges. Travelling behaviour, on the other hand, had highest probability to occur in continuous forest areas and close to riparian habitats.

While the available literature suggests that forest and riparian areas are essentially used by genets for foraging (Sarmento et al. 2009; Pereira and Rodríguez 2010) and resting (Virgós et al. 2001; Sarmento et al. 2009), our models suggest that travelling was the most frequent behaviour. Our results support the role of riparian habitats as movement corridors (documenting that observed movement parameters are compatible with travelling movement) and, therefore, of significance for landscape connectivity and mitigation planning. In fact, previous results state that, despite the presence of roads decreases landscape connectivity for genets, this effect can be minimised when riparian corridors are present, given the presence of culverts that are used as road crossing structures (Carvalho et al. 2018; Craveiro et al. 2019). This corridor effect from riparian habitats is of special importance when embedded in open agricultural areas (Pereira and Rodríguez 2010; Carvalho et al. 2016). In fact, one genet (animal C) crossed the highway using two different crossing structures (a culvert and an underpass) installed in a riparian corridor.

Implications for road mitigation

To mitigate the negative effects of roads on genet populations, we must first understand the processes that affect the behavioural responses towards roads and existing mitigation (Klar et al. 2009). According to our results, culverts and underpasses should be in close proximity to forest and riparian habitats, as those areas seem to promote travelling behaviour of genets and might be used more frequently in road crossing events. For culverts, it is important that these structures are wide or include dry ledges, as these increase the success of crossings by genets and other carnivores (Villalva et al. 2013; Craveiro et al. 2019). The implementation of effective fences along roads should also be considered, as these may help to guide movements towards road-crossing structures (Ascensão et al. 2014), while increasing safety of genets' movements on road verges.

Study limitations

Our results should be viewed as preliminary, as we used an unsupervised HMM approach and the inferred states were not validated by direct observations of the animals in the field. However, all the diurnal resting sites identified through VHF signal during daytime (when downloading movement data during daylight hours) overlapped spatially with most locations inferred as resting states in HMM. Thus, we are confident that the obtained state classification captured most of the variation in the genet movement behaviour.

A second potential limitation is related with the number of tracked individuals and sampled period. Our sample size of individual genets was relatively small, male-biased and did not cover the entire annual cycle. Space use by genets may possibly vary throughout the year as result of seasonal changing in resource availability and reproduction cycle (Camps and Llobet 2004). On the other hand, the breeding period sampled here corresponds to the season of greatest activity, since males usually explore areas beyond their usual home range in search of receptive females as these are not yet with cubs and are, therefore, not spatially restricted (Camps and Llobet 2004). The genets' breeding period also corresponds to a period of increasing abundance of their main prey, the wood mouse, before reaching maximum densities in spring, both in road and roadless areas (Galantinho et al. 2017). Thus, although we have sampled a limited portion of the annual cycle, it should clarify the main environmental constraints influencing genet behaviour. Future HMM studies covering larger and more balanced sample sizes may be able to refine these results and accommodate inter-sexual differences, along with individual and seasonal variability on movement behaviour of genets.

Conclusions

Our results support evidence that the proximity of roads, along with more heterogeneous and fragmented areas, might favour foraging opportunities for genets, though this may also increase genet exposure to road threats. We emphasise that road-engaged stakeholders need to consider the movement behaviour of genets when targeting management practices to maximise road permeability.

Author contributions

SMS, EMF and AM conceived the study; EMF, JC, NF and PC conducted fieldwork; EMF, FV and DM developed the analysis protocol; EMF and FV analysed the data; EMF, FV and SMS wrote the first manuscript draft; all authors revised the work and gave final approval for publication.

Acknowledgements

The authors are grateful to Filipe Carvalho for field support and discussions. Professor Joana Reis (Veterinarian Hospital, University of Évora) supervised the handling and anaesthesia of captured genets and Joaquim Martins and Filipe Dias collaborated in the veterinarian procedures. EMF, FV and DM were supported by a PhD fellowship, funded by Fundação para a Ciência e a Tecnologia (SFRH/BD/146037/2019, SFRH/BD/122854/2016 and SFRH/BD/104861/2014, respectively). This work was supported by the projects POPCONNECT (PTDC/AAG-MAA/0372/2014) and LIFE-LINES (LIFE14 NAT / PT / 001081) Linear Infrastructure Networks with Ecological Solutions (60% co-financed project by the LIFE – Nature and Biodiversity Programme of the European Commission).

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Supplementary material 1

Figures S1–S3

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Data type: Images

Explanation note: Additional files regarding 1) HMM model performance, 2) percentage of state occupancy of each tracked genet, and 3) density distribution plots of behavioural states as a function of each predictor considered in analyses.

Link: https://doi.org/10.3897/natureconservation.47.72781.suppl1

Nature Conservation 47: 177–196 (2022)
doi: 10.3897/natureconservation.47.71864
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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The effect of habitat reduction by roads on space use and movement patterns of an endangered species, the Cabrera vole *Microtus cabrerae*

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Academic editor: Cristian Remus Papp | Received 20 July 2021 | Accepted 8 November 2021 | Published 25 March 2022

http://zoobank.org/21152CC6-AAEE-4C84-A367-0225E9E67E5F

Citation: Fernandes N, Ferreira EM, Pita R, Mira A, Santos SM (2022) The effect of habitat reduction by roads on space use and movement patterns of an endangered species, the Cabrera vole *Microtus cabrerae*. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 177–196. https://doi.org/10.3897/natureconservation.47.71864

Abstract
Roads are among the most widespread signs of man's presence around the globe. From simple low traffic trails to wide and highly used highways, roads have a wide array of effects on wildlife. In the present study, we tested how habitat reduction by roads may affect the space use and movement patterns of the Cabrera vole (*Microtus cabrerae*), a near-threatened Iberian endemism, often living on road verges. A total of 16 voles were successfully radio-tracked in two habitat patches with different size and proximity to roads. Results showed that individuals from the smaller patch (Verge patch) had smaller and less complex home-ranges than those from the larger patch (Meadow patch). Movement patterns were significantly influenced by the day period but only in individuals from the Verge patch. There was evidence of a barrier effect in both habitat patches, being this effect much more noticeable in the verge population. Overall, this study shows that space use and movement patterns of Cabrera voles near roads may be affected by the degree of habitat reduction imposed by these infrastructures. This suggests that species space use and movement patterns at fine-scale should be accounted for in road planning, even for species that may benefit from road verge habitats as refuges.

Keywords
Barrier effect, Cabrera vole, fragmentation, road ecology, small mammals

Introduction

Roads are a widespread sign of human presence across the globe, imposing several contrasting effects on wildlife species, from positive to negative (Forman 2000). Positive effects of roads include increased availability of foraging habitat and food supplies, low predation pressure, hunting areas for avian predators, or even attractive microclimate conditions of road surface (Morelli et al. 2014). Road verges are frequently the only remaining favourable habitat for many species in human-modified landscapes, providing refuge, habitat, or dispersal corridors (Way 1977; Porto-Peter et al. 2013; Redon et al. 2015). This is probably the case for many small prey species that find in road verge habitats protection from predators, which have been shown to be negatively affected by roads (Fahrig and Rytwinski 2009). This is supported by several studies showing a higher abundance of small mammals in road verges when compared with the surrounding habitats (e.g. Adams and Geis 1983; Sabino-Marques and Mira 2011; Porto-Peter et al. 2013; Redon et al. 2015).

The negative effects of roads are however more frequent than positive effects, being mainly related to direct mortality, habitat fragmentation, disturbance, and chemical pollution (Forman and Alexander 1998; Trombulak and Frissell 2000; Seiler 2001). Roads also act as barriers to movement for many species, thereby decreasing their access to mates, water, food or other resources (Trombulak and Frissell 2000; Brown et al. 2006), with both genetic and demographic costs to populations, increasing local extinction risk (Shepard et al. 2008). For instance, it has been shown that road proximity can have negative impacts on mammal species abundance or activity (Kozel and Fleharty 1979; Garland and Bradley 1984; Clark et al. 2001), this effect decreasing with the distance to the road (Benítez-López et al. 2010; Medinas et al. 2019). Roads have been also shown to decrease edge permeability for some small mammal species such as the montane akodont *Akodon montensis* (Ascensão et al. 2017). Habitat fragmentation caused by road development might therefore result in high risk of extinction (Crooks et al. 2017), due to associated habitat loss and increased patch isolation (Bennett 2003), reducing the chances of local (re)colonization (McGregor et al. 2008). Besides, in addition to the reduction in animal populations, species movement behaviour may be impacted near roads (Coffin 2007).

Although the negative effects of roads on wildlife are well-documented for many species (Forman et al. 2003; Shepard et al. 2008), few studies have focused on the behavioural consequences of roads to individual animals or their populations (see Shepard et al. 2008). Understanding behavioural responses of animals to roads provides insights into the causes and mechanisms of the effects of linear infrastructures on wildlife, allowing more informed mitigation and conservation planning (Roedenbeck et al. 2007). Existing evidence suggests that responses vary considerably across species (Goosem 2001; Bissonette and Rosa 2009; Rytwinski and Fahrig 2012; Porto-Peter et al. 2013; Grilo et al. 2018) and depending on the landscape context. Galantinho et al. (2017) found that in *montado* systems, wood mouse (*Apodemus sylvaticus*) populations living near roads have a lower fitness than those living far from roads. Moreover, small mammals with high site fidelity and slow movements are more susceptible to the negative effects of roads (Coffin 2007). This was documented by Rico et al. (2007) that observed a lower crossing rate in less mobile rodent species. Even dirt roads may confine individual home ranges and inhibit their movements, as shown for the Abert's squirrel (*Sciurus aberti*) (Chen and Koprowski 2016). In general, terrestrial species with small and fragmented populations, and specific habitat or environmental requirements should be particularly vulnerable to impacts of road barrier effects, though compelling evidence supporting this idea is still scarce (Goosem 2001; McDonald and St Clair 2004).

The Cabrera vole (*Microtus cabrerae* Thomas, 1906) is an Iberian endemism with a patchy distribution across all its range. It is considered "Vulnerable" both in Portugal (Queiroz et al. 2005) and in Spain (Fernández-Salvador 2007) and shows a spatial pattern consistent with a metapopulation structure, with frequent local extinctions and colonizations (Pita et al. 2014), and with home ranges typically < 1000 m^2 (Fernández-Salvador et al. 2001; Pita et al. 2010, 2014). In highly modified landscapes, the specific habitats selected by the species (tall and dense wet herbaceous patches) are often restricted to marginal areas, including along road verges (Fernández-Salvador 1998; Pita et al. 2006, 2007; Santos et al. 2007). Despite the exposition to traffic noise and increased mortality risk by roadkill (Santos et al. 2007; Valerio et al. 2020), road verge habitats may still provide important resources for species living on them. However, the behavioral consequences of roads to the species are still largely unknown, even though these may impact local population viability.

In the present study we evaluated how living in road verges influences space use and movement patterns of Cabrera volesin southern Portugal. Specifically, we assessed whether space use of Cabrera voles may change when occupying road verge patches that are spatially limited and linearly shaped, with individuals exhibiting less complex home range boundaries (Ford 1983; Hiller et al. 2016) or increasing intrasexual overlap (Madison 1980; Ims et al. 1992; Collins and Barrett 1997). We also assessed whether home ranges in road verges are smaller and more linear, as predicted for other small mammals (Stumpf and Mohr 1962), due to the higher availability of food and shelter, potentially attracting a high number of individuals compared to the surrounding matrix habitats. In addition, we assessed whether movement paths are shorter and more linear when compared with those of more extensive habitat patches (Maclagan et al. 2019). Furthermore, because vehicles pass closer to animals in road verge habitats, we assessed whether individuals may adjust their movement periods to avoid higher traffic hours as observed for other mammals (Chen and Koprowski 2016; Kušta et al. 2017). Finally, we assessed whether voles living in road verges might cross the road more often due to the recolonization dynamics of metapopulations (Pita et al. 2007) and to increased intraspecific competition typical of small habitat patches (Ims et al. 1992). In order to test these predictions, we derived the following hypotheses: i) individuals occupying road verges have smaller home ranges with lower shape complexity, smaller and lower number of core areas and/or higher intrasexual spatial overlap; ii) have shorter movement paths, iii) have more linear movement paths, iv) make shorter movements during high traffic periods, and v) cross the road more frequently than those living in larger habitats.

Overall, we expect our study will contribute for a better understanding of the behavioral consequences of roads to small mammals, which should be critical for species management planning and road impacts mitigation.

Materials and methods

Study area

The present study took place in Alentejo, southern Portugal (38°41'42"N, 08°04'46"W; Figure 1A). The climatological normal mean (1981–2010) varied between 14.3 °C and 21.4 °C for the study area (IPMA 2018). The landscape is mainly characterized by the agroforestry system commonly known as "montado". It is characterized by an open tree layer with Cork oak (*Quercus suber*) and/or Holm oak (*Quercus rotundifolia*), with sclerophyll shrubs and annual grasses (Pinto Correia et al. 2011). There is one main road in the study area (N4 national road) with an annual traffic of 3882 motorized vehicles (3424 during daytime and 458 during night-time) and connecting Lisbon to Spain (EP 2005) (Figure 1B).

Study design

We used radio-telemetry data from individuals captured in two habitat patches with different size and road proximity (Meadow and Verge; Figure 1B). The patches were identified after previous searches for species presence signs in areas near the main roads of the study region (October 2016 to February 2017). The two patches presented abundant and conspicuous pathways among grasses, latrines of dark-green droppings and the fresh cut grasses, typical and undoubtably recognizable as Cabrera voles presence signs (Pita et al. 2006). Both patches were located along the same N4 road and separated by 1.5 km from each other (Figure 1B).

The Meadow patch (38°41'30.76"N, 08°05'14.33"W) is a large patch (24 589 m^2) with high habitat availability for the species. Dominant vegetation here is sedge/rush and tall perennial grass communities with isolated cork trees in the periphery. The Meadow patch is also crossed by a very small stream, only flooding after abundant rainfall. This area is separated from the road by a fence and a fire break. This patch is flanked by N4 road at North side and by a smaller dead-end road at the West side, with very low traffic. Vole presence signs suggested high local population abundance and were all located outside the road verge habitat (SM Santos, pers. observ.).

The Verge patch (38°41'54.94"N, 08°04'14.26"W) is a small patch (2 021 m^2) spatially constrained between two paved roads, N4 at North, and a smaller and less used road at South providing access to private property. The dominant vegetation in this patch is mainly annual grass communities with isolated shrubs (*Cytisus* spp., *Genista* spp.), typical of road verge communities (Santos et al. 2007). This patch is closer to the road, without a physical separation, such as a fire break or a fence. This means that the Verge patch is adjacent to the road pavement.

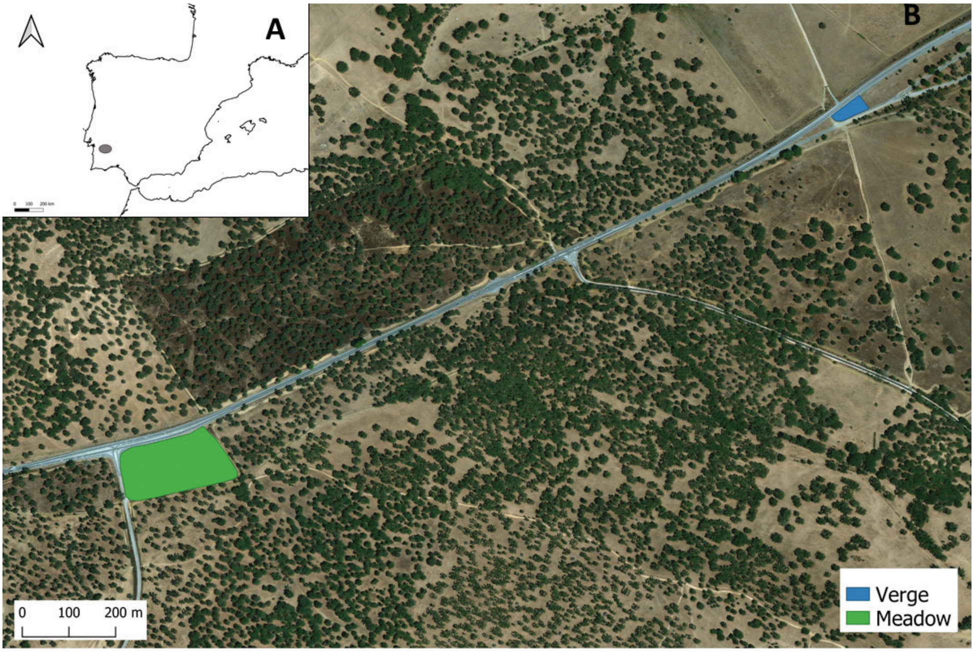

Figure 1. Panel **A** study area location within the Iberian Peninsula; Panel **B** selected habitat patches along the N4 road for the study of space use and movement patterns of Cabrera voles in southern Portugal (green- Meadow patch; blue – Verge patch).

Both patches are bordered by the same road, but the habitat is much more reduced at the Verge patch when compared to Meadow patch. While the centroid of Verge patch is 14 m from the nearest road, the centroid of the Meadow patch is 60 m away. Therefore, the road effects are expected to be much more evident in the Verge patch. Given the mean home ranges of 300–400 m^2 for Cabrera voles in Mediterranean areas (Pita et al. 2014), we assume that the Meadow patch is a control area for assessing the effects of roads on Cabrera voles living in the road verges.

Capture and radio-telemetry

Voles were captured with Sherman live traps (7×23×9 cm) laid in clusters where the species signs were more concentrated and fresher. Apple and carrot were used as bait, and hydrophobic cotton and grass were provided as bedding (Pita et al. 2011). A total of 14 trapping sessions were conducted (April to June 2017). The sampling period corresponded to the end of the wet season, which is when reproduction should be higher (Pita et al. 2014). The traps were set in the morning at 7:00 a.m. and disabled at 1:00 p.m. to avoid prolonged time of animals inside traps. The average trapping effort was 58 traps per day. Animals from other species were released immediately at the site of capture with no further manipulation or intervention.

All Cabrera voles captured were weighed and sex determined in the field to immediately exclude animals with low weight, and pregnant or lactating females, to avoid any negative impacts on local populations. Voles with conditions to be radio-collared (good physical condition and body weight > 36g) were sedated with a subcutaneous injection of Dormitor (0.5 mg/kg) combined with Clorketam (40 mg/kg) to reduce handling stress during collar fitting, following all animal welfare conditions for animals used in research. During sedation, the reproductive status was confirmed based on the presence of descendent testes or perforated vulva and nipple development. Radio transmitters (SOM-2018; Wildlife Materials, Inc., Murphysboro, IL, USA) were attached with collars to voles. The transmitters weighed 2.0 g and represented an average 4.2% (range: 3.1–5.3%) of voles' body mass (range: 38 – 65 g) in order to ensure that additional energetic costs were kept to a minimum (Sikes et al. 2011). Voles were additionally fitted with PIT tags to easily identify them in case of future recaptures. Voles were then induced out of sedation with Antisedam (0.2 mg/kg). Before release in the field, collared animals were kept a few hours for observation, ensuring that they were wide awake during their release. Animals were released close to their place of capture and radio tracking begun at least 4 h after their release (adapted from Pita et al. 2011).

Eighteen voles were fitted with collar radio-transmitters: 9 voles in Meadow patch (7 females; 2 males) and 9 in Verge patch (4 females; 5 males). All voles tracked were non-juveniles (> 28g), as recommended elsewhere (Fernández-Salvador et al. 2005; Pita et al. 2010).

From 7th April to 14th June 2017 the collared voles were tracked on foot using the "homing-in" method (White and Garrott 1990) and by multiple triangulations when the observer was close to the animals, with a hand-held 2-element Yagi antenna and a SIKA radio receiver (Biotrack, United Kingdom).

Due to the short battery life, it was decided to use a clustered sampling scheme, with discontinuous tracking at 15 min intervals, to access space use and movement patterns (Pita et al. 2010; Santos et al. 2010). Hence tracking was done in six 4-h sessions, comprising 16 position fixes each and separated at least 4h from the next session in order to sample the entire 24h cycle (05–09h, 09–13h, 13–17h, 17–21h, 21–01h, 01–05h). The nocturnal session (01–05h) was sampled only once per animal as Cabrera voles are more active during the daytime (Fernández-Salvador et al. 2005; Pita et al. 2011). This allowed to optimize sampling to the periods of higher activity. Voles were seen on several occasions during tracking, and appeared little affected by the presence of the observer. At each position fix, a coordinate was recorded using a Garmin eTrex handheld GPS. Mean fix error was 1.2 m (n = 35; 0.2 – 3.1m).

Whenever possible, tracking was carried out until at least a minimum of two session replicates were reached for each individual (excepting the nocturnal session), corresponding to 176 location fixes. At the end of field work a new trapping session took place to remove the collars from tracked animals, though this was only possible for a few of them (n = 4) due to the low recapture rates.

Data analysis

Response variables

To assess differences in animals' space use between habitat patches, the individual home ranges, shape complexity index, extension and number of core areas, and the female spatial overlap were estimated. Movement patterns were assessed through path length and linearity, and road crossing rates.

Individual home ranges were estimated using biased random bridge kernel (BRBK) at 95% (where animals spend 95% of their time) and 50% utilization distribution contour (core areas). The BRBK estimator is based on the biased random walk model and deals with serial autocorrelation of the fixes (Millspaugh et al. 2006; Benhamou 2011). Movement step distances of less than the average location error (1.2 m) were assumed as non-movement (Lmin). The maximum step duration for defining successive relocations was defined as 4h (Tmax) and the minimum smoothing parameter was set to 1.2 in all animals (hmin). The contours of utilization distribution (UD) were adjusted to the road limit whenever necessary. All BRBK estimates were based on more than 140 location fixes.

The shape complexity index (C) was calculated for each animal to infer differences in resource use between patches as $C = L/(2*\sqrt{(A\pi)})$, where L is the UD contour perimeter length (m) and A is the area (m^2) of contour UD. A perfectly circular contour has C = 1 (Hiller et al. 2016).

Differences in the degree of spatial interactions were examined calculating home range overlap between females for 95% BRBK (Frère et al. 2010). The utilization distribution overlap index (UDOI) was used to measure space-use sharing between two females (Fieberg and Kochanny 2005). The UDOI ranges from 0 when two home ranges do not overlap and equals 1 if both home ranges are uniformly distributed and have 100% overlap (Fieberg and Kochanny 2005).

To assess differences in movement patterns between individuals from the two habitat patches, two responses were calculated from radio-telemetry data: path length and path linearity index.

In the present study, a step is assumed as the movement measured in 15 min, and the path is the group of 16 steps measured during a period of 4 h (15 min × 16). Before these calculations, telemetry data was converted into a time-regular trajectory data from which standard parameters were extracted for each telemetry session: step length, step absolute angle and step relative angle (i.e., turning angle) (Calenge et al. 2009). Step lengths lower than 3 m (maximum fix error) were corrected to zero (along with the respective absolute and relative angles) and classified as no movement.

The path length expresses how active an individual was in each session, and it allows to monitor the periods of activity and behavioural patterns (e.g. nocturnal species will have higher path lengths during the night) (Edelhoff et al. 2016).

The linearity index was calculated for each observed path as the net displacement distance (the Euclidean distance between the start and the final point of a path), divided by the total length of the path (Almeida et al. 2010). This index varies from 0 to 1 and quantifies the searching efficiency of the animal while adjusting its path to the most profitable route in terms of resource acquisition (Benhamou 2004). Linearity indices closer to 1 are indicative of higher search efficiency (Almeida et al. 2010).

In the present study it was assumed that all movements were routine daily movements as the individuals were adults and never abandoned their home range.

Explanatory variables

For each individual the sex and patch where the tracking took place were registered. For each position fix recorded in the field, we also registered the time at which the fix was taken, together with several variables describing microhabitat composition and structure (Suppl. material 1: Table S1). A detailed digital elevation model (pixel: 1 × 1 m^2) was built for the two habitat patches based on a detailed topographic field measurement (CL Topografia, Lda) from which elevation was extracted for each position fix. Because each patch is at a different elevation, we calculated the difference between the elevation in each fix and the lowest elevation in the respective patch. Regional meteorological conditions at each hour (air temperature, relative humidity and amount of rainfall) were obtained from Centro de Geofísica de Évora (University of Évora; Mitra station) and later added to the dataset.

A total of 23 explanatory variables were initially considered for movement pattern analyses: 9 in the step dataset and 17 in the path dataset. The explanatory variables of path dataset are a summary (sum, average, median or mode) of steps variables comprising each path (Suppl. material 1: Table S1).

Statistical analyses

All defined response variables were screened for their distribution and the need of transformations. Path length, BRBK (95% and 50%), and Number of core areas were log transformed. For the movement pattern analyses, the paths and steps with zero length were discarded.

The area of individual home ranges (95% BRBK), core areas (50%BRBK), the number of core areas (No BRBK50), the shape complexity index, and female overlap index (UDOI) were compared between the two habitat patches with a Wilcoxon rank-sum test (W) to assess differences between patches in space use parameters (Sokal and Rohlf 1997). Because there were no effects of sex on home range and core area sizes, neither on the number of core areas and shape complexity (Suppl. material 1: Table S2), sexes were combined in space use analyses.

To assess the influence of explanatory variables (including the habitat patch and day period) in movement patterns, Linear Mixed Models (LMM) were applied to path length and path linearity index (Zuur and Ieno 2016). The two response variables were modelled as a function of explanatory variables, with individual voles as a random intercept to deal with pseudo-replicationarising from repeated measures made on the same individual (Zuur and Ieno 2016). Model selection was based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

Before model building, the collinearity among explanatory variables was verified. Thus, for variable pairs showing high collinearity (Pearson correlation: $r > 0.7$), only the one with strongest correlation with response variables was retained for further analysis. To reduce the number of competing candidate models and avoid spurious effects, each non-collinear explanatory variable was individually tested against the response variable with a Generalised Linear Model (GLM) and this model AIC compared with the respective Null model (a GLM with only the intercept). Explanatory variables that produced models with an AIC higher than the Null model were not considered in mixed models.

Mixed models showing an AIC within two units of the best model ($\Delta AIC < 2$) were considered to be equally supported by the data (Burnham and Anderson 2002). In these circumstances we performed model averaging accounting for the average parameters on the group of models with $\Delta AIC < 2$ (Burnham and Anderson 2002). Explanatory variables included in these models were considered significant if their confidence intervals did not overlap zero (Burnham and Anderson 2002). Models were also globally evaluated through the comparison of their AIC with the AIC of the Null model. Models with an $\Delta AIC > 2$ relative to the Null model were assumed to have considerable support.

To assess road barrier effect, the number of observed road crossings was compared to the expected number of road crossings through Pearson chi-square test. The expected number of road crossings was generated with correlated random walk (CRW) models (Calenge et al. 2009). CRW models (Kareiva and Shigesada 1983) were parameterized using observed telemetry data as follows: the concentration parameter (r) was obtained using the Wrapped Normal Maximum Likelihood estimate for observed turning angles; the scaling parameter (h) was calculated from each observed path; and the spatial coordinate to start from. A total of 100 simulated paths were produced for each observed path from which the number of times each path crossed a road were extracted (Rondinini and Doncaster 2002). If a vole significantly avoided roads, then the number of observed road crossings should be below the 95% of the distribution of predicted crossings (i.e. one-tailed $P < 0.05$) generated from the individual's simulated movement paths (Shepard et al. 2008). The expected number of road crossings was generated for all voles together in each habitat patch, and then for individual voles.

Analyses were performed in QGIS (2.18 Las Palmas) software and R environment, version 3.4.4 (R Development Core Team 2017), and using the packages adehabitatHR, adehabitatLT, MuMIn, lme4 and nlme.

Results

General results

A total of 16 voles were successfully tracked. Radio-telemetry provided 3886 position fixes collected over 904h for 16 animals. Mean ± SE fixes per animal was 217.8 ± 48.3. Three

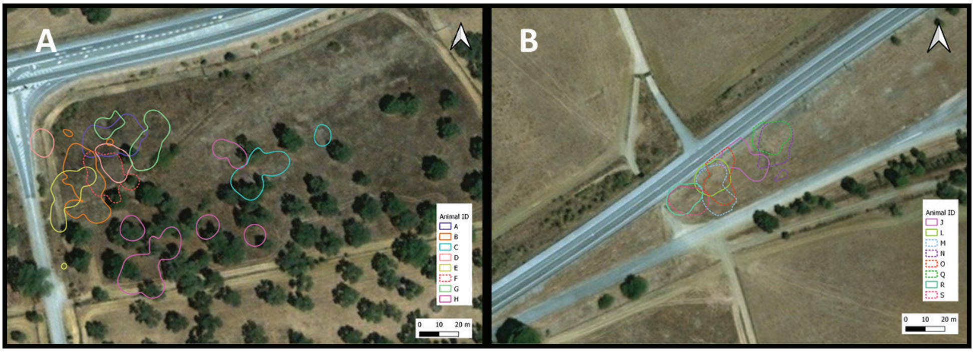

Figure 2. Home range (BRB Kernel 95%) of each radio-tracked Cabrera vole in southern Portugal; Panel **A** meadow patch; Panel **B** verge patch. Females are represented with continuous home range outline, while males are represented with discontinuous home range outline.

batteries failed before the end of the study, one vole was predated by a snake, and another possibly removed the collar. The animals included in analyses have at least a full 24-h period sampled (16 voles). The maximum number of voles tracked simultaneously was four.

Cabrera voles showed home ranges (95% BRBK) between 175 and 815 m^2 (mean ± SD: 352 ± 163m^2). Core areas (50% BRBK) varied between 37 and 175 m^2 (mean ± SD: 62 ± 34 m^2).

Steps and paths of zero length were calculated as 73.1% and 14.3% of observations respectively, and were not included in the analyses of movement patterns. Thus, steps length (movement within 15 min) varied between 3 and 28 m (mean ± SD: 5.8 ± 3.5 m), while path length (movement within 4h) varied between 3 and 94.8 m (mean ± SD: 27.4 ± 21.3 m).

Space use patterns

Voles from the Verge patch showed significantly (P-value < 0.05) smaller home ranges (95%BRBK) and lower shape complexity index (sh_complex) when compared with voles from the Meadow patch (Figure 2; Table 1). Mean home range in the Meadow was 451 m^2, while in the Verge patch was 255 m^2. The extent of core areas (50%BRNK), the number of core areas (No BRBK50) and female spatial overlap (UDOI index) were not statistically different (P-value > 0.05) between patches (Table 1).

Differences in movement patterns between patches

The length of movement paths was explained by a group of five models (ΔAICc < 2), the first model had a weight of 0.37 and an AIC improvement relatively to the Null model of 38. (Null model AIC = 422; best model AIC = 384).

According to the average model, there were differences in path length between day periods, according to the patch type: paths were longer for the 5–9h period (dawn) when compared with the three following periods (9–13h, 13–17h, 17–21h) in Verge

Table 1. Summary results of Wilcoxon rank tests applied to the space use parameters of Cabrera voles with observed values for the two habitat patches (mean ± SD), also showing the value of the test statistic (W) and the p-value for the test (P-value); 95%BRBK: biased random bridge kernel (BRBK) at 95% utilization distribution contour; 50%BRBK: biased random bridge kernel (BRBK) at 50% (core areas); No BRBK50: number of core areas; sh_complex: shape complexity index; UDOI: utilization distribution overlap index.

	Meadow	Verge	W	P-value
95%BRBK [a]	450.5 ± 178.4 (m^2)	254.8 ± 60.6 (m^2)	56	0.01
50%BRBK [a]	71.2 ± 45.7 (m^2)	52.2 ± 12.2 (m^2)	39	0.505
No BRBK50 [a]	2.1 ± 2.0	1.6 ± 0.9	34.5	0.815
sh_complex	1.7 ± 0.4	1.1 ± 0.1	61	0.001
UDOI [b]	0.013 ± 0.033	0.000011 ± 0.000017	152	0.375

a) log transformed. b) square root transformed

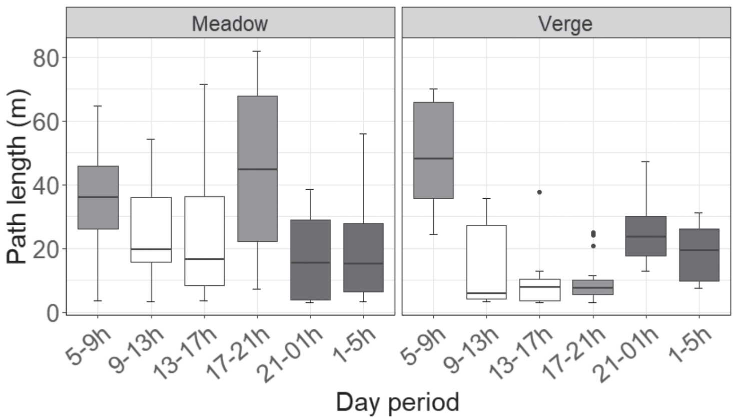

Figure 3. Variation of path length according to habitat patch (Meadow and Verge) and day period of Cabrera voles in southern Portugal (dark gray: nocturnal periods; medium gray: sunrise and sunset periods; white: diurnal periods).

patch (but not in Meadow patch). This interaction effect is more noticeable between the periods 5–9h (dawn) and 17–21h (sunset; Figure 3; Suppl. material 1: Table S3). In addition, paths were longer during lower ambient temperatures in both habitat patches (Suppl. material 1: Table S3).

None of the path linearity models had a fit superior to the Null model (AIC = 56.4).

Frequency of road crossing by animals

There were no crossing events recorded for any of the radio-tracked voles. The overall expected road crossing percentage in the Meadow patch was 10.2% (Pearson chi-square = 12.25; p-value = 0.0005) while the expected value for the Verge patch was 54.2% (Pearson chi-square = 101.79; p-value = 0.0000; Table 2). This shows that, for both habitat patches, the observed crossing rates were significantly lower than

Table 2. Comparison between the observed and the expected paths through a Pearson chi-square test by patch; for each comparison is also presented the crossing estimate, Chi-square and P-Value.

	Positive Observed crossings	Negative Observed crossings	Positive Expected crossings	Negative Expected crossings	Estimate	Chi-square	P-Value
Meadow	0	108	1190	10485	0.102	12.245	<0.001
Verge	0	83	5640	4485	0.542	101.79	<0.001

Table 3. Comparison between the observed and the expected paths through a Pearson chi-square test by individual with the crossing estimate, Chi-square and P-Value.

Patch	Animal	Positive Observed crossings	Negative Observed crossings	Positive Expected crossings	Negative Expected crossings	Estimate	Chi-square	P-Value
Meadow	A	0	18	254	1641	0.134	2.782	0.095
	B	0	16	275	1370	0.167	3.205	0.073
	C	0	17	1	1644	0.000	0.010	0.919
	D	0	7	147	853	0.147	1.205	0.272
	E	0	14	400	1245	0.243	4.486	0.034
	F	0	14	49	1451	0.033	0.473	0.492
	G	0	13	51	1194	0.041	0.555	0.456
	H	0	9	13	1087	0.012	0.108	0.743
Verge	J	0	12	833	912	0.477	10.893	0.001
	L	0	12	849	596	0.587	16.896	<0.001
	M	0	14	980	520	0.653	25.933	<0.001
	N	0	9	471	774	0.378	5.453	0.02
	O	0	11	626	474	0.569	14.340	<0.001
	Q	0	7	345	500	0.408	4.803	0.028
	R	0	9	843	257	0.766	28.756	<0.001
	S	0	9	693	452	0.605	13.636	<0.001

predicted by chance, although the difference between observed and expected was much higher in the Verge patch (-0.102 for Meadow and -0.542 for Verge; Table 2).

When analyzing crossing events for individual animals, all voles presented road crossing rates lower than expected, although the differences were not statistically significant for most voles from the Meadow patch (Table 3). Accordingly, the expected crossing percentage of paths of individual voles from the Meadow varied between 0.0006% and 24% (mean of 9.7%) with only statistical significance for one individual (Pearson chi-square = 4.49; p-value = 0.034) which occupied a home range near the road verge of the Meadow patch (vole E; Table 3). The expected crossing percentage of paths of individual voles from the Verge patch varied between 37.8% and 76.6% for each vole (mean of 55.7%) with statistical significance for all individuals (all p-values < 0.05; Table 3).

Discussion

Despite the potential positive role of vegetated road verges for biodiversity conservation, they are subject to periodic vegetation removal (by road companies), are linearly shaped, and are bordered by the road surface and, often unsuitable matrix habitat, thus providing challenging conditions for population establishment and persistence. This underlines the importance of fully understanding how road verges affect species of conservation concern, particularly its behavioral patterns such as space use and movements. Our results seem to support the first hypothesis (i), that individuals occupying road verges have smaller home ranges with lower shape complexity. As for movement patterns, the model results did not support the hypotheses that individuals living in the road verge have shorter paths (hypothesis ii), and more linear paths (hypothesis iii). These results suggest that movement behaviour is little affected by the degree of habitat reduction. However, there was an interaction effect between habitat patch and day period for path length, which partially supports the hypothesis that individual movements during high traffic periods (daytime and sunset) are more constrained in smaller habitat patches adjacent to the road (hypothesis iv). Road crossing results do not support the hypothesis that individuals living in smaller habitat patches cross the road more frequently than those in larger patches (hypothesis iv), although it suggests the existence of a strong road-barrier effect for individuals living in road verges.

Differences in space use in the Verge patch

As predicted, individuals occupying the Verge patch showed smaller home ranges with lower shape complexity than those in the larger area (Meadow patch). However, there were no significant differences in core areas, number of core areas and female overlap, as observed in previous studies with other vole species testing social organization over time and space (e.g. Madison 1990, Ims et al. 1992). This seems to indicate that habitat reduction by roads may hinder individual's home ranges, but the characteristics of core areas and social structure are maintained. Although road verges have been associated to a lower nutritional quality of food resources (Santos et al. 2007, Rosário et al. 2008), home ranges with circular shapes (i.e., lowest shape complexity) suggest that road verges might present evenly distributed resources, which tend to minimize energy expenditure, contrasting with heterogeneous distribution of resources in larger patches that originate more complex home ranges (Hiller et al 2016).

Differences in movement patterns in the Verge patch

The path length was similar among both patches. However, there was an interaction between the day period and the habitat patch. This interaction points to longer paths in the period of 5–9h (sunrise) in the Verge patch when compared with the 9–21h period. This has not happened in the Meadow patch. Since traffic intensity is higher during the day (and sunset), animals in Verge patch may have decreased their path length in response to increased traffic as was observed by Chen and Koprowski (2016) in Arizona (USA) with Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*). The higher proximity of animals to the road pavement in the Verge patch, when compared to the Meadow patch, may explain this interaction effect. By being restrained in a smaller habitat patch, voles may be forced to adapt their behavior by decreasing their activity during some periods of the day. There was also an influence of temperature on movement length, with longer path lengths occurring during coolest hours of the day, for both habitat patches. This is confirmed by previous studies on activity rhythms of this species (Pita et al. 2011; Grácio et al. 2017) and can explain why path length seems shorter during midday, since it coincides with higher temperature period. Also, the differences in the vegetation structure between habitat patches (lower abundance of shrubs in the Verge patch) could be another possible explanation for the differences in path length, as Verge patch might offer less protection from avian diurnal predation (e.g., buzzards and kites that are frequently observed along the studied road).

Due to their poor ability to move further away from the road, voles seem to have adapted their movement patterns to accommodate the exposure to the road disturbance. While animals in the Meadow patch showed no significant differences in movement patterns throughout the daily cycle (beyond what would be expected in diurnal animals), in the Verge patch, movement patterns may have changed or even been hindered during at least part of the day. Traffic disturbance could be the reason for the disparity of results between habitat patches, as the changes in the movement patterns coincided with the period of increased traffic (day and sunset periods). This agrees with observations for moose (*Alces alces*), which remain further away from roads during high traffic periods (Neumann et al. 2013).

Road barrier effects

When analyzed at the patch scale, there were significant differences between observed and random paths in both patches. Although results indicates that the voles from both habitat patches avoided the road, this avoidance signal was 5 times stronger in the Verge patch. This explains why most animals from the Meadow patch showed individually non-significant differences in crossing estimates. Thus, the disparity between crossing estimates by animals in the different patches may be explained by the spatial location of home ranges in Meadow patch being further away from the road than in Verge patch. As individuals in Verge patch are restricted to a smaller area, it is more likely that any expected path would cross the road, whereas in Meadow patch, by being further away from the road, this is less likely. This could suggest that voles in Verge patch are more exposed to the barrier effect and thus more prone to local extinction events (Seiler 2001).

Overall, the present study is in accordance with other studies (e.g. McDonald and St. Clair 2004; Grilo et al. 2018), showing that roads can have influence on small mammal space use and movement patterns. The difference in space use and movement patterns between habitat patches may have been caused by traffic disturbance or by the less heterogeneous vegetation structure in the Verge, which may offer less protection against avian diurnal predators, and therefore may promote a different response from the voles during certain periods of the day. While we acknowledge that the number of study patches and individuals, and the particular period of the year considered may limit our inferences to other geographical areas and seasons, we believe that our study highlights the need to recognize in future studies the importance of road effects on the space use and movement patterns of the Cabrera vole and other species that are often associated to road verge habitats.

Main Conclusions

This study suggests that, although road verges can have several potential advantages for Cabrera voles, the small habitat patches typical of verges may restrict vole space use and movement patterns, and even act as a behavioural barrier to vole road crossings. Despite the extensive number of studies about the effect of roads on small mammals, few have focused on the behavioural traits related to individual space use and movement of an endangered species that often occur on road verges, such as the Cabrera vole. Due to the "Vulnerable" status of this species, the present study should be particularly relevant in terms of conservation. The results point to the importance of promoting wide and unrestricted verges for the species conservation. In the present case, it is possible that road crossing structures, such as small culverts, could soften the road-barrier effect, especially in the Verge patch.

Acknowledgements

Prof. Joana Reis from Veterinary Hospital of Évora University (HVUE) gave invaluable support in anesthetizing and handling of the captured voles. We thank Carmo Silva, Sofia Eufrázio, Vânia Salgueiro and Tiago Mendes for helping with captures and telemetry. This study was supported by the projects POPCONNECT (PTDC/AAG-MAA/0372/2014) and LIFE LINES (LIFE14 NAT/PT/001081).

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Supplementary material 1

The effect of habitat encroachment by roads on space use and movement patterns of an endangered vole

Authors: Nelson Fernandes, Eduardo M. Ferreira, Ricardo Pita, António Mira, Sara M. Santos

Data type: Docx file.

Explanation note: Details of predictors analysed and detailed tests and model results.

Link: https://doi.org/10.3897/natureconservation.47.71864.suppl1

Nature Conservation 47: 197–213 (2022)
doi: 10.3897/natureconservation.47.67979
https://natureconservation.pensoft.net

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Are several small wildlife crossing structures better than a single large? Arguments from the perspective of large wildlife conservation

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Academic editor: Cristian Remus Papp | Received 28 April 2021 | Accepted 12 January 2022 | Published 25 March 2022

http://zoobank.org/776CD073-0E1A-493A-87BD-9EB492DECC15

Citation: Helldin JO (2022) Are several small wildlife crossing structures better than a single large? Arguments from the perspective of large wildlife conservation. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 197–213. https://doi.org/10.3897/natureconservation.47.67979

Abstract

Crossing structures for large wildlife are increasingly being constructed at major roads and railways in many countries and current guidelines for wildlife mitigation at linear infrastructures tend to advocate for large crossing structures sited at major movement corridors for the target species. The concept of movement corridors has, however, been challenged and pinching animal movements into bottlenecks entails risks. In this paper, I address the SLOSS dilemma of road ecology, i.e. the discussion whether a Single Large Or Several Small crossing structures along a linear barrier would produce the most benefit for wildlife, using the case of crossing structures for large wildlife in Sweden. I point out risks, ecological as well as practical, with investing in one large crossing structure and list a number of situations where it may be more beneficial to distribute the conservation efforts in the landscape by constructing several smaller crossing structures; for example, when the ecological knowledge is insufficient, when animal interactions are expected to be significant, when the landscape changes over time or when future human development cannot be controlled. I argue that such situations are often what infrastructure planning faces and that the default strategy, therefore, should be to distribute, rather than to concentrate passage opportunities along major transport infrastructures. I suggest that distributing passage opportunities over several smaller crossing structures would convey a risk diversification and that this strategy could facilitate the planning of wildlife mitigation. What to choose would however depend on, inter alia, landscape composition and ecology and on relationships amongst target species. A single large structure should be selected where it is likely that it can serve a large proportion of target animals and where the long-term functionality of the crossing structure can be guaranteed. New research is needed to support trade-offs between size and number of crossing structures. Cost-effectiveness analyses of wildlife crossing structures are currently rare and need to be further explored. Camera trapping and video surveillance of crossing structures provide opportunities to analyse details concerning, for example, any individual biases according to sex, age, status and grouping and any antagonism between species and individuals. Wildlife ecology research needs to better address questions posed by road and railway planning regarding the importance of specific movement routes and movement distances.

Keywords
Mitigation planning, Sweden, SLOSS, wildlife crossing structure

Introduction

Crossing structures for wildlife

One of the most significant ecological impacts of roads and railways are their barrier effects for terrestrial wildlife (Forman and Alexander 1998; O'Brien 2006; Beckman and Hilty 2010; Barrientos and Borda-de-Água 2017). By obstructing movements and, thereby, restricting the access to resources and the opportunities for migration and dispersal, linear infrastructures may inhibit the individual fitness and genetic diversity of wildlife and negatively impact population demography and conservation status. After the emergence and growth of the applied scientific field of road ecology in the last decades (for example. Forman et al. 2003; van der Ree et al. 2015), the barrier effects for large wildlife, such as ungulates and large carnivores, are now well recognised in countries worldwide (Clevenger and Huijser 2011; Wingard et al. 2014; Georgiadis et al. 2015, 2018; Collinson and Patterson-Abrolat 2016; van der Grift et al. 2018; Hlaváč et al. 2019). Accordingly, transport agencies increasingly construct adapted culverts, tunnels and vegetated bridges to provide wildlife with safe opportunities to cross major roads and railways (Iuell et al. 2003; Clevenger and Ford 2010; Rijkswaterstaat 2011; Smith et al. 2015).

Monitoring of over- and underpasses for large wildlife has provided frequent proof that they are used by a variety of species (van der Ree et al. 2007; Smith et al. 2015). In general terms, larger (wider, higher) constructions are used by larger species, by a broader array of taxa and by a larger proportion of target populations (Rodriguez et al. 1996; Clevenger and Waltho 2000; Bhardwaj et al. 2020), although other aspects of their design may affect the frequency of use, such as human disturbances, occurrence of vegetation and cover and siting in relation to preferred habitats (Clevenger and Waltho 2000, 2005; Ascensão and Mira 2007; Glista et al. 2009; van der Ree and van der Grift 2015; Andis et al. 2017).

Despite having recognised both the problem with barrier effects and its potential solution, in infrastructure planning practice, many transport agencies still seem to consider crossing structures for wildlife to entail external or unexpected costs. Accordingly, such constructions have to be argued for on a case-by-case basis and often end up being rather few. In response, environmental planners tend to advocate for as large wildlife crossing structures as possible and put much effort into finding the ideal locations for those crucial constructions. This situation is reflected not least in current European guidelines for mitigation of barrier effects at transport infrastructures; many of these have their focus on methods to identify major wildlife corridors and state ideal rather than optimal dimensions of crossing structures (Iuell et al. 2003; Alterra 2008; Jędrzejewski et al. 2009; Nowak et al. 2010; Vejdirektoratet 2011; Statens Vegvesen 2014; Ciabò et al. 2015; Reck et al. 2018; Hlaváč et al. 2019).

Size vs. number of crossing structures

While crossing structures may be necessary measures to safeguard the connectivity for wildlife across large linear infrastructures, they inevitably create bottlenecks for animal movements, irrespective of location and size. Funnelling animals from larger areas into movement bottlenecks may have a number of ecological disadvantages, for example, increased predation (Little et al. 2002; Mata et al. 2015) or exaggerated social interactions between animals. Moreover, the concept of natural movement corridors has been criticised for lacking solid theoretical and empirical foundations (Simberloff et al. 1992) and that its frequent application in land-use planning satisfies political and economic interests rather than ecological requirements (Van Der Windt and Swart 2008; Shilling 2020). For large terrestrial wildlife, well-defined, predictable migratory paths do occur in some populations (Andersen 1991; Berger et al. 2006; Kauffman et al. 2018), but seem to be the exception rather than the rule to how animals move between areas.

The size is one of the most cost-driving factors for crossing structures and, in the infrastructure planning reality, the cost-effectiveness of measures has to be considered. Wildlife crossing structures, from culverts to viaducts and green bridges, may range in investment cost by orders of magnitude (Sijtsma et al. 2020; see also Fig. 1) and considerable savings can be made if the optimal trade-off is found between number and size of crossing structures with the aim of reaching the maximum infrastructure permeability for wildlife. While some guidelines for wildlife measures at transport infrastructures do acknowledge that a large number of narrow wildlife crossings may be more effective than a single, wide one (Iuell et al. 2003; Jakobi and Adelsköld 2011; Reck et al. 2018), the required cost-benefit analyses are rarely conducted (Sijtsma et al. 2020).

The question of size vs. number of wildlife crossing structures is analogous with that of the so-called SLOSS dilemma in conservation, i.e. the question whether a Single Large Or Several Small protected areas would be more effective for species conservation (Diamond 1975; Simberloff and Abele 1976). That question remains a dilemma as it has no universal answer; the best strategy depends on, inter alia, to what extent the smaller areas share species, on the environmental variability in and amongst areas and on the distance between areas (Simberloff and Abele 1976; Akcakaya and Ginzburg 1991). The SLOSS dilemma of road ecology – the trade-off between single large or several small crossing structures (Karlson et al. 2017) – is likely to share many characteristics with that of protected area designation.

Figure 1. Examples of differently sized crossing structures in Sweden used by large wildlife, with rough estimates of investment costs. The precise costs depend on a number of site-specific factors, and values given are intended to serve as indications. Images by courtesy of Trafikverket and PEAB.

The issue of SLOSS wildlife crossing structures has previously been addressed by Karlson et al. (2017), using a theoretical approach to compare the outcome in model landscapes with different levels of habitat contrast and aggregation. They concluded that in homogenous (low-contrast, low-aggregation) landscapes, a number of smaller crossing structures are better than one large, given that each still meets minimum ecological design criteria. This conclusion derived simply from geometry; with passage opportunities evenly distributed along an infrastructure, the distance to a crossing structure from an average point in the landscape will be shorter. In heterogeneous landscapes, on the other hand, the outcome will depend on the habitat quality in and around the crossing structures; fewer animals would cross through a structure located in low quality habitat. Accordingly, in heterogeneous landscapes, more care must be taken to the location of crossing structures in relation to the habitat requirements of target species.

Aim of the paper

In this paper, I develop the SLOSS dilemma of road ecology using the case of crossing structures for large wildlife in Sweden. Based on ecological and pragmatical arguments, I list a number of situations where it may be more beneficial to distribute the conservation efforts in the landscape by constructing several small crossing structures rather than one or a few large. I argue that the situations described for Sweden are not unique, but may apply to other taxa and geographical regions. I conclude by suggesting how the SLOSS discussion could provide information for planning of wildlife mitigation at linear infrastructures and by proposing some directions for future research in the field.

Planning for crossing structures for large wildlife in Sweden – a case study

Large mammal distributions and movements

Populations of many large mammals are currently relatively strong in Sweden and species such as moose (*Alces alces*), deer (red deer *Cervus elaphus*, fallow deer *Dama dama*, roe deer *Capreolus capreolus*), wild boar (*Sus scrofa*) and large carnivores (wolf *Canis lupus*, bear *Ursus arctos*, lynx *Lynx lynx*) range over large parts of the country (Bergström and Danell 2008; Liberg et al. 2010; Chapron et al. 2014). Natural or semi-natural habitats, such as managed forest, wetland or mountain make up some 80% of the Swedish land area (Gerell et al. 1996). While most large mammals do show some preferences for forested areas, they also use agricultural land and built-up areas, particularly in night-time when the human disturbance is low (Winsa 2008; Godvik et al. 2009; Milleret et al. 2018; Fattebert et al. 2019; Richter et al. 2020) or during seasons with available crop (Thurfjell et al. 2009; Olsson et al. 2011). Accordingly, these species tend to occur in most habitats and most landscapes and their movements are less likely to be strongly funnelled to specific habitat corridors. One exception may be seasonally migratory ungulates in the north (primarily moose and semi-domestic reindeer *Rangifer tarandus*), which follow routes along river valleys and other topographic landscape elements that may be maintained between generations or even decades (Sweanor and Sandegren 1988; Andersen 1991; Singh et al. 2012; Lindberg 2013; St John et al. 2016).

Within the managed boreal forest, ungulates may prefer certain stand types, for example, clear-cuts, young or dense forest stands and linear landscape elements, such as riparian areas and edge zones (Winsa 2008; Thurfjell et al. 2009; Bjørneraas et al. 2011). However, the spatial distribution of forest stands is likely to change over decades, i.e. within the expected lifespan of a bridge or culvert, due to forest growth or management activities. Additionally, in less intensively managed landscapes, habitats are expected to undergo changes due to natural disturbances, succession or climate change, with potential change in animal movement patterns over time as a result.

Animal movements may also change due to sudden human influences in the surrounding landscape, such as new housing, mining or industry and increased outdoor recreation adjacent to crossing structures (Singh et al. 2012). While such developments should be addressed in landscape level physical plans and environmental impact assessment (Clevenger and Ford 2010; Ryegård and Åkerskog 2020), not all can be foreseen during the planning stage of fauna mitigation schemes. Moreover, transport agencies have limited authority over the land use outside the road or railway right-of-way, so the long-term functionality of a wildlife crossing structure depends on the compliance of surrounding landowners and land users.

Extensive site-specific empirical data on wildlife movements are in short supply, in Sweden as in other countries (Clevenger and Ford 2010; Helldin and Souropetsis 2017). Identification of movement corridors – which is often required in the planning practice – has to rely on the distribution of natural or wildlife habitat, wildlife accident data or expert opinion (van der Grift and Pouwels 2006; Clevenger and Ford 2010; Olsson et al. 2019). However, such indirect approaches have their flaws (Clevenger and Ford 2010; Helldin and Souropetsis 2017; Sjölund et al. 2020) and the true spatial distribution of wildlife movements remain obscure, with few and localised exceptions.

Some Scandinavian mammals are territorial, amongst these being roe deer and large carnivores (Linnell and Andersen 1998; Mattisson et al. 2011) and may, therefore, expel other individuals of the same species and gender from a crossing structure. Similarly, interspecific competition occurs frequently amongst ungulates (Latham et al. 1997; Feretti 2011; Pfeffer 2021; La Morgia et al. in review) and amongst carnivores (Mattisson et al. 2011), which may lead to a dominant species effectively expelling subdominants. Although such "ecological plugs" are probably only partial, they could inhibit the movement of subdominant individuals or species through a crossing structure.

In addition, game and prey species, such as ungulates, may adapt their spatial distribution, habitat choice and activity patterns to the risk of being hunted or predated (Cromsigt et al. 2013; Lone et al. 2014, 2015; Zbyryt et al. 2018). Similarly, hunting and poaching are main causes of mortality for large carnivores in Scandinavia (Andrén et al. 2006; Liberg et al. 2012) and, consequently, these species avoid human interaction (Ordíz et al. 2011; Carricondo-Sanchez et al. 2020). Hunting in the direct vicinity of over- or underpasses occurs in Sweden (own observations), but how frequent this happens is not known. Incidents of natural predation on ungulates near wildlife crossing structures have been reported, but appear to be rare (Little et al. 2002; Plaschke et al. 2021). Yet, only the presence of ambushing predators or hunters in the area may temporarily inhibit the structure´s effectiveness for target species (Mata et al. 2015).

Where and when may several small crossing structures be better than a single large structure?

This Swedish case of large wildlife ecology describes a number of situations that – each individually and all taken together – suggest that distributing conservation efforts on several small crossing structures may perform better than a single large crossing, namely:

- In relatively intact or homogenous landscapes, where animal movements are dispersed.
- Where animal movement routes are expected to gradually change over time due to landscape changes.
- Where future human development cannot be controlled and natural habitats surrounding crossing structures may suddenly deteriorate.
- Where animal movement habits simply are not known.
- When wildlife mitigation needs to target multiple species with different habitat choices and no ideal site can be appointed.
- When target species are territorial or competitors and there is a risk that some individuals or species monopolise the area in and around the crossing structure.
- When target species are sensitive to hunting, poaching or predation and enemies (human or natural predators) may ambush at sites where movements of prey are pinched.

Current planning for large wildlife crossing structures

The Swedish Transport Administration (STA), the responsible manager for the public road and railway network in Sweden, currently works along a strategy for landscape connectivity for large wildlife that partly take a SLOSS approach. According to the national ecological standards (Trafikverket 2019), safe passageways for large mammals (ungulates and large carnivores) should be provided at a maximum distance of 6 km along all major roads and railways; a requirement based on the assumption that large mammal movements are ubiquitous and dispersed or at least ought to be so. Via supporting documents (Seiler et al. 2015 and references therein), the standards point out moose and roe deer as focal species (*sensu* Lambeck 1997); moose, in particular, because it is supposedly one of the most demanding large mammal species in Sweden when it comes to crossing structure design and one of the most problematic when it comes to wildlife-vehicle accidents and barrier effects.

The standards describe a range of larger to smaller crossing structures as suitable for moose and roe deer (Seiler et al. 2015; Trafikverket 2021a, 2021b) and it also takes into account the predicted wildlife connectivity provided by bridges constructed for other purposes, for example, watercourses, trails and low-traffic roads (Seiler et al. 2015). Accordingly, the standards provide a framework allowing, but not requiring, that trade-offs are made between functionality and number of crossing structures on the level of a longer road section or an infrastructure network.

Due to the lack of an explicit SLOSS approach in the planning for large wildlife mitigation, opportunities for better ecological function and more cost-effective mitigation measures may still be missed. For example, regional differences in data availability, plasticity in animal movements or target species for mitigation would imply different output depending on the region. In northern Sweden, investing in few large crossing structures at major migration routes may be warranted. Thorough ecological data should be collected and compiled to identify the ideal sites for these crossing structures and considerable efforts should be made to secure their long-term effectiveness through adapted management of the surrounding landscape. In more southern parts of the country, however, sufficient overall permeability of infrastructures may be achieved by several smaller crossing structures, including non-wildlife bridges which tend to be plentiful along most major roads and railways.

Discussion

Implications for the planning of wildlife mitigation

Though based on the specific case of Swedish large wildlife, I believe that many of the situations described above are what infrastructure planning often faces. Site-specific knowledge of animal movement patterns tends to be sparse (Clevenger and Ford 2010) and, in many biomes, it is likely that movement routes will change over time due to natural landscape dynamics or anthropogenic impacts. With mitigation schemes targeted to multiple wildlife species, it will be difficult to find the perfect site for a crossing structure and target species are likely to interact at the site. In these cases, the connectivity delivered by each individual crossing structure cannot be guaranteed and distributing investments over several structures would convey a risk diversification. Moreover, this is not only an economical or practical consideration; transport agencies should aim at allowing dispersed or flexible animal movements wherever they occur and avoid the ecological predicaments that pinched animal movements may entail. In principle, these aspects could apply similarly to other animal taxa that are frequent targets for crossing structures at roads and railways, such as medium-sized mammals and amphibians (Iuell et al. 2003; Langton 2015).

Following this line of argument and with support from the results from the modelling approach adopted by Karlson et al. (2017), I suggest a default strategy for transport agencies to construct several small crossing structures rather than concentrating the passage opportunities along major transport infrastructures to a single large structure. What to choose should, however, depend on the context: for example, the degree of habitat heterogeneity (aggregation and contrast), habitat predictability, the dimension requirements of target species and the spatial overlap between species (Mata et al. 2005; Karlson et al. 2017). Single large structures may be selected at sites where it is likely that the crossing structure can serve a large proportion of target animals (species and individuals), for example, where animal movements follow distinct routes and where target species have a large overlap in habitat requirements and little social or trophic interference. However, going for a single large structure should require that the long-term functionality of the crossing structure could be guaranteed, for example, in areas that are legally protected or when solid agreements can be made with adjacent land-users to protect the crossing structure and its surroundings from significant impacts. There may be situations where an intermediate or mixed (single large combined with several small) approach may be the best choice.

A planning strategy aiming at several smaller crossing structures rather than a single large structure could facilitate the planning of wildlife mitigation in a few ways. It may not be necessary to put as much effort into finding the best siting or design of each crossing structure, which may save both time and costs at early planning stages. Instead crossing structures may have a standard design and be spaced out on pre-defined intervals along the infrastructure or where the ground conditions (topography and soil) are ideal from a technical perspective. Non-wildlife bridges or culverts used by wildlife may also be included in the wildlife mitigation plan. While the goal of wildlife mitigation plans should not be to save money, but to minimise wildlife-traffic conflicts, the SLOSS issue will open the question of how to get the most out of available investments or how to reach conservation goals with a minimum of cost and it may, therefore, help the matter by redirecting the focus in planning from costs to savings.

Some implications for future ecological research

Trade-offs between size and number of crossing structures in wildlife mitigation schemes may require that road ecology research take a somewhat different angle than that currently prevailing. Research and monitoring of over- and underpasses during the last decades have provided a basic understanding of how well different type of structures correspond to the demands of different species or taxa (Jędrzejewski et al. 2009; Clevenger and Ford 2010; Smith et al. 2015), but comprehensive comparisons of structures of different size and design are still few (but see Clevenger and Waltho 2005; Mata et al. 2005; Taylor and Goldingay 2010; Cramer 2012; Bhardwaj et al. 2020; Sijtsma et al. 2020). Moreover, the costs for the constructions, including any costs for planning, traffic diversion during construction, long-term maintenance etc., are rarely integrated into the analyses (Sijtsma et al. 2020). Seiler et al. (2016) and Sijtsma et al. (2020) point out some directions for how cost-effectiveness analyses of wildlife crossing structures can be set up, but the field needs to be further explored. Monitoring of wildlife-use of crossing structures should be conducted following a standardised protocol to be able to make a just comparison of the performance of a range of crossing structures and to be able to add new monitoring results over time to a global analysis (Helldin and Olsson 2015).

A strategy to construct several small crossing structures should entail an increased demand for research on how to make also narrower crossing structures more functional for wildlife, for example, by adapting vegetation and limiting human disturbance. However, squeezing down the size of crossing structures would also mean approaching a lower limit for functionality and, in the light of this, a much better understanding of the ecology of narrow crossing structures is needed.

I suggest a stronger emphasis in monitoring of crossing structures, not only on how different species use them differentially (such as described by, for example, Cramer 2012; Mata et al. 2015), but also differences between animal categories within species, for example, between sexes and ages, individuals of different status or condition and individuals in groups of different size and composition. It is likely that different animal individuals or categories show differences in vigilance and sensitivity to disturbance (Liley and Creel 2008) and crossing structures that deter certain categories of animals are less likely to provide functional connectivity for the population, irrespective of the absolute number of individuals using the structure.

To this, we need better knowledge of what happens between animals at crossing structures, for example, predation risk (real and perceived), interference competition, territoriality, dominance and other antagonistic types of behaviour that can expel some target animals from the sites. The well-developed methods, using camera traps and video surveillance of crossing structures, provide opportunities for studying both animal categories and types of behaviour to a larger extent than is currently done.

Finally, I call for more efforts in wildlife ecology research to develop the knowledge of animal movements, to specifically address the questions posed by road and railway planning, of movement routes (importance of certain routes, their stability over time and reliable methods to map them) and potential movement distances along fences to find safe passages (Bissonette and Adair 2008). While this has been studied for some large and charismatic species (e.g. moose in Sweden), these aspects are largely unknown for most species, including important target species for wildlife crossing structures.

Acknowledgements

This paper is based on conference presentations held at ICOET (Raleigh, NC, USA, 20–24 September 2015), ACLIE (Skukuza, South Africa, 10–15 March 2019) and IENE (Online, 12–14 January 2021). I thank Manisha Bhardwaj, Lars Nilsson, Heinrich Reck and academic editor Cristian Remus Papp for helpful comments on earlier drafts of the paper. The writing was financed by the Swedish Transport Administration, through the research project TRIEKOL (https://triekol.se/).

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Nature Conservation 47: 215–233 (2022)
doi: 10.3897/natureconservation.47.73710
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Sensitivity mapping informs mitigation of bird mortality by collision with high-voltage power lines

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Academic editor: Manisha Bhardwaj | Received 31 August 2021 | Accepted 31 January 2022 | Published 25 March 2022

http://zoobank.org/8B24CDB2-6402-4BEE-9450-79735E7F73AC

Citation: Paquet J-Y, Swinnen K, Derouaux A, Devos K, Verbelen D (2022) Sensitivity mapping informs mitigation of bird mortality by collision with high-voltage power lines. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 215–233. https://doi.org/10.3897/natureconservation.47.73710

Abstract

Mapping the relative risk of impact on nature by a human infrastructure at a landscape scale ("sensitivity mapping") is an essential tool for minimising the future impact of new development or for prioritising mitigation of existing impacts. High-voltage power lines ("transmission lines") are known to increase bird mortality by collision. Here we present a method to derive a high resolution map of relative risk of transmission line impacts across one entire country, Belgium, from existing bird distribution data. First, all the bird species observed in Belgium were systematically assessed using literature and casualty records to select those to be included in the sensitivity map. Species were selected on the basis of their intrinsic susceptibility to collision and the conservation relevance of avoiding additional mortality for that species in Belgium. Each of the selected species was included in one or several spatial layer constructed from existing data, emerging from citizen science bird monitoring schemes. The resulting 17 layers were then combined into one final sensitivity map, where a "risk score" estimates the relative collision risk across Belgium at a 1×1 km resolution. This risk score is relatively robust to the subtraction of any of the 17 layers. The map identifies areas where building new transmission lines would create high risk of collision and, if overlapped with existing power lines, helps to prioritise spans where mitigation measures should be placed. Wetlands and river valleys stand out as the most potentially dangerous areas for collision with transmission lines. This sensitivity map could be regularly updated with new bird data or adapted to other countries where similar bird data are available.

Keywords
Belgium, bird, mitigation, sensitivity mapping, strategic planning, transmission lines, waterbird

Introduction

Power lines have been identified as one of the major causes of man-induced mortality in birds (Loss et al. 2015). Direct mortality by collision with overhead wires is known to occur with any type of lines but has been especially studied for the so-called transmission grid, or high-voltage power lines (Bernardino et al. 2018), while medium-voltage lines (the so-called distribution grid, from 1 to 30 kV in Belgium) additionally induce electrocution risk for larger birds (Guil and Pérez-García 2022). Flying birds might collide with wires especially under low visibility conditions during crepuscular or nocturnal movements or during bad weather. Despite the difficulties inherent to such quantification, casualty numbers are undoubtedly very high. An annual estimate of 8–57 million birds killed by collision with transmission lines was made for the USA alone (Loss et al. 2014). Despite these impressive figures, only in very few instances has a link been established between population dynamics (e.g. the decline of a given population of a single bird species) and power line mortality (Bernardino et al. 2018; D'Amico et al. 2018). Possible demographic impacts mostly concern endangered species: 12% of the entire Blue Crane *Anthropoides paradiseus* population was estimated to be killed annually by collision with power lines in South Africa (Shaw et al. 2010). On the other hand, low mortality rates do not mean that no significant impact exists, e.g. by historical depletion of local populations (Ascensão et al. 2019). Even if a population effect of power line mortality cannot be readily established, it is important to reduce this human-induced mortality as much as possible in an attempt to minimise the impact of this ever-growing infrastructure. An estimated 65 million kilometres of medium- to high-voltage lines was already covering the world a decade ago (Jenkins et al. 2010). With the anticipated change towards a more decentralised production, transmission grids are expected to grow constantly in the near future (Barov 2011; Bio Intelligence Service 2012; Biasotto and Kindel 2018). Therefore, minimising bird fatalities on both existing and future power lines is critical and a prerequisite to increase public support for such a development.

Construction of underground lines is the best solution to prevent any further casualties. However, this is not always possible from a technical point of view or economically viable, especially when existing aerial lines have to be brought underground. Wire marking in order to increase visibility of the cables for birds is therefore the most widespread measure to reduce mortality. A recent review of wire-marking effectiveness (Bernardino et al. 2019) concluded that mortality rates on average are reduced by half (95% confidence interval: 40.4–58.8% across 35 studies).

Strategic planning has been proposed as a first necessary step to mitigate power line impact, both to avoid building new power lines in vulnerable areas and to act on mitigation measures on existing dangerous lines (Bernardino et al. 2018; D'Amico et al. 2018). Sensitivity mapping is routinely used in several instances of interaction of fauna with human infrastructure as a basic planning tool when new infrastructure has to be built (Allinson et al. 2020). It also helps to prioritise where mitigation measures should be taken (European Commission 2018). However, there are very few examples of sensitivity maps for a countrywide transmission line network (but see (D'Amico et al. 2019) for Portugal and Spain). Here, we present a method based on large-scale citizen science data to map the relative collision risk associated with transmission lines for birds, for any given location in Belgium. We also propose a prioritisation process to mitigate the risks associated within the existing 5,614 km of aerial transmission lines (70–380 kV) in Belgium.

Identifying existing transmission lines presenting a high collision risk for birds or drawing attention to potentially harmful future lines can be attempted at a regional scale by looking at some natural habitat features or spatial characteristic (Martín Martín et al. 2019), but mapping areas where collision-susceptible species are particularly abundant would always give a better assessment of the risk, especially on a larger scale. Indeed, not all species are facing the same risk when confronted with power lines since some species are more prone to collisions than others (Bevanger 1998). These susceptible species could congregate in large numbers at specific places used on a daily basis, like communal night roosts or breeding colonies, hence increasing the number of potential casualties around those areas. Besides the intrinsic probability of collision for a given species, the conservation value (for example, their IUCN status) or demographic sensitivity to higher adult mortality could also guide the choice of lines to be targeted for mitigation.

The building of the collision risk map in Belgium followed several steps. First, a list of bird species prone to collision with power lines has been compiled based on a review of the literature and casualty records in Belgium. This list was then matched with available recent data on bird distribution and abundance, provided by different schemes of large-scale bird monitoring and a citizen-science portal. Several layers of spatial information on birds were then combined using a scoring system to create a sensitivity map at a resolution of 1×1 km. When overlapped with the existing transmission line network, this map highlights power line spans presenting high collision risk for birds and is now used by the transmission system operator in Belgium, Elia, to define priority sectors for mortality surveys and, more importantly, mitigation actions. Furthermore, the risk map allows for the planning of new developments of the transmission grid minimising collision risk, but not precluding the necessity of environmental impact assessment to detect possible collision issues before any new line construction.

Methods

Study area

Belgium is a low-lying country in North-Western Europe, characterised by a landscape gradient ranging from densely populated flat areas in the northern part, largely occupied by intensive farmland and urban areas, to hilly parts in the South, culminating slightly under 700 m, with a more forested and rural landscape. Including rare and vagrant species, but excluding introduced or escaped species, about 460 different wild bird species have been reported in Belgium. Although a small and densely populated country, Belgium hosts no fewer than 184 regular breeding bird species, of which 62 are of European Conservation Concern (BirdLife International 2017). During the winter, waterbird populations of international importance (several species of geese and ducks) are observed, especially in Flanders. For example, the coastal polder complex between Bruges and Ostend is home to 30% of the total biogeographic population of Pink-footed Geese *Anser brachyrhynchus* (Devos and Kuijken 2020). On average, an estimated 374,000–594,000 waterbirds -gulls not included- winter in Belgium, mostly in Flanders (Paquet et al. 2019). Due to its central position in Europe and along the southern edge of the North Sea, millions of birds also travel across Belgium during prenuptial and postnuptial migrations, some of them even without a stop or roosting only for a few hours or days.

Belgium has a long industrial history and is a very densely populated country, equipped with a dense power line network: 5,614 km of aerial high-voltage lines (voltage of 70–380 kV, here after "transmission network") are managed by Elia, the transmission system operator for Belgium, additionally to more than 5,000 km of aerial medium voltage power lines managed by several electricity distributors (Synergrid 2022). The medium-voltage transmission network (30–36 kV) is largely underground. The density of aerial transmission lines in Belgium (about 18 km/100 km^2) is similar to the one in France but higher than in Spain (about 8.3 km/100 km^2) and in Germany (about 9 km/100 km^2; Data: ENTSO-E). In the present study, we focused only on the transmission network, for which a detailed map in vectorial format was provided by Elia. The vectorial format of the transmission network is composed of more than 22,000 linear segments of lines between two pylons (named "spans" in the rest of the study). Spatially explicit vectorial data on the distribution grid for the whole of Belgium was not available for this study.

Sensitivity map development

The development of the collision-risk map followed the general guidance for wildlife sensitivity mapping (Allinson et al. 2020), which was established primarily for renewable energy development but is also relevant for any potentially impactful large-scale infrastructure.

Identification of susceptible bird species

Several criteria were used to select bird species that need to be considered as prone to collision with power lines (those species are named "susceptible species" in the rest of this study), for which we therefore need to include information about numbers and distribution in the next steps of this process.

The species list that we considered (Suppl. material 1: Table S1) is the reference list used in the reporting under Article 12 of European Union Directive 2009/147/EC, known as the "Birds Directive". This list follows the taxonomy of BirdLife (BirdLife International 2021) and contains all the breeding bird species, the species that winter in large numbers and some abundant passage migrants in Belgium. Intrinsic susceptibility to collision of individual bird species was evaluated. Not all bird species are equally susceptible to collision with the horizontal cable structures; birds with poor manoeuvrability, i.e. small wings related to body weight, are more prone to collision (Bevanger 1998). Other factors like poor eyesight may also play a role (Martin and Shaw 2010; D'Amico et al. 2019). However, some species groups which are expected to present a low collision risk given their body aspect or physiology are frequently encountered as victims: this is the case for gulls, probably because of their social behaviour and frequent movements in crepuscular conditions when commuting between their feeding grounds and their communal nocturnal roosts (Bevanger 1998). Based on these studies, several lists of collision susceptible species have been published (Bern Convention on the Conservation of European Wildlife and Natural Habitats 2004; Prinsen et al. 2011) and these lists were used as a basis for our own sensitive-species list.

In order to optimally adapt our approach to our local conditions, information about collision frequency in Belgium was also examined. Statistics of bird casualties resulting from probable collision cases with power lines were taken from two sources: Firstly, 719 cases of dead birds found opportunistically under high-voltage power lines recorded in the most popular nature recording platform in Belgium (named Waarnemingen.be in Dutch and Observations.be in French) were examined. This relatively high number of cases is due to an active promotion campaign since 2016 among the public of nature conservation organisations to record such casualties. From this list of 91 species, we retained those with more than 4 cases as being susceptible to collision (Suppl. material 2: Table S2). Secondly, a wounded bird found under high-voltage power lines recorded by wild bird care centres in Belgium was used in the same way (Suppl. material 2: Table S3) to refine the list of susceptible species. By this process, bird species from Belgium were classified into three "collision susceptibility" categories: 0 – Null, almost never cited in mortality studies or in review, never found as victims in Belgium; 1 – Sometimes cited in studies as found injured or dead, but not regularly in Belgium; 2 – Regularly cited in studies or encountered in Belgium as injured or dead by collision with power lines (see Suppl. material 1: Table S1, column J).

Along with the concept of susceptibility to collision, the "conservation relevance" of preventing collision was considered for each species. If the conservation status of a species is already degraded, any supplementary mortality is important to avoid. The most recent regional red lists of endangered birds in Wallonia, Flanders and Europe (Devos et al. 2016; BirdLife International 2021; Paquet et al. 2021) were used to classify the species according to their conservation relevance: in Belgium: 0 – not red listed in any of the three lists considered no; 1 – listed as "Neath-threatened – NT" in at least one of the three lists; 2 – Red listed (at least Vulnerable) in at least one of the three lists. A few species were also listed as "2" because Belgium is hosting an important part of the global population (wintering arctic geese); in that case, reducing mortality in Belgium is also of conservation interest.

Susceptible species (value of 2 for that criteria) and of high relevance for conservation (value of 2 for that criteria) were retained for building the risk map thanks to spatially explicit information about that species (the "spatial layers"), but some exceptions are to be noted: waterbird species often congregating in large numbers or in large communal roosts in winter and migrant birds known to fly over Belgium in very large numbers, sometimes a significant part of the overall European population, such as for the Common Crane *Grus grus* (Kever et al. 2018). All these exceptions are detailed in Suppl. material 1: Table S1 (column N).

Compiling and preparing the bird spatial layers

In order to capture the actual spatial risk of collision for a selected species within the collision risk map, different types of geographical information were used, according to distribution patterns of the species and the behaviour increasing the risk. For the selected species with a diffused distribution pattern across the country, the relative bird density was calculated at high spatial resolution (1×1 km). Bird species which are naturally concentrated on a few sites e.g. waterbirds during wintering or migration period were treated differently. For those species, using site perimeters, we evaluated the relative importance of these sites using individual numbers of each species regularly counted inside these perimeters. A special case is the social species. They breed or roost together in relatively small areas, sometimes in very large numbers. However, they can also disperse over larger areas to forage. The social congregations add a supplementary risk of collision because of the commuting habits for many birds at the same time. Therefore, the spatial location of roosts and breeding colonies was used, rather than their dispersed distribution when foraging.

Table 1 is describing the different bird layers used in the compilation of the collision risk map. Some susceptible species are treated in more than one geographical layer (see Suppl. material 1: Table S1); this could be the case if a species has a breeding population at risk but also a wintering population that congregate in roosts or in important wintering sites for waterbirds. Some layer types are included in the collision risk map as one synthetic layer for several species, while others are declined in several individual layers, one for each species (for further explanation see Table 1).

Here we describe how each of the spatial layers was derived from the raw data. Bird data from the period 2010–2019 were used, except when mentioned differently.

"Important waterbird sites" were derived from mid-monthly counts of wintering waterbirds carried out in Belgium for several decades by hundreds of volunteers (Devos et al. 2019; Jacob et al. 2019). For this spatial layer, Flanders and Wallonia administrative regions were considered separately, as we wanted to assess the importance of the sites at the regional (and not national) level. Each participant counted all the waterbirds present from a specific wetland (or watercourse) on a specific weekend (the closest to the 15th of the month from October to March in Flanders and from November to

Table 1. Description of the spatial layers containing bird distribution or abundance information used in sensitivity mapping.

Bird layer type	spatial information type	Explanation	Number of layers included in the collision risk maps	Species concerned (see also Suppl. material 1: Table S1)
Important waterbird sites	Site perimeters and distance buffer around these sites (several species in one synthetic layer; see table 2 for the buffer distances)	Layer based on regular surveys performed at specific sites, during which all present waterbirds are counted. Each site may be used by several sensitive species and the relative risk associated with the sites depends on the number of species and individuals regularly seen at the site, compared to the regional estimated population of those species.	1	48 species of wintering waterbirds
Important roosts	Buffers around a point location (several species in one synthetic layer; see table 2 for the buffer distances)	These layers are based on the distance from a specific location (point) where a colony or a roost of a sensitive species is established. The closer a colony or roost is to a power line, the higher the collision risk, because of the flight trajectory to and from the site.	1	10 sensitive species regularly forming roosts
Important colonies			1	11 sensitive species breeding in colonies
Foraging goose areas	Presence or absence of each of the considered species at a 1×1 km spatial resolution	Maps at 1-km^2 resolution indicating the presence or absence of sensitive species, estimated by a spatial model constructed on the basis of raw data of species presence (extracted from citizen science data portals; see text) combined with environment variables. Sensitive species are deemed 'present' in a given 1-km^2 area if the probability of occurrence of the species (estimated by the spatial model) is above a cut-off value. The use of spatial modelling reduces the risk of bias associated with observers' tendency to visit certain locations and the lack of data in other locations, where few people are recording birds.	3	Goose species wintering in large numbers: Greylag, Pink-footed and Greater White-fronted Goose
Widespread breeding birds			5	5 species of widespread breeding birds (Grey Partridge, Green Woodpecker, Black Woodpecker, Middle Spotted Woodpecker, European Turtle Dove)
Woodcock areas			1	Areas where displaying Eurasian Woodcock are present
Plover group areas			3	Charadriidae species with a tendency to form large groups in very open countryside: Eurasian Dotterel, Golden Plover, Northern Lapwing
Rare bird areas	Number of rare breeding species in 1×1 km square (several species in one synthetic layer)	Maps at 1-km^2 resolution with a count of the number of species (in our case, rare breeding bird species) recorded in that cell.	1	22 species of susceptible rare bird with high conservation value
Migration corridors	Low resolution very large perimeters (several species in one synthetic layer)	Very low-resolution maps of the main 'corridors' for large numbers of migrant birds in transit	1	Migration corridors for general migrants (coastline) and two very abundant migrants: Woodpigeon and Common Crane

February in Brussels and Wallonia). Maximum counts per winter, for each species and each site, were calculated. The regional wintering population for each species was estimated using a multiple imputation method to account for missing values (Onkelinx and Devos 2019). Only species with a mean regional population of at least 10 individuals were taken into account. To assess the relative importance of a counting site, the total number of individuals (all species together) and the relative importance of the site population for a given species were considered. For each species, the winter maximum for any given site was compared with the regional population estimate. A site is deemed as "fairly important" If between 100 and 1,000 individuals are regularly counted. A site was deemed “important” if 2% of the regional population of at least one waterbird species or more than 1,000 individuals (all species taken together) are regularly recorded. A site was deemed “very important” if 15% of the regional population of at least one species is regularly recorded (Everaert et al. 2011). Here, “regularly” means at least half of the years in which one count was available (some sites were not counted every year). Non-indigenous species and gulls were excluded from all calculations here.

“Important roost or colonies” counts were extracted from the databases of coordinated counts of roosts and colonies maintained by the Research Institute of Nature and Forest in Flanders and Natagora in Brussels and Wallonia. These data were complemented by records extracted from the main nature observations recording portals used by birdwatchers in Belgium, named www.observations.be in French and www.waarnemingen.be in Dutch (Paquet et al. 2013). Colonies and communal night roosts can be specifically recorded in this data portal so that all relevant records can be easily extracted. Communal roosts are defined as “very important” if more than 1,000 individuals. or at least 2% of the regional population, are counted in at least half of the available counts during the period 2010–2019. They are deemed as ‘important’ if between 100 and 1,000 individuals are regularly (i.e. for half of the available counts) counted. Colonies were defined ‘important’ if 10 to 100 breeding pairs are regularly counted (i.e. at least 50% of the available counts; when several counts are available for one season, the highest count is taken into account), and ‘very important colonies’ if more than 100 breeding pairs are regularly recorded or if it holds at least 2% of the regional breeding population.

Layers of presence-absence of the considered species at 1 km^2 resolution were obtained by spatial modelling. Observational data for the target species were extracted from the portal www.observations.be/www.waarnemingen.be during the period 2012–2019. To model the distribution of the species considered at a resolution of 1×1 km, 20 environmental variables were calculated for each grid cell of 1×1 km across Belgium. These variables describe land use (calculated from the 2006 version of the CORINE land cover map, published by the European Topic Centre on Land Use and Spatial Information) and bioclimatic variables calculated from the WordClim dataset (Hijmans et al. 2005). MaxEnt, a presence-only technique widely used in distribution work (Phillips et al. 2006), was used to model the presence-absence of the considered species. MaxEnt uses the square where the focus species was observed (redundant observations in the same square are discarded) as the training dataset for modelling the relationship between the presence of the species and its environment as described by the 20 variables. The projected result of the model is a map estimating the probability of occurrence of the target species (ranging from 0 to 1) for every 1×1-km square in the model’s grid. The model was created based on 75% of the data, leaving out 25% for validation. This modelling procedure was repeated 10 times, with the final model providing the average of the 10 repetitions. A species is considered ‘present’ in a given square if the probability of occurrence is above a certain cut-off value. This cut-off is proposed by MaxEnt and corresponds to the probability value for which the omission rate is closest to 20% (meaning that the model omits 20% of the actual occurrence in the validation set). This should help to keep the risk of false negatives (stating that the species is absent when it is actually present) at around 20% while minimising the total range predicted for the species (and therefore minimising the risk of false positives). Observational data used as raw data in these modelling procedures were selected to correspond to the behaviour of the targeted species (i.e. territorial behaviour for breeding bird species, large groups for foraging geese). If the raw data used to build the model corresponds to a particular criterion (i.e. 'groups larger than 10 individuals'), then the model also reflects the chance of presence of the same form of bird presence (groups rather than just the simple presence of an exemplar).

The list of species identified as being prone to collision with power lines includes several rare breeding bird species. For some species, all known breeding sites are monitored each year. Point records of breeding rare birds were extracted from data portals; records were selected on the basis of breeding evidence given by the observers (i.e. a territorial behaviour, the presence of a nest or pulli, or behaviour indicating a nest). The number of breeding species of this particular list for each 1×1 square in Belgium was retained for the layer type "rare breeding bird".

Mapping specific corridors for seasonal bird migration is especially difficult in a low-lying country. While in mountainous areas clear migrant funnels can be observed, Belgium lacks such strong geographical bottlenecks. As a result, millions of migrant birds fly over the country, crossing a wide area each year. However, some concentrations of migrating birds are observed along the North Sea coastline or along some river valleys. To consider migration in a layer, we started from migration corridors already defined for wind-farm sensitivity mapping in Flanders (Everaert et al. 2011) and we added approximated corridors for the main migration of the Common Crane *Grus grus*, known to migrate in rather well-defined corridors, and one of the most abundant migrant birds, the Wood Pigeon *Columba palumbus*, as deduced from migration counts recorded in the portal trektellen.org (Troost and Boele 2019).

Combining bird layers into a risk map

The bird layers were combined into a risk map using a scoring system (Table 2), with the intention of providing an assessment of the relative risk of bird collisions, in other words 'weighting' spatial units in relation to bird collision risk with power lines. As explained above, we hypothesised that the most detrimental power line effects would be close to important waterbird areas, especially roost sites and colonies, as they involve regular movements of large numbers of birds entering and leaving these areas. We also postulated that focusing on mitigation efforts for lines crossing sensitive rare bird areas would be relevant, as it makes sense in terms of concentrating on conservation measures, given that regional authorities as well as nature-conservation organisations are often already investing in these areas to protect target species. Other sensitive species, like widespread breeding species and migrating birds in certain corridors, are also present around some power lines but because power lines probably pose a 'diluted' risk for these species, we advocate handling these factors only as a secondary priority criterion.

Table 2. Priority scoring system for the spatial units in the final map.

Spatial layer considered (Table 1)	Distance buffer from the site				
	Inside the site	Less than 1 km	Between 1 and 3 km	Between 3 and 5 km	Over 5 km
Important waterbird site	If very important, 30; if important, 25; if fairly important, 20	14	9	4	0
Important roosts	If very important, 25; if important, 20	14	9	4	0
Important colonies	If very important, 25; if important, 20	14	9	4	0
	(no buffer considered below)				
Rare-bird area	10 points for an area with one rare species, 20 for an area with two or three rare species, 25 for an area with four or five rare species, and 30 for an area with more than five species				
Migration corridor	8 points if inside, 12 if it is the coastal corridor				
Plover staging area	5 points for each of the three species, when presence cut-off is reached				
Widespread breeding bird	4 points for each species, when presence cut-off is reached				
Woodcock area	4 points if Woodcock presence cut-off is reached				
Geese foraging area	5 points in the areas of occurrence defined by the spatial models				

All these considerations are reflected in the scoring system. The bird layers and the score system were combined, adopting the following procedure. We used a regular 31,472 km^2 grid covering Belgium – in fact, the same 1×1-km grid used to build the bird layers in Table 1. The highest possible score for a given layer intersecting each square was selected for that square and summed over all layers. For the score depending on the distance to waterbird sites, the distance from the centroid of the square to the nearest important site was used. Therefore, each 1×1-km^2 square received a final score made up of 17 sub-scores corresponding to all the possible bird layers.

Checking the risk map robustness

The importance of the different spatial layers and their effect on the final risk score of the grid cells was calculated by comparing the results from the complete risk map with the map resulting from reduced maps in which a single data layer was removed. Since the risk map is designed to identify the most vulnerable locations, the main interest of the reduced risk maps is to study how consistently these vulnerable locations are identified when removing a single data layer from the global risk map. To examine this, the grid cells within the top 10 percentile highest-risk scores were identified, next we examined how many of these grid cells were also classified as among the top 10 percentile most dangerous in each of the reduced risk maps.

Results

The list of susceptible species to be considered for collision risk with transmission lines amounts to 83 bird species in Belgium (see Suppl. material 1: Table S1 for the complete list). This represents 38.4% of all regularly observed bird species in Belgium. Thanks to regular coordinated monitoring of wintering waterbirds, colonial breeding birds and some socially roosting species, together with a very popular bird recording system (about 2 million bird records in Belgium every year), a large number of data could be used to draw the 17 thematic layers (all presented as Suppl. material 4: Figs S1–S17).

The application of the scoring system resulted in a map at 1×1 km spatial resolution for collision risk with power lines for Belgium, presented in Fig. 1. This map is independent of the presence of actual power lines; it represents a hypothetical risk based on the additive presence of the identified sensitive species.

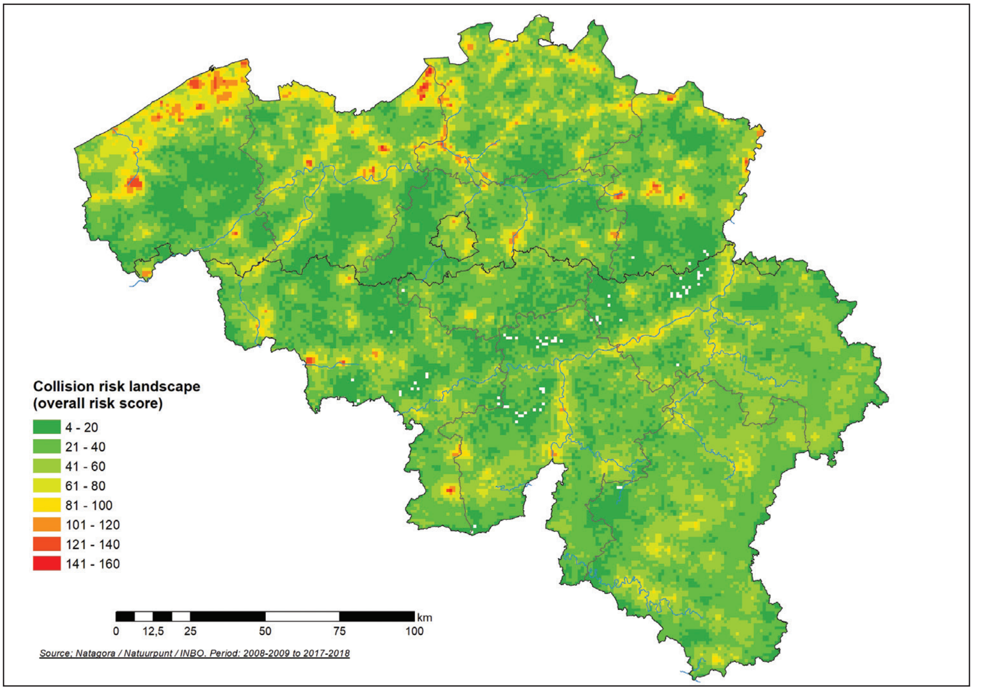

Figure 1. The transmission lines collision risk map for the whole of Belgium, shows the risk at any location in the country. This is a theoretical score not accounting for the current presence/absence of a power line, based only on the additive presence or high abundance of the sensitive species.

Combining all the possible maximum scores for each layer, the theoretical highest possible score is 176. In our present assessment, the highest observed score is 153. There is a clear gradient of risk from the lowlands in northern Belgium, where most wetlands are located, to southern, more elevated parts of the country, where risk is more diffused except along the main river valleys. The polder areas are the most critical areas as these are major concentration sites for waterbirds. Inland wetlands are also focal points for collision risk.

When overlapped with the risk maps, power-line spans (the linear segment of lines between two pylons) can be classified according to the relative risk they represent to birds (Fig. 2). The most dangerous span in the present assessment is predicted to be the line crossing a nature reserve along a major tributary of the Scheldt river, with a score of 133.

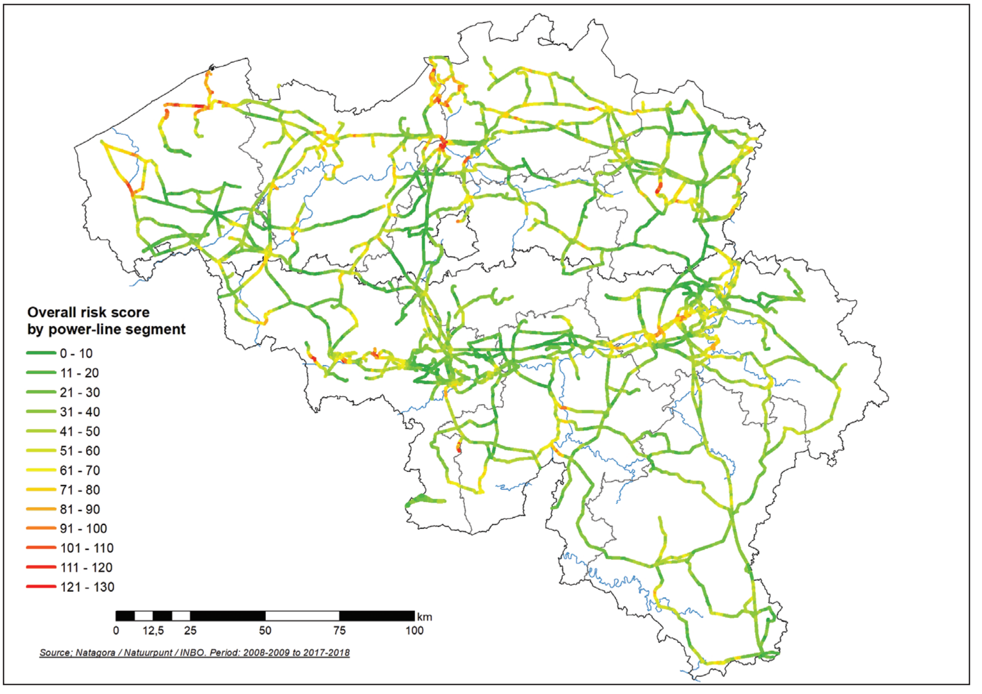

Figure 2. Map of the existing transmissions lines, colour-coded according to the bird collision risk they represent. Most of the high-priority lines are close to important waterbird sites, but numerous segments are also located in the central part of the country, in the historically industrial river valleys.

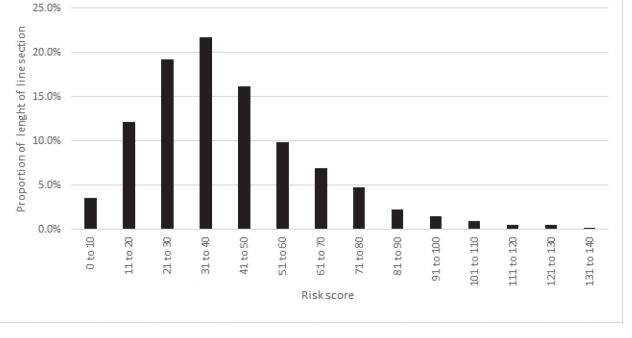

Figure 3. Frequency distribution of grouped risk scores for the total length of overhead line spans (for the whole of Belgium).

Most of the lines run through medium- or low-risk score areas (Fig. 3). Looking at the grid as a whole, 5.8% of the total length has a score above 80.

Depending on which data layer was removed, 81.6% – 90.1% of the most dangerous grid cells (as identified by the complete risk map) remained within the top 10% of the most dangerous grid cells (according to the reduced risk maps, Suppl. material 3: Table S4). This indicates a certain robustness from the collision risk map to the removal of one specific data layer.

Discussion

Reducing the risk of bird mortality along transmission lines is an important goal to achieve in a context where electricity transport system will inevitably expand throughout the world. Here we propose a method based on existing bird data to identify the "dark spot" where collision risk is relatively higher at a country scale, the scale at which the transmission line companies are operating. We believe that such an approach could inform the strategic planning of new transmission lines to be installed but more directly could be used to target mitigation actions – wire marking – on existing lines, once the existing network is overlapped with our risk map. A similar sensitivity mapping approach was developed previously in Spain and Portugal, taking into account susceptible breeding bird distribution at the scale of 10×10 km (D'Amico et al. 2019). Here, both breeding and wintering bird abundances were brought into the map at a resolution of 1×1 km, thanks to the spatially explicit data provided by several citizen-science schemes.

Our results indicate that the risk of bird collisions with high-voltage power lines is unequally distributed over Belgium. This knowledge is important for multiple reasons. Firstly, for existing power lines, it contributes to focusing efforts to mitigate effects as efficiently as possible, where every investment has the highest return translated into prevented collision casualties. Secondly, the country wide risk assessment (independent of the presence of a transmission line) can be used to compare potential trajectories of new proposed power lines.

The collision risk map was entirely based on data about the avifauna. However, the risk of bird collision is not only depending on the species richness and the abundance of birds, but also on the technical configuration of the pylons and consequently the power lines. Spacers, which separate the lines of the phase, can increase visibility (Bevanger 1994). The height of the power line is also likely to affect the bird collision risk, as is the number of vertical wire levels, the wire diameter and the presence of an earth wire (Bernardino et al. 2018). Although currently not available nationwide (Mortier, J. pers. comm.), the addition of a technical data layer to combine with the risk derived from the avifauna data could refine the current results. Furthermore, there is the possible effect of the surrounding landscape. A power line located in a heavily forested habitat with power pylon height lower than the average tree height poses limited risk to possibly susceptible species since they are forced to fly above the trees and the power lines (Jenkins et al. 2010). We suggest taking these landscape elements into consideration for fine-tuning of the wire marking once mitigation has been targeted with the help of the countrywide risk map. However, even with a further refinement of this theoretical approach, it should not replace a detailed field survey of mortality along existing lines or the necessary field expertise necessary for a proper Environmental Impact Assessment.

A key issue in this sensitivity mapping approach is the availability of bird data at a country-wide scale. Our study area, Belgium, benefits from a high density of amateur birdwatchers and long-term coordinated monitoring schemes. But we think that our approach could be used even in less surveyed regions. Spatial modelling techniques are now available to produce reliable predictive spatial models based on citizen-science records, taking into account strong spatial bias in their collections (Tang et al. 2021). These citizen-science records are now starting to accumulate almost everywhere in the world and are generally available as open source data (Callaghan and Gawlik 2015; de Vries and Lemmens 2021). In our case, for species with a low detection rate, as Eurasian Woodcock, we could use the limited number of available data to estimate the total range at 1×1 km resolution. Scarcity of data should not prevent attempting to perform a risk map analysis in other regions of the world as we have shown that prioritised segments are rather constantly highlighted by the risk maps, even when removing one layer.

A common problem with many conservation assessments published is that they often do not result in any conservation action (Knight et al. 2008; Arlettaz et al. 2010; Schuwirth et al. 2019). Our sensitivity mapping was commissioned by Elia, the transmission lines operator in Belgium. An earlier version of the risk map (Derouaux et al. 2012) was already used by the company to prioritise mitigation actions and to equip with wire marking around 115 km of lines until 2021 across Belgium (around 2% of all lines; data Elia). Some of this wire marking already took place before the production of the first version of the risk map, but already 7.4% of the transmission lines with a risk score higher than 80 are now equipped with wire marking (Elia data). In several of these spans, before-after control impact treatment involving field searches of bird casualties are now under way. Future field work analyses will allow for an assessment of the effectiveness of the prioritised wire markings but also will provide an evaluation of the theoretical mapping approach presented here.

Once established, our risk map analysis could be easily updated with new data, as bird monitoring and data collecting programs involved are running continuously and bird numbers and distributions are often susceptible to rapid changes. Another potential use of our risk analysis method is to assess further needs in wire marking (or burying) in the case of major natural wetlands restoration programmes (Decleer et al. 2016) that could result in large-scale bird distribution changes (Bregnballe et al. 2014) and thus changing the collision risk associated with existing transmission lines.

Acknowledgements

This work was only made possible thanks to the dedication of thousands of enthusiast field observers and ornithologists. The value of their mostly voluntary field work is further enhanced by the expert validators, census organisers and database curators of Natuurpunt, Natagora, Département d'Études des Milieux Naturels et Agricoles from the Service Public de Wallonie, the Research Institute of Nature and Forest in Flanders. This work was commissioned by Elia. The authors specially wish to thank Johan Mortier (Elia) for his continuous support. An earlier version of this manuscript was greatly improved thanks to the suggestions of two anonymous referees.

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Supplementary material 1

Table S1

Authors: Jean-Yves Paquet, Kristijn Swinnen, Antoine Derouaux, Koen Devos, Dominique Verbelen

Data type: Excel table

Explanation note: List of all considered bird species in Belgium with the classification into several categories according to the type of presence in Belgium, the susceptibility to collision with transmission lines, the conservation relevance. The type of spatial layer where the data from the considered species was used is also indicated.

Link: https://doi.org/10.3897/natureconservation.47.73710.suppl1

Supplementary material 2

Table S2, S3

Authors: Jean-Yves Paquet, Kristijn Swinnen, Antoine Derouaux, Koen Devos, Dominique Verbelen

Data type: Excel table

Explanation note: List of species recorded as victim of collision with power lines in Belgium: Table S2. From data portal. Table S3. From care centre in Belgium in 2010 and 2011 (source: Vogelbescherming VL).

Link: https://doi.org/10.3897/natureconservation.47.73710.suppl2

Supplementary material 3

Table S4

Authors: Jean-Yves Paquet, Kristijn Swinnen, Antoine Derouaux, Koen Devos, Dominique Verbelen

Data type: docx. file

Explanation note: Robustness of the final risk map, estimated by removal of one of the bird information layers.

Link: https://doi.org/10.3897/natureconservation.47.73710.suppl3

Supplementary material 4

Figures S1–S17

Authors: Jean-Yves Paquet, Kristijn Swinnen, Antoine Derouaux, Koen Devos, Dominique Verbelen

Data type: Maps in a docx document

Explanation note: Individual maps of all the spatial layers contributing to the final sensitivity map of the collision risk for birds with transmission power lines in Belgium.

Link: https://doi.org/10.3897/natureconservation.47.73710.suppl4

Nature Conservation 47: 235–270 (2022)
doi: 10.3897/natureconservation.47.73060
https://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
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Co-use of existing crossing structures along roads by wildlife and humans: Wishful thinking?

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Academic editor: Sara Santos | Received 16 August 2021 | Accepted 16 February 2022 | Published 25 March 2022

http://zoobank.org/EFE0C206-D299-4305-8ACA-98F005009B49

Citation: Warnock-Juteau K, Bolduc V, LoScerbo D, Anderson M, Daguet C, Jaeger JAG (2022) Co-use of existing crossing structures along roads by wildlife and humans: Wishful thinking? In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 235–270. https://doi.org/10.3897/natureconservation.47.73060

Abstract

This study assesses existing human-purpose underpasses below an unfenced high-traffic 4-lane highway in the Appalachian region of Quebec, Canada, as potential crossing structures for native mammal species. Eight underpasses of three types (five water culverts with minimum height and width of 1.8 m, one low-use gravel road byway, and two railroad underpasses) were continuously monitored by motion-detection infrared camera traps for time periods spanning up to 778 days (September 2016 to November 2018). We asked how the ratios of successful crossings through the structures (termed full crossings) and aversions to the structures (termed aversions) differed between species and we explored the influence of human activity levels on the use of these structures by wildlife. All monitored crossing structures had low human observations (with averages of less than 35 human activities per day). Our results provide evidence that 21 species of mammals in the study area successfully crossed through at least one of the eight observed underpasses on a minimum of one occasion. Some species were observed crossing through some of the underpasses on a regular basis, namely raccoon, red fox, and white-tailed deer. We propose a classification of mammal species into five human co-use classes (no or low co-use to very high co-use) to explore the relationship between mammal use of the structures and human presence. We found that humans and mammals were observed sharing passages for the four mammal species identified as tolerant of human co-use (high and very high co-use classes), but co-use was observed to be limited or not occurring for most other species. The strengths of this study include the length of time during which monitoring took place, as well as the placement of four cameras at each structure (two facing inward and two facing outward) to determine whether individuals successfully crossed through the structures or displayed avoidance behaviour. The results suggest select species of mammals show some co-use with humans at existing underpasses. The activity patterns of mammals documented over the two-year study can assist with future estimates of highway permeability. Further, measurements of human and mammal co-use have species-specific implications for retrofitting existing structures and constructing wildlife fences and purpose-built wildlife passages.

Keywords
Camera traps, culverts, existing structures, landscape connectivity, road mitigation, underpasses, wildlife movement, wildlife passages

Introduction

Roads have become ubiquitous features in landscapes around the world. In the contiguous United States, 82% of the total land area is within 1 km of a road (including unpaved and private roads) (Riitters and Wickham 2003); in Europe, 50% of all land area is located within 1.54 km of the nearest paved road or railway line (Torres et al. 2016). Roads and vehicular traffic have complex impacts on wildlife and biodiversity, such as increased wildlife-vehicle collisions (WVCs), habitat fragmentation, and decreased habitat quality (Forman and Alexander 1998; van der Ree et al. 2015). When an animal confronts a road, it is either forced to move in a different direction, i.e., access to habitats on the other side is inhibited, or it must attempt to cross, thus being exposed to traffic. In severe cases, road avoidance behaviour may significantly impede dispersal of individuals to new habitat patches, reducing genetic exchange and overall, decreasing population persistence (Jaeger et al. 2005).

A developing solution to habitat fragmentation by roads is the installation of crossing structures. Successful road crossings by way of under- and overpasses have been documented for numerous species such as black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), moose (*Alces americanus*), cougar (*Puma concolor*), wolf (*Canis lupus*), white-tailed deer (*Odocoileus virginianus*), weasel (*Mustela nivalis*), and stoat (*Mustela erminea*) (Rodriguez et al. 1997; LaPoint et al. 2003; Dodd et al. 2004; van Vuurde and van der Grift 2005; Ford et al. 2017). Facilitation of gene flow across subpopulations was shown in populations of Eurasian elk (*Alces alces*) through use of wildlife overpasses in Sweden (Olsson et al. 2008) and in populations of grizzly bear and black bear in Canada (Sawaya et al. 2013; Ford et al. 2017). Although implementing wildlife passages appears to be a simple solution, there are structural and functional factors that need to be considered to ensure their efficiency as wildlife crossing structures.

A poorly understood covariate of crossing structure use is the recreational co-use of wildlife passages by humans (van der Ree and van der Grift 2015). A crossing structure designed for both wildlife and recreational use by humans is called a multi-use crossing structure, whereas a structure designed intentionally for sole use by human transportation (i.e., road or train underpass) or water divergence (i.e., culvert or bridge) is termed an existing (or human-use) crossing structure. Wildlife may use existing structures to cross above or below roads, yet this type of use was not intended for in the construction or design. If humans and animals are able to use the same crossing structures (multi-use or existing), fewer additional structures would need to be constructed for wildlife, saving transportation agencies considerable expenses. This ideal situation of shared passages, however, cannot be assumed for all species, as human use of crossing structures may be a deterrent for many species and may defeat the intended mitigation efforts (Rodriguez et al.1997; Grilo et al. 2008). Human use can encompass many different types of anthropogenic presence, including pedestrians, cyclists, motorized vehicles (automobiles and off-road vehicles such as snowmobiles and all-terrain vehicles (ATVs)), as well as trains.

For multi-use passages, one study found no significant effect of recreational human co-use on crossing structure use by small and medium mammals and roe deer (*Capreolus capreolus*), so long as certain structural requirements were met, including a large width of structure and the presence of screening between wildlife and human paths (van der Ree and van der Grift 2015). However, another study found that human co-use of multi-use passages deterred use by carnivores such as badgers (*Meles meles*) and genets (*Genetta genetta*) (Grilo et al. 2008). For large mammals such as black bear, grizzly bear, cougar, wolf, and ungulates, it has been observed that recreational human co-use of multi-use passages acts as a severe hindrance to mammal presence (Clevenger and Waltho 2000). For other mammals, such as wildcat (*Felis silvestris*) and red fox (*Vulpes vulpes*), human presence in the form of trains had no significant effect on mammal passage (Rodriguez et al. 1997). Often, these findings cannot be generalized across species since animal sensitivity to traffic noise and human presence varies considerably. Research on existing crossing structures is sparse, and a better understanding of the relationships between their use by wildlife and the factors that may encourage or discourage use is needed for effective mitigation of habitat fragmentation by roads.

Here, we (1) assessed the use of existing crossing structures by wildlife, and (2) explored the influence of human activity levels on the use of existing crossing structures by wildlife. Specifically, we addressed the following questions:

a) Which species are using the structures and how often?

b) How do the ratios of successful crossing through the structure (full crossings) and aversion to the structure (aversions) differ between species?

c) How much does the use of existing crossing structures by wildlife and humans vary during the course of the day?

d) How does the daily frequency of use by wildlife relate to the daily frequency of human activity?

Methods

Study area

Our research focused on eight existing (human-use) crossing structures in the Appalachians of southern Quebec, Canada, more specifically in the Northern Green Mountain linkage. Extending across 83 million acres from Northern Massachusetts, USA, to the north of the Gaspe Peninsula in Quebec, Canada, the Northern Appalachian-Acadian ecoregion retains the largest expanse of intact forest in the contiguous United States (Anderson et al. 2006). Within this ecoregion, the Northern Green Mountain linkage straddles northern Vermont and southern Quebec (Staying Connected Initiative 2018) and is home to numerous wide-ranging mammals including black bear, moose, bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Pekania pennanti*), as well as American marten (*Martes americana*), North American river otter (*Lontra canadensis*), and American mink (*Neovison vison*) (Gratton and Bryant 2012). The Northern Appalachian-Acadian ecoregion remains one of the most forested yet vulnerable ecoregions in Eastern North America, due to a lack of protected natural areas and the proximity of human infrastructure to undeveloped areas (Trombulak et al. 2008). While large carnivores such as the wolf and cougar have been extirpated from the ecoregion, there remain many wildlife species within the area that are listed as needing immediate conservation action, including woodland caribou (*Rangifer tarandus*) and maritime shrew (*Sorex maritimensis*) (Anderson et al. 2006).

A section of the four-lane Highway 10 East bisects the Northern Green Mountain linkage and fragments the northern Estrie and Monteregie regions from the Sutton Mountain range to the south (Daguet 2015). This high-traffic highway exposes populations to high levels of mortality while also acting as a potential barrier to those species presenting road avoidance behaviour (Jaeger et al. 2005). Each year, an average of 89 white-tailed deer, 7 moose, and 1.5 black bear have been reported to be killed in WVCs along Highway 10 East (i.e., the section between km 68 and 143) in the Appalachians of southern Quebec, in addition to over 69 collisions with medium-sized mammals such as coyote, red fox, and porcupine (*Erethizon dorsatum*) (Ministère des Transports du Québec, unpublished data). These high yearly mortality events, especially of large mammals, cause great economic damage (Bissonette et al. 2008) and can result in loss of human lives. At the time of this study, there were no WVC mitigation measures in place along Highway 10 East, other than some warning signs advising drivers of deer presence in the area.

Eight existing crossing structures were selected for monitoring within the Northern Green Mountain linkage along a 75 km stretch of Highway 10 East between the towns of Granby (km 68) and Sherbrooke (km 143) (Fig. 1). The study sites are numbered 1, 2, and 4 through 9; Site 3, a road underpass, was not included in this study due to time constraints for data analysis (due to extremely high human use). The site numbering was left as originally assigned to allow for future analysis of the sites and comparisons to the findings from this study. A variety of underpass types were selected for this study, including train underpasses, a gravel road byway, and water culverts (Fig. 2). The study sites are located on average 4.4 kilometres from one another, with a maximum distance of 11 kilometres between two adjacent study sites and a minimum distance of less than one kilometre.

The first monitored train underpass, site 1, is located 22.4 metres from the forest edge (calculated as the mean distance to forest from both openings) and has a height of

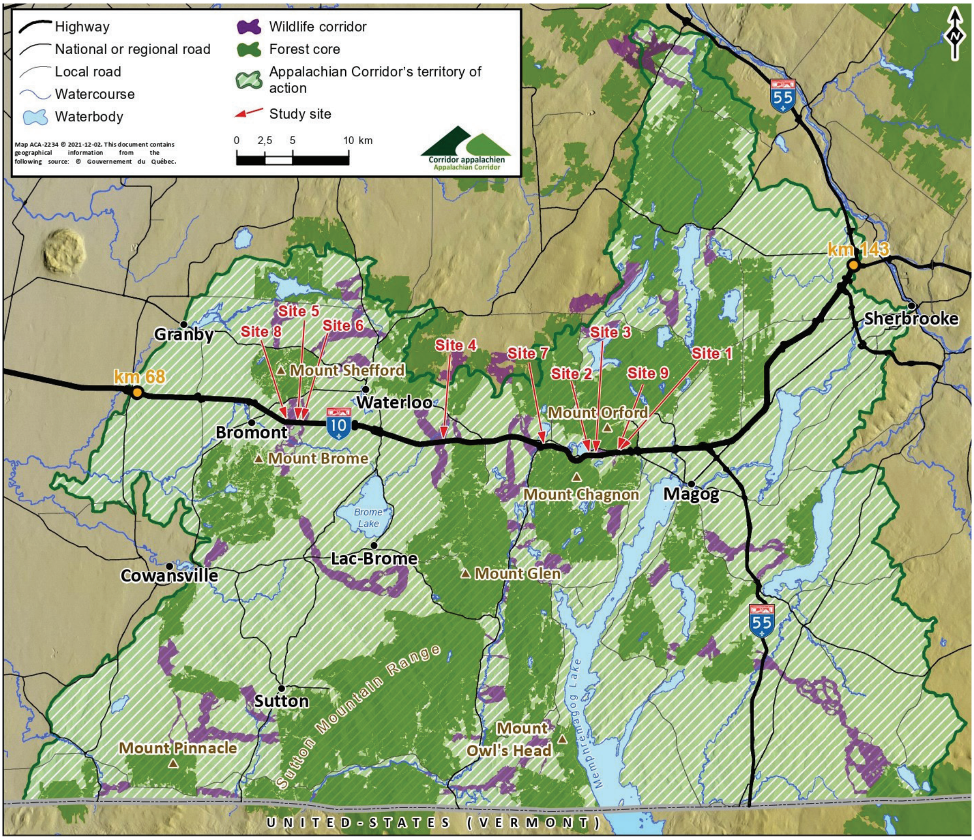

Figure 1. Predicted wildlife corridors in the Appalachians of southern Quebec based on GIS modeling of landscape connectivity, habitat validation on the ground, and mammal tracking. Large unfragmented forest blocks of more than 10 km^2 are shown in dark green. Following preliminary results from the multivariate analysis by Salvant (2017), several sections of Highway 10 East were selected to monitor human and mammal activity at a total of nine suitable multi-use underpasses (i.e., sites 1–9, although site 3 was not considered in this paper due to time constraints for data analysis). Adapted from Rapport sur l'identification des corridors fauniques de part et d'autre de l'autoroute 10 - Phase II (Daguet 2015).

8.0 metres and a width of 12.0 metres (Table 1). The underpass is 67.2 metres long and covered with a coarse gravel substrate, with one train track running through the center. The underpass is in proximity to a main road (Route 112, several hundred metres), a gas pipeline with open vegetation (less than a dozen metres), and a residential lot with a mowed lawn and artificial lake. The second monitored train underpass, site 4, is located 17.5 kilometres west of site 1 and 14.0 metres from the forest edge. The underpass has a height of 15.0 metres, a width of 25.0 metres and a length of 61.9 metres. Site 4 is covered with a mix of gravel substrate and vegetation within the underpass with one train track running through the center. Site 4 has the highest openness ratio (calculated as height × width / length) of all structures at 6.06 metres, while site 1 has

Figure 2. Photos of all eight existing underpasses observed in this study, none of which are dedicated wildlife passages. Sites 1 and 4 are train underpasses. Site 5 is a gravel road underpass. Sites 2 and 6 through 9 are water culverts (photos: Michelle Anderson and Daniella LoScerbo).

an openness ratio of 1.43 metres, the third highest of all monitored crossing structures. The train underpass is located far from any main road or residential development and the high openness ratio allows for natural light within the underpass.

The gravel road underpass, site 5, is located 29.1 metres from the forest edge and has a height of 7.0 metres and a width of 16.0 metres. The underpass is 41.9 metres long with an openness ratio of 2.67 metres, the second highest of the monitored underpasses. The road is a low-use gravel byway with two 1.0-metre-wide vegetated drainage ditches running along each side of the road.

The water culvert at site 2 is a circular concrete water culvert with a height of 1.8 metres, a width of 1.8 metres, and is 76.9 metres in length (resulting in an openness ratio of 0.04 metres, the lowest of all monitored underpasses). The culvert is located 4.8 metres from the forest edge. The box water culvert located at site 6 is made of concrete with a height of 2.6 metres, a width of 6.8 metres, and is 48.4 metres in length (resulting in an openness ratio of 0.37 metres). The culvert is located 11.0 metres from the forest edge and from September to June, water fills the culvert completely. During the summer months of July to August, the water within the culvert will dry partially, exposing a dry path on either side of the steam. The circular concrete water culvert at site 7 has a height of 1.9 metres, a width of 2.3 metres, and is 60.8 metres in length (resulting in an openness ratio of 0.07 metres). The culvert is located 11.0 metres from the forest edge. From September to June, water fills the culvert completely. During the summer months of July to August, the stream within the culvert runs dry. The box water culvert at site 8 is a concrete culvert with a height of 1.8 metres, a width of 2.3 metres, and is 50.5 metres in length (resulting in an openness ratio of 0.08 metres). The culvert is located 10.0 metres from the forest edge and is filled with water year-round (no dry path). The final water culvert, at site 9, is a circular concrete water culvert with a height of 4.0 metres, a width of 4.2 metres, and is 94.3 metres in length (the longest of all studied underpasses). The structure has an openness ratio of 0.18 metres and is adjacent to the forest edge. The culvert is filled with water year-round with no dry path. More information about the structure height, width, and length of each underpass, as well as substrate type and the presence of water, is given in Table 1.

Camera trapping

Each monitored crossing structure was equipped with four Reconyx Hyperfire HC600 infrared motion-detection camera traps, which provided continuous observation of the study sites for a minimum of 461 days (site 5) and a maximum of 778 days (sites 1, 2, and 4). The two train underpasses (sites 1 and 4) were monitored continuously from October 2016 to November 2018. The road underpass (site 5) was monitored continuously from October 2016 to December 2017. The camera traps at site 5 were removed from the field in December 2017 due to theft of one of the four cameras at the site, prompting the removal of the remaining cameras by the research team. The five water culverts were monitored continuously from October 2016 to November 2018 (site 2 for a total of 778 continuous observation days), October 2016 to June 2018 (site

Table 1. Structural characteristics of eight monitored underpasses (Fig. 2) below Highway 10 East in Quebec, Canada. Distance to forest is the average taken from the two entrances of the structures.

Site	Type	Road km	GPS Coordinates	Height (m)	Width (m)	Length (m)	Openness (m)	Substrate type	Water presence	Dist. to forest (m)
1	Train	112.5	-72.228503°E, 45.291720°N	8.0	12.0	67.2	1.43	Gravel	No	22.4
2	Culvert	105.5	-72.253064°E, 45.282949°N	1.8	1.8	76.9	0.04	Concrete	Yes	4.8
4	Train	95	-72.428521°E, 45.302273°N	15.0	25.0	61.9	6.06	Vegetation, gravel	No	14.0
5	Road[a]	83.5	-72.593076°E, 45.319216°N	7.0	16.0	41.9	2.67	Vegetation, gravel	Yes	29.1
6	Culvert[b]	84	-72.589380°E, 45.319051°N	2.6	6.8	48.4	0.37	Concrete	Yes	11.0
7	Culvert[b]	106	-72.314650°E, 45.297190°N	1.9	2.3	60.8	0.07	Concrete	Yes	11.0
8	Culvert	82	-72.607100°E, 45.319600°N	1.8	2.3	50.5	0.08	Concrete	Yes	10.0
9	Culvert	112.5	-72.230790°E, 45.291150°N	4.0	4.2	94.3	0.18	Concrete	Yes	0.0

[a] Site 5 is a gravel road with vegetation and two 1 m wide drainage ditches running along each side of the road. [b] From September-June, water fills culvert width completely. In the summer months of July-August, the stream dries partially (site 6) and completely (site 7), expanding the dry path width through the culvert.

6 for a total of 619 continuous observation days), and July 2017 to November 2018 (sites 7, 8, and 9 for a total of 493, 498, and 493 continuous observation days, respectively). The camera traps at site 6 were removed from the study site in June 2018 due to vandalism. The camera traps at water culvert sites 7, 8 and 9 were installed in July 2017, following the installation of cameras at the other study sites in October 2016, to increase the number of crossing structures monitored for the study.

Over the past decade, there has been a significant increase in research using camera traps as a non-invasive method to study the presence and behaviour of wildlife (Wearn and Glover-Kapfer 2019). Camera traps allow for continuous data collection during the day and night with minimal environmental and wildlife disturbance, as well as low labour costs (Henschel and Ray 2003; Rowcliffe et al. 2008). However, some studies suggest that animals can detect the location of camera traps through auditory localisation acuity, which occurs when an animal is alerted to the presence of a camera due to the high-frequency sound emitted as the camera captures an image (Meek et al. 2016). While this can potentially result in avoidance behaviour toward the area in which the camera is located, overall, cameras remain an efficient and widely used method of wildlife monitoring.

For this study, two camera traps were installed at each of the northern and southern extremities of the underpasses, one facing outward and one facing inward (Fig. 3). We installed the cameras to the walls of the structures approximately four feet above the ground and positioned them horizontally at a slight downward angle, to maximize detection of small-, medium-, and large-sized mammals. The cameras were installed in metal lockboxes to prevent theft, and laminated cards were placed next to the cameras to inform readers of the research project and to deter vandalism. Triggered by movement or heat signatures within their detection ranges, the outer-facing cameras detected approaches by wildlife and humans in proximity of the underpass openings. The inner-facing cameras were used to confirm whether an animal crossed through the full length of the underpass and exited at the opposite opening from which it entered (termed a full crossing), or whether an animal doubled back inside the structure and exited through the opening from which it had entered (termed an aversion). All camera traps collected data simultaneously and were programmed to continuously take a sequence of five photographs when triggered, until the movement or heat signature was no longer within the detection range of the camera. The research team visited the study sites monthly to replace SD cards and camera batteries, as well as to reorient any cameras that may have shifted since the last maintenance visit. The research team wore gloves when manipulating the cameras to prevent odor transfer. No lures or bait were used to attract mammals near the study sites. We use standardized camera trapping terminology consistently for reporting results in this paper (Meek et al. 2014; Wearn and Glover-Kapfer 2017).

Photo analysis

Each photo depicting an animal was assessed for the following: date, time, temperature, species, number of animals in the group, and direction of movement. The sequence of

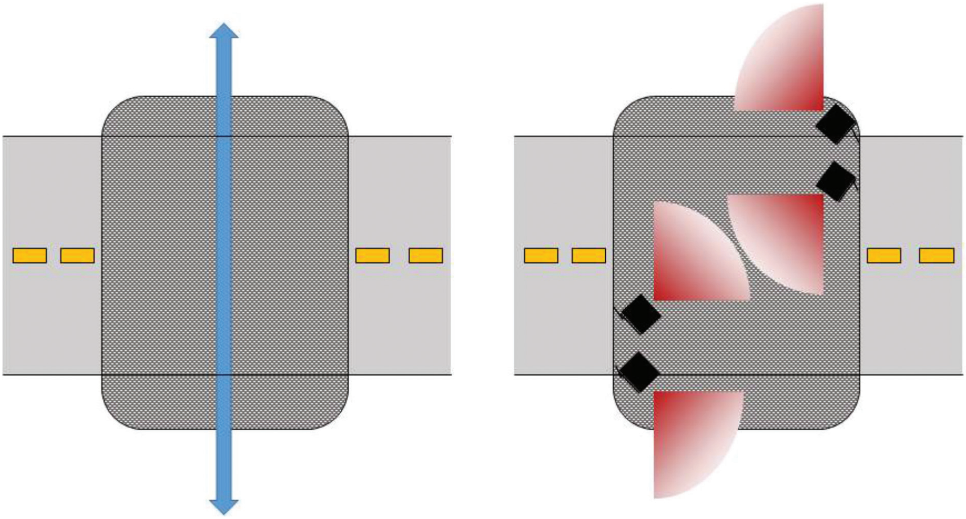

Figure 3. Display of layout for monitoring of human and animal activity by cameras in eight underpasses below Highway 10 East. The grey crosshatched rectangles indicate the underpass structure. The blue arrow suggests the theoretical path of movement through the underpass to cross below the highway. The four black boxes represent the *Reconyx Hyperfire HC600* motion and infrared detection cameras. The range of detection for each camera extends to roughly 60 feet and is represented by the red arcs.

photos that captured an animal near the entrance of or within a crossing structure was used to confirm the presence of a certain species. In the event that multiple individuals of the same species were observed in one sequence of photos, we considered the observation event as having multiple detections of the same species. When an animal or group of animals was detected by more than one camera trap simultaneously at a study site, we considered it as one observation event. If the animal was observed by any combination of camera traps showing that it successfully crossed through the underpass, this was deemed a full-crossing event. If the animal was observed to turn around, or pass near the underpass without entering, this event was termed an aversion. When the outcome of a wildlife observation was uncertain, the event was termed unknown. We calculated the crossing-success ratio for each species per study site as follows:

Crossing-success ratio = (Full crossings / Confirmed detections)

Confirmed detections are equal to the sum of confirmed full crossings and confirmed aversions. The detections for which the outcome is not confirmed (unknown) are not considered in this equation as it is uncertain how many of them were full crossings or aversions. Any events of the same species that occurred more than 5 minutes apart were considered independent observation events (to allow for sufficient time to pass through the structure).

Human activities observed at the study sites were classified into four categories, namely train, automobile/road vehicle, ATV (including snowmobile), and non-motorized activity (cyclist, pedestrian, horseback rider, etc.). All human activity was assessed for the following: direction of movement, date, time, and duration of each event. The visits by the research team (for replacement of SD cards and camera batteries) were included in the tally of human activity at each site.

We calculated the Shannon Diversity Index (H) of each crossing structure to characterize the species diversity observed at each study site, as follows:

$$H = - \Sigma\, p_i \cdot ln(p_i),$$

where p_i indicates the proportion of the entire community made up by species i. The Shannon Diversity Index accounts for both abundance and evenness of the species present within a community (Shannon and Wiener 1963). We calculated the Shannon Diversity Index for each monitored crossing structure for all mammals observed (termed overall diversity index) and for all mammals confirmed to have successfully crossed through the structure (termed full-crossing diversity index), resulting in two diversity values for each crossing structure.

Mammal classification

Wildlife species often perceive humans as predators and will display avoidance behaviour toward areas that experience high human activity, which in turn can generate population-level consequences (Frid and Dill 2002; Preisser et al. 2005; Ellenberg et al. 2006). To explore the relationship between the use of existing crossing structures by wildlife and the presence of humans at our study sites, we chose to classify the mammal species into groups that exhibit different levels of human co-use, which may reflect different levels of tolerance to humans (Samia et al. 2015). To do so, we grouped all observation days (24 hours) across all study sites based on the number of human activities per day. All observation days that showed no human activity were placed in one group; days that showed one human activity were placed in another group; and so on. We then standardized each group to represent a period of 50 days, following the recommendation of maximal smoothing histograms by Terrell and Scott (1985). Since our study sites experienced mostly low daily rates of human activity, we averaged down for the groups with low daily human activity. For groups that had less than 50 overall observation days for a particular human activity level (i.e., days with high human activity), we combined these days with days that showed similar daily human activities to produce standardized groups of 50 observation days. In total, 20 daily human activity groups were formed (Table A1 in Appendix 1).

The wildlife activities and associated full crossings within each daily human activity group were then examined for visible trends in the data. Mammal species with at least 10 detections throughout the study were classified into five categories based on their level of correlation with the aforementioned groups of daily human activity. Mammal species that were never observed fully crossing through an underpass above four daily human activities were classified into the “very low or no human co-use” category (Table 2). Species that were observed fully crossing through the structures at least once above the level of four daily human activities, while the number of full crossings above this level was very low compared to the total number of full crossings, were classified in the "low" human co-use category. The "moderate" human co-use category includes species with a negative correlation between increasing levels of human activities and the number of full crossings. The "high" human co-use category includes species that were observed having no relationship between the level of daily human activity and the number of full crossings. Finally, species that displayed a positive correlation between full crossings and increasing daily human activity levels were classified into the "very high" human co-use category.

Table 2. Mammal species classifications based on observed human co-use levels.

Level of human co-use	Criteria	Species names
Very low or none	No full crossings above 4 human activities per day	Mouse spp., muskrat, North American porcupine, rat spp., squirrel spp.
Low	Very low number of full crossings above 4 human activities per day compared to the total number of full crossings	American mink, bobcat, snowshoe hare
Moderate	The average number of full crossings for 50 days decreases with the increase in the number of daily human activities	Red fox, white-tailed deer
High	The average number of full crossings for 50 days stays the same with the increase in the number of daily human activities	Coyote, domestic cat, groundhog
Very high	The average number of full crossings for 50 days increases with the increase in the number of daily human activities	Racoon

We conducted Kendall's Tau tests (using Excel 2016) for species with the highest detection rates across the study to explore the correlation between the species' presence with human activity at the study sites. We calculated the Tau-values for these species for all detections and for all confirmed full crossings, resulting in two Tau-values for each species. Kendall's Tau is a non-parametric test used to understand the strength of the relationship between two variables. More specifically, the Kendall Tau-*a* test is used when there are no ties in the data and the Kendall Tau-*b* test is used to correct for ties in the data (Laurencelle 2009). The tests provide both a Tau-value to determine the direction of the relationship (positive or negative) and a *p*-value. We did not conduct a Kendall's Tau test on any species in the "very low or none" co-use classification as there were not enough data (detections) for these species to reflect statistical significance.

Results

Which species are using the structures?

Mammal movement at eight existing crossing structures was documented between 461 (site 5) and 778 (sites 1, 2, and 4) continuous observation days (total sampling effort of this study was 19,592 camera trap days), encompassing over 1.3 million photos (Fig. 4) and 3459 mammal detections across 23 species, including black bear, bobcat, coyote, moose, raccoon (*Procyon lotor*), red fox, and white-tailed deer (Table 3). Other non-focal animals observed included various bird species, including wild turkey (*Meleagris gallopavo*), great blue heron (*Ardea herodias*), American crow (*Corvus brachyrhynchos*), duck species, as well as turtle species. Across all study sites, nine animal detections were not identified by species due to low photo resolution (termed unknown species in Table 3).

How do the ratios of successful crossing through the structure (full crossings) and aversion to the structure (aversions) differ between species?

Of the total number of mammal detections, 1832 were confirmed as successful crossings through the monitored underpasses (full crossing), 1285 exhibited aversion behavior toward the structures (aversion), and 342 outcomes could not be confirmed (unknown). This results in an overall crossing success ratio of 58.8% across all mammal detections. Raccoon, white-tailed deer, and red foxes were the predominant users across all structures and were the only three species observed at all eight study sites. Among the three species recorded at all eight study sites, raccoons had the highest crossing success ratio at 85% (1212 full crossings over 1423 confirmed detections), followed by red foxes (47%, 196 full crossings over 420 confirmed detections) and white-tailed deer (24%, 222 full crossings over 910 confirmed detections). However, regarding the type of crossing structure, of the 564 white-tailed deer detections recorded at the water culverts (sites 2 and 6–9), only 16 were confirmed as successful crossings through the structures, an overall culvert success ratio of only 3% (16 full crossings over 553 confirmed detections).

The eight crossing structures observed in this study vary greatly in structural characteristics, human activity, and animal activity. To illustrate potential patterns of human-animal co-use across these diverse sites, the following sections detail human and animal activity by crossing structure type.

Train underpasses

The railroad at site 1 was visited by American mink, bobcat, coyote, groundhog (*Marmota monax*), moose, raccoon, red fox, and white-tailed deer for a total presence of 236 mammal detections. Red foxes (100) and white-tailed deer (97) showed the highest presence at site 1. Notably, all raccoons (46) detected at site 1 crossed through the underpass, similarly for bobcat (2) and coyote (2). White-tailed deer were the least likely to cross through this structure at 51% (47 full crossings over 93 confirmed detections). There was an average of 3.4 daily human activities at site 1, mainly consisting of trains, maintenance vehicles, and monthly research team activity. Site 1 had the third-highest overall diversity index (1.32) and third-highest overall full crossing ratio (79%) of all study sites, resulting in a full crossing diversity index of 1.37, the second highest of all crossing structures.

The railroad at site 4 was visited by bobcat, coyote, domestic cat (*Felis catus*), fisher, groundhog, raccoon, red fox, weasel (*Mustela ermine*), and white-tailed deer. White-tailed deer (221) and raccoon (32) had the highest presence at site 4. All bobcat (20) observed at the site used the crossing structure within the month of February 2017. While the red fox was the dominant species observed at the train underpass at site

Table 3. Total numbers of individuals detected at each existing underpass for mammal species (confirmed detections + unknowns). A confirmed detection is an instance where an animal was detected at the structure and either crossed through the structure (full crossing) or avoided the structure (aversion); the number of detections for which an animal was detected at a structure, but the outcome is not known (unknown) is given after the + sign. The number in brackets represents the percentage of full crossings out of the confirmed detections. Daily human activity is the average calculated from the total (24-hour) days observed at each site and includes trains, automobiles and other road vehicles, ATVs (including snowmobiles), pedestrian, cyclists, equestrian riders, as well as the research crew visiting sites for maintenance.

Species	Total number of mammals detected at existing underpasses (% of full crossing)							
	Train underpass		Road underpass	Culvert				
	1	4	5	2	6	7	8	9
Neovison vison (American mink)	1 (100%)	-	-	4 (75%) + 29	4 (0%)	26 (81%) + 1	1 (0%) + 1	11 (18%)
Ursus americanus (Black Bear)	-	-	-	1 (100%)	1 (100%)	-	-	-
Lynx rufus (Bobcat)	2 (100%)	20 (100%)	2 (50%)	2 (100%)	1 (0%)	-	-	2 (0%)
Tamias striatus (Chipmunk)	-	-	-	-	-	- + 1	-	-
Canis latrans (Coyote)	2 (100%)	1 (100%)	4 (100%)	-	-	-	3 (0%)	2 (0%) + 6
Felis catus (Domestic Cat)	-	10 (90%)	19 (89%) + 2	-	1 (0%)	-	-	-
Pekania pennanti (Fisher)	-	1 (100%)	-	1 (0%) + 1	-	-	-	-
Marmota monax (Groundhog)	10 (90%)	11 (91%) + 4	9 (22%)	3 (100%)	2 (0%)	4 (75%)	2 (0%)	-
Alces alces (Moose)	3 (100%)	-	-	-	1 (0%)	1 (0%)	-	-
Mus spp. (Mouse spp.)	-	-	-	-	- + 1	14 (29%) + 8	3 (0%)	-
Ondatra zibethicus (Muskrat)	-	-	-	-	-	17 (82%) + 9	-	-
Castor canadensis (North American beaver)	-	-	-	1 (100%)	-	-	-	-
Erethizon dorsatum (North American porcupine)	-	-	1 (100%)	-	-	16 (88%)	-	-
Lontra canadensis (North American river otter)	-	-	-	1 (100%)	-	5 (100%)	- + 1	-
Procyon lotor (Raccoon)	47 (100%)	30 (73%) + 2	602 (96%) + 48	141 (88%) + 20	201 (88%) + 59	284 (88%) + 5	29 (52%) + 15	89 (0%) + 10
Rattus spp. (Rat spp.)	-	-	-	-	-	20 (100%)	-	-
Vulpes vulpes (Red fox)	90 (93%) + 10	5 (80%) + 1	3 (67%) + 1	3 (0%)	2 (0%)	298 (36%) + 23	1 (0%)	18 (0%)
Rodentia (Rodent)	-	-	-	9 (0%)	-	-	-	-
Sciurus spp. (Squirrel spp.)	-	-	-	3 (100%)	-	77 (13%) + 4	-	1 (0%)
Mephitis mephitis (Striped skunk)	-	-	-	-	-	4 (100%)	-	-
Lepus americanus (Snowshoe hare)	-	-	-	6 (0%)	-	1 (0%)	3 (33%)	4 (50%)
Mustela erminea (Weasel)	-	1 (100%)	-	1 (100%)	-	-	-	-

Species	Total number of mammals detected at existing underpasses (% of full crossing)							
	Train underpass		Road underpass	Culvert				
	1	4	5	2	6	7	8	9
Odocoileus virginianus	93 (51%)	181 (77%)	82 (24%)	106 (0%)	109 (12%)	60 (3%)	216 (0%)	62 (0%)
(White-tailed deer)	+ 4	+ 40	+ 24	+ 2	+ 5	+ 2	+ 2	
Unknown	1 (100%)	-	2 (0%) + 1	2 (50%)	-	1 (0%)	2 (0%)	-
All mammals	249 (79%) + 14	260 (80%) + 47	724 (86%) + 76	284 (49%) + 52	322 (59%) + 65	828 (55%) + 53	260 (7%) + 19	189 (2%) + 16
Overall diversity index	1.32	1.04	0.66	1.37	0.81	1.70	0.74	1.36
Full-crossing diversity index	1.37	0.99	0.37	0.59	0.28	1.44	0.24	0.69
Daily human activity	3.4	2.6	33.9	0.1	1.3	0.2	1.1	0.1
Total days observed (site-based camera-trap days)	778	778	461	778	619	493	498	493
Total sampling effort (site-based camera-trap days x number of cameras)	3,112	3,112	1,844	3,112	2,476	1,972	1,992	1,972

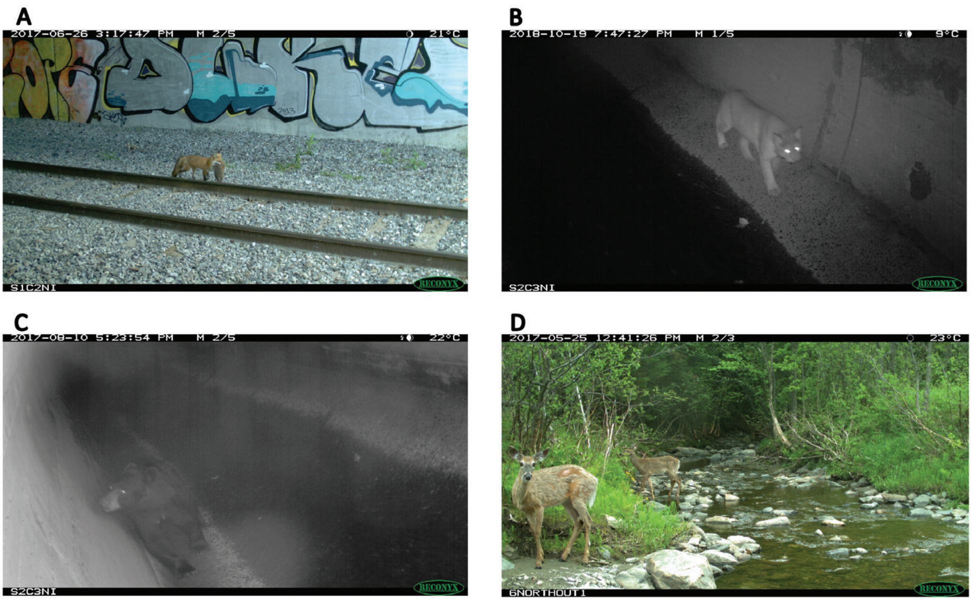

Figure 4. Select photos of mammals at various monitored structures. In photo (**A**), a red fox (*Vulpes vulpes*) walked along the railroad at site 1 with prey in its mouth. A bobcat (*Lynx rufus*) was detected crossing through a water culvert at site 2 (**B**). A black bear (*Ursus americanus*) successfully crossed through a water culvert (site 2) during summer months when the water level was lowest and a dry path was present (**C**). In photo (**D**), a white-tailed deer (*Odocoileus virginianus*) and its fawn were observed outside a water culvert (site 6).

1, only six red fox detections were recorded at site 4. However, site 4 had the second highest overall crossing-success ratio across observed species of all underpasses at 80%. The overall diversity index for site 4 (1.04) was slightly lower than for site 1 (1.32) even though site 4 was visited by a higher number of mammal species (9 and 8, respectively). This is due to the number of white-tailed deer (221) observed visiting the site, which made up 72% of wildlife detected around or within the railroad underpass. Site 4 also saw a lower full-crossing diversity index (0.99) compared to site 1 (1.37), due to the smaller number of species that crossed through the structure. The average daily human activity at site 4 was 2.6 per day, once again consisting primarily of trains, maintenance vehicles, and monthly research team activity.

Road underpass

The gravel road at site 5 was visited by bobcat, coyote, domestic cat, groundhog, North American porcupine, raccoon, red fox, and white-tailed deer. Site 5 was the second-most visited study site (following site 7) with 800 mammal detections, consisting mostly of raccoon (650), white-tailed deer (106), and domestic cat (21). The overall full crossing success ratio across all mammal species for site 5 was 86%, i.e., the highest of all structures, largely due to raccoon with a crossing-success ratio of 96%. Although visited by eight mammal species throughout the course of the study, this structure had the lowest diversity index of all monitored underpasses (H = 0.66) due to the disproportionate number of raccoons. The high proportion of raccoon (578 of 623 total full crossings) resulted in the third-lowest full-crossing diversity index (0.37) of all structures studied. Moreover, site 5 had the highest observed daily human activity at 33.9, consisting primarily of vehicle traffic driving through the underpass.

Water culvert underpasses

Site 2 - circular water culvert: At site 2, 334 mammal detections from 14 confirmed species (and two unknown) were recorded at the structure, consisting mainly of raccoon (161) and white-tailed deer (108). The only North American beaver (*Castor canadensis*) detected was confirmed to have crossed through this culvert, alongside one of the only two detected black bears in the study. Notably, all 106 confirmed detections of white-tailed deer resulted in avoidance behaviour toward the structure, as did all observed red fox (3), rodent species (9), and snowshoe hare (*Lepus americanus*, 6). High mink activity was observed during the month of March 2016 (25 detections of 33 detections in total). The overall diversity index for site 2 was 1.37 but the full-crossing diversity index was only 0.59. Site 2 showed the lowest daily human activity level of all monitored structures at 0.1 per day, alongside site 9, which consisted mainly of monthly research team activity.

Site 6 - box water culvert: At site 6, ten mammalian species were detected, consisting mainly of raccoons (260) and white-tailed deer (114). While both species were observed crossing through the structure, white-tailed deer displayed a crossing-success ratio of only 12%. Raccoons had an overall crossing success ratio of 88%, and one of the only two black bears observed during the study crossed through this structure. Site 6 had the third lowest overall diversity index (0.81) and the second lowest full-crossing diversity index (0.28). Average daily human activity level for site 6 was 1.3 per day, consisting mainly of ATVs and monthly research team activity.

Site 7 - circular water culvert: Site 7 exhibited the highest number of mammal detections (881) across fifteen mammal species, including red foxes (321), raccoons (289), and white-tailed deer (62), resulting in the highest overall diversity index (1.70) and the highest full-crossing diversity index (1.44). While raccoons were observed to have a high crossing-success ratio of 88%, other species exhibited avoidance behaviour toward the structure, including white-tailed deer (3%), squirrel species (13%), and red fox (36%). However, all detections of striped skunk (*Mephitis mephitis*, 4), rat species (20), and North American river otter (5) were confirmed as crossing through the structure. Daily human activity level at site 7 was the second lowest of all monitored structures at 0.2 per day, consisting primarily of monthly research team activity.

Site 8 - box water culvert: Site 8 had 289 mammal detections across nine confirmed species and an overall crossing-success ratio of only 7%. White-tailed deer (218) and raccoons (44) dominated mammal activity at site 8. Only two species were observed to successfully cross through the structure, namely raccoons (52%) and snowshoe hares (33%). The full-crossing diversity index at the site was 0.24, lower than the overall diversity index of 0.74. Site 8 was observed to have an average daily human activity level of 1.1 per day, which consisted mainly of ATVs and monthly research team activity.

Site 9 - circular water culvert: Site 9 had the lowest crossing-success ratio (2%) of all underpasses and the lowest average daily human activity level (0.1 per day), alongside site 2. Only two of the eight species observed were confirmed to have crossed through the structure, namely two American mink (18%) swam through the structure in May 2018 and two snowshoe hares (50%) travelled through the structure in January 2018, when the water was frozen over. This water culvert had an overall diversity index of 1.36 (the third highest of all structures) and a full-crossing diversity index of 0.69. No humans, apart from the research team, were observed at the site.

How much does the use of existing crossing structures by wildlife and humans vary during the course of the day?

Average daily human activity at the study sites varied between 0.1 and 33.9 events per day, with a maximum of 114 observation events at site 5 on October 23, 2017. Across all study sites, human activity levels were highest during the daytime hours (between 6:00 a.m. and 8:00 p.m.) and peak daily human activity levels were reached in the early evenings, at roughly 5:00 p.m. (Fig. 5). Contrarily to human activity, average daily mammal activity levels were highest during nocturnal hours (between 8:00 p.m. and 7:00 a.m.) with peak activity levels reached between 1:00 a.m. and 7:00 a.m. We chose to classify raccoon observations apart from other mammal species, as they were observed much more often than any other species and also exhibited a much higher overall crossing-success ratio (85%, 1212 full crossings over 1423 confirmed detections). Raccoons were almost exclusively detected during crepuscular and nocturnal hours (between 6:00 p.m. and 7:00 a.m.) with peak activity levels between 4:00 a.m. and 7:00 a.m. Full crossings across all mammal species (excluding raccoon) were highest during crepuscular hours.

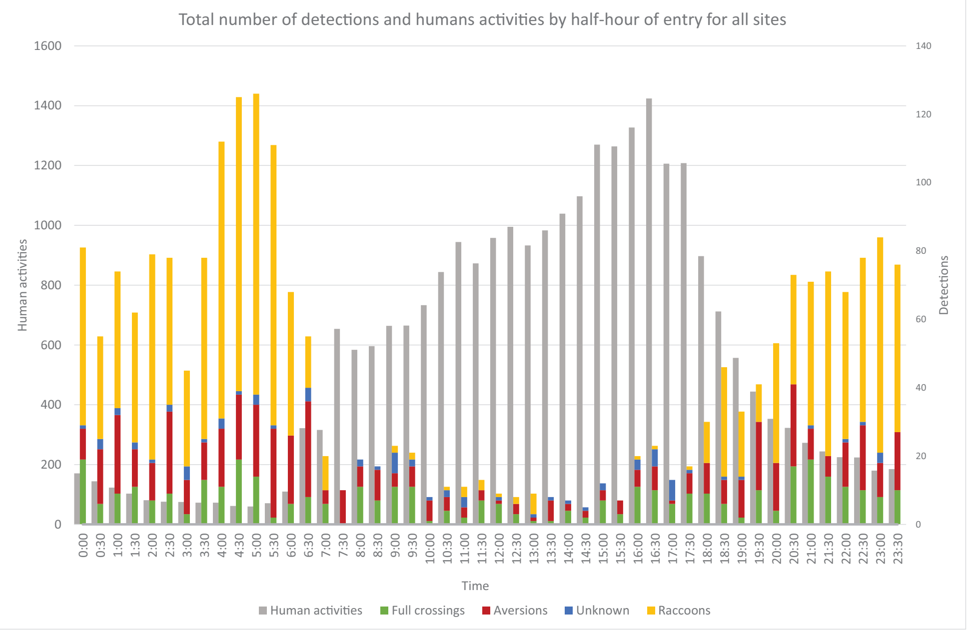

Figure 5. The total number of human and mammal detections by half-hour across all study sites. The results for raccoon (*Procyon lotor*) were removed from the other mammal species to prevent a skew due to the high numbers of raccoons observed throughout the study. Grey bars indicate human observations. Green bars indicate confirmed full crossings for mammal species and red bars indicate confirmed aversions for mammal species (excluding raccoon). Blue bars indicate mammal observations for which the outcome is unknown (excluding raccoon). Yellow bars indicate raccoon detections.

How does the daily frequency of use by wildlife relate to the daily frequency of human activity?

To relate wildlife activity in underpasses to human activity levels, we compared the total numbers of detections for each species across 50 days (Tables A1–A3) with the associated daily human activity across all sites (Fig. 6).

Very low or no human co-use

Mouse species, muskrat (*Ondatra zibethicus*), North American porcupine, rat species, and squirrel species displayed very low or no human co-use at the existing underpasses (Table 2). All species in this group, excluding squirrel species, were never observed successfully crossing through a structure on days when human activity occurred. Squirrel species were not observed successfully crossing through a structure on days with more than four human activities.

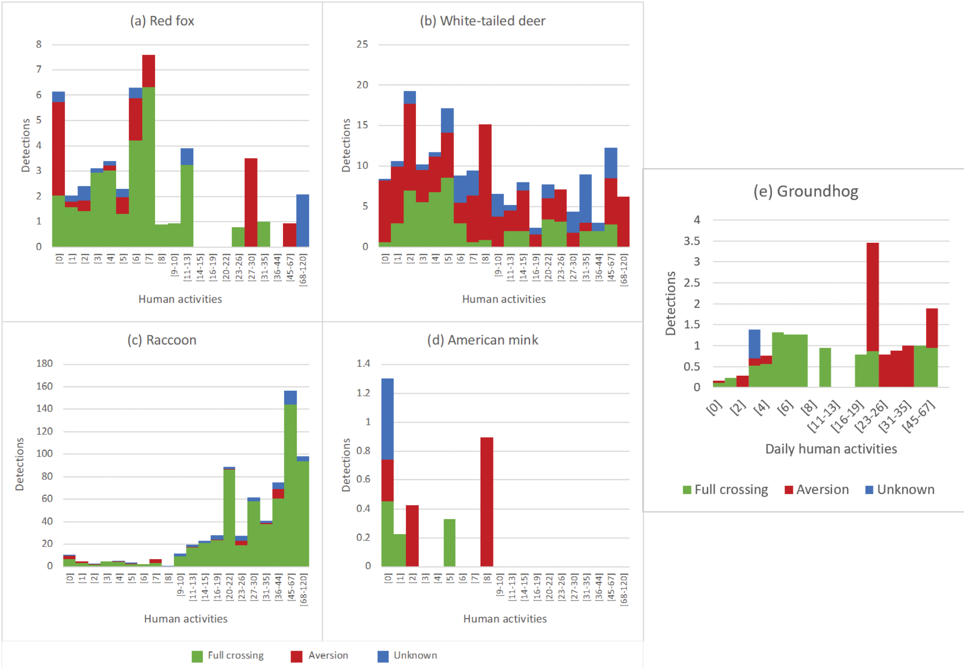

Figure 6. The average number of detections of (**a**) red fox, (**b**) white-tailed deer, (**c**) raccoon, (**d**) American mink, and (**e**) groundhog over 50 days by daily human activity levels. Green bars indicate confirmed full crossings, red bars indicate confirmed aversions, and blue bars indicate detections for which the outcome was unknown.

Low human co-use

American minks were observed crossing through the structures on 26 occasions on days with no human activity and only once on a day with five human activities (Fig. 6). Snowshoe hares were observed on 14 occasions throughout the study and only one detection occurred on a day with more than four human activities. Bobcats, the final species in the classification, were observed only three times on days with more than 4 human activities (out of 29 detections). We conducted a Kendall's Tau-*b* test on American mink for both full crossings and total observation events to explore the relationship with human presence. For full crossings, we obtained a Tau-value of -0.253 (p = 0.0154) and for total observation events, we obtained a Tau-value of -0.345 (p = 0.007) (Table 4), indicating a negative correlation between American mink's use of the existing crossing structures and human presence.

Moderate human co-use

Species in this class included white-tailed deer and red fox (Fig. 6). The majority of full crossings for red fox were observed on days with fewer than 14 human activities. On

Table 4. Results obtained from the Kendall's Tau tests (*a* and *b*) performed on raccoon, white-tailed deer, red fox, American mink, and groundhog to measure the correlation between human presence at the study sites and full crossings by wildlife, as well as number of detections.

Species	Full crossings			Total detections		
	Test	Tau-value	*p*-value	Test	Tau-value	*p*-value
Raccoon	Tau-*a*	0.642	7.55×10^{-5}	Tau-*a*	0.674	3.28×10^{-5}
White-tailed deer	Tau-*b*	-0.236	0.150	Tau-*a*	-0.389	0.016
Red fox	Tau-*b*	-0.492	0.002	Tau-*b*	-0.298	0.068
American mink	Tau-*b*	-0.253	0.015	Tau-*b*	-0.345	0.007
Groundhog	Tau-*b*	-0.064	0.686	Tau-*b*	0.128	0.434

days with 14 or more human activities, there were on average no more than 3.5 red fox detections and no more than one full crossing per 50 days. White-tailed deer were most often observed crossing through the structures on days with less than seven human activities but were nonetheless also observed crossing on days with up to 67 human activities.

We conducted Kendall's Tau-*a* and Tau-*b* tests for white-tailed deer and red fox for full crossings and total detections. For white-tailed deer, we conducted a tau-*b* test for full crossings (to correct for ties) and a tau-*a* test for total detections (no ties). We obtained a Tau-value of -0.236 (p = 0.150) for full crossings (non-significant) and a Tau-value of -0.389 (p = 0.016) for total observation events, suggesting a negative correlation for total observation events. For red fox, we conducted a Tau-*b* test on both datasets and obtained a Tau-value of -0.492 (p = 0.002) for full crossings, and for total detections we obtained a Tau-value of -0.289 (p = 0.068, i.e., marginally significant).

High human co-use

Coyote, domestic cat, and groundhog showed similar patterns of underpass use independent of human activity level. The full crossings by groundhog remained relatively stable across all daily human activity levels, with no more than 1.5 full crossings on average over 50 days, regardless of human activity level (Fig. 6). The observations for coyote and domestic cat showed similar trends, with observations remaining relatively stable across all daily human activity levels. Kendall's Tau-*b* test for groundhog resulted in a Tau-value of -0.064 (p = 0.686) for full crossings and a Tau-value of 0.128 (p = 0.434) for total detections. Both results are non-significant and do not indicate a relationship between groundhog use of the existing structures and human presence.

Very high human co-use

Raccoon was the only species exhibiting a positive correlation between full crossings and high daily human activities (Fig. 6). Almost half of all observed raccoons' full crossings occurred at the gravel road underpass at site 5 (47.6%), which is the site that displayed by far the highest average daily human activity (33.9 per day) across all study sites. Additionally, raccoons represented 92.5% of all full crossings at site 5. Kendall's Tau-*a* test (since there were no ties) resulted in a Tau-value of 0.642 ($p = 7.55 \times 10^{-5}$) for full crossings and a Tau-value of 0.674 ($p = 3.28 \times 10^{-5}$) for total detections, indicating a clear positive correlation between raccoon use of the structures and human presence at the study sites.

Species that were observed less than 10 times throughout the study and therefore were not considered in the classification of human co-use included black bear, chipmunk (*Tamias striatus*), fisher, moose, North American beaver, North American river otter, striped skunk, and weasel. Of these, only fisher, moose, and weasel were observed crossing through a structure on a day with more than two human activities.

Discussion

Use of existing crossing structures by wildlife: Species distribution and frequencies of use

In an effort to estimate the permeability of Highway 10 East to wildlife, we found that 21 mammalian species used at least one of the eight observed underpasses at least once to cross under the highway, and a few species frequented some of the underpasses on a regular basis, namely raccoon, red fox, and white-tailed deer.

Train underpasses

Railroad underpasses show promise in facilitating mammal crossing, with considerable rates of full crossings detected for a diverse range of species within this study. Notably, medium- and large-sized mammals known to frequently cause VWCs along Highway 10 East in the region were detected at train underpass structures, including moose, white-tailed deer, bobcat, coyote, and raccoon. Remarkably, each of the three moose detected at a railroad underpass (site 1), which is darker and more coarsely gravelled than site 4, were confirmed to have fully crossed through the structure. Similar patterns were observed for American minks, bobcats, coyotes, and raccoons, for which all detections resulted in confirmed full crossings at the darker train underpass (site 1). Additionally, all bobcat detections (20) that occurred at the train overpass which exhibited more natural light, in addition to having vegetation and a soil substrate on either side of the train tracks (site 4), were confirmed to have successfully crossed through the structure. Of those bobcat detections, 15 occurred during the same month (February 2017), which suggests one or a few individuals may have revisited the train underpass throughout the month. Similarly, the brighter, more vegetated train underpass facilitated a larger number of white-tailed deer detections, with the species accounting for 72% of the total wildlife detected around or within the railroad underpass at site 4. In contrast, at the darker, more coarsely gravelled train underpass (site 1), white-tailed deer detections made up only 37% of total wildlife detections. These differences in wildlife use of the railroad underpasses suggest that species behaviour may be influenced by the structural and environmental differences between the underpasses. This notion has been confirmed in earlier studies, which have determined that high openness ratios (short in length, as well as high and wide) facilitate higher rates of usage by grizzly bears (*Ursus americanus*), wolves, and deer (Clevenger and Waltho 2005), and that natural substrates throughout crossing structures encourage full crossings by wildlife by connecting habitat (Yanes et al. 1995).

Human activity remained relatively similar in both underpasses, consisting mostly of trains and monthly visits by the research crew. This leads us to believe that the significant variation in crossing-success ratios at both train underpasses may be due to the height and width differences, i.e., the openness ratio of the structures (1.43 m at site 1 and 6.06 m at site 4) and substrate differences between the structures.

Road underpass

The unpaved road underpass had the greatest frequency of mammal use, where on average nearly two wildlife individuals crossed per day. However, this result was driven by raccoons, a species of low concern to conservation organizations or transport and wildlife authorities. A significant number of white-tailed deer (108 individuals) also visited the site, perhaps due to the large openness ratio of the structure and the presence of vegetation along the sides of the road. However, only 24% of detected white-tailed deer were observed crossing through the structure, suggesting avoidance behaviour to certain characteristics of the gravel road underpass, possibly the presence of vehicles and nearby cottages. Our observations and the very low full-crossing diversity index (0.37) suggest that road underpasses are suitable for co-use by raccoons and white-tailed deer but are unlikely to be used by other species.

Water culverts

Numerous species were detected using water culverts to cross below the highway: black bear, raccoon, white-tailed deer, American mink, river otter, striped skunk, snowshoe hare, red fox, and rodent species. Moose, fisher, and chipmunk were detected at culvert sites, but were never observed crossing through successfully. Water culverts are much less frequented by humans than both train and road underpasses but have structural features that can limit wildlife use. Deer were only observed crossing through the culvert with the highest openness ratio (site 6), and only during the summer seasons, when water levels were lowest. Flooded conditions of culverts likely impeded use by mammals, namely white-tailed deer. Reports of ungulate use of culverts are rare, as most research points to their strict aversion of enclosed spaces with low openness (Foster and Humphrey 1995; Clevenger and Waltho 2005; Kintsch and Cramer 2011). Alternatively, high water levels can facilitate crossings for some mammal species such as American mink, which was detected swimming through the water culvert at site 9 in late spring. In winter, ice formations at water culverts can also affect crossing success. Snowshoe hares were detected using the water culvert at site 9 in winter when the water was fully frozen over. For much of each winter season, snow and ice pile-up obstructed the entrances to one culvert (site 2) almost entirely, leaving only a small opening for access to the structure. Minimal wildlife full crossings were detected during the winter months at this site compared to the other non-obstructed culverts. Interestingly, this obstructed culvert became a winter burrow for an American mink during the winter months of 2016, highlighting the multiple ways that water culverts can serve both humans and animals.

While various species were detected using culverts to cross below the highway, our findings indicate that water culverts are frequented considerably less often than the other studied structures, namely a gravel road underpass and two railroad underpasses. Research conducted on the same highway at nearby water culverts of smaller size (with heights less than 1.8 metres and widths less than 1.8 metres, including one rectangular culvert with a height of 3.0 metres and a width of 6.0 metres) concluded that the culverts were used considerably less than one could expect for designated wildlife passages (Brunen et al. 2020). The study found that out of 20 species observed in the vicinity of the culverts, only about half of the species were detected making a full crossing, and only two species known to be tolerant to water, namely raccoons and American minks, were observed crossing through the culverts with regularity (Brunen et al. 2020). These results may be in part due to the significant structural and environmental differences between the structure types, including the smaller openness ratio of the studied water culverts, the concrete substrate, and the presence of water. Water culverts are a common structural component of highway systems, and our findings support previous work documenting their use by some mammal species; however, water culverts also show limited use compared to larger, more open structures. The potential for water culvert use by wildlife to be improved based on modifications, maintenance, and structural design is an important topic for future work, e.g., retrofitting with ledges to allow small- and medium-sized mammals to use culverts without having to enter the water (Trocmé and Righetti 2012).

Species of special interest

A number of species are of particular interest for conservation purposes, due to large home ranges which bear significance to inform land conservation prioritization at a local or regional scale, where habitat fragmentation, functional ecological connectivity, and adaptation to climate change are key elements of interest (Koehler and Pierce 2003). Several species of interest were detected throughout the course of our study, including black bear (2), bobcat (29), coyote (12), and moose (5), all of which were observed crossing through one or several structures. A recent study in the same region exclusively on water culverts also detected black bear and bobcat near the openings of the structures, but no entries were observed (Brunen et al. 2020), likely due to the significantly smaller size of monitored culverts compared to the size of structures monitored in our study. However, these observations are noteworthy as they indicate the species' presence near the highway, and, in our case, their ability and willingness to enter and cross through some of the existing structures. All species of special interest have naturally low population densities within the region and large home ranges, believed to be a function of food distribution and abundance (Leptich and Gilbert 1989; Koehler and Pierce 2003). Urbanization and habitat fragmentation have significant adverse impacts on wildlife species, especially mammalian carnivores, in large part due to their habitat size and preferences (Riley et al. 2003). Monitoring the effects of habitat fragmentation and investing in mitigation measures (including fencing and wildlife passages) could facilitate the movement of these species and decrease the number of WVCs within the region (Rytwinski et al. 2016).

Species rarely detected

Among species we might have expected to detect more frequently, fisher (2) is especially noteworthy due to its conservation interest. Fisher presence in the region is frequently confirmed both by trapping records and winter tracking information that is collected by trained volunteers and coordinated by various local or regional conservation organizations (including Appalachian Corridor, Conservation des vallons de la Serpentine, and Ruiter Valley Land Trust). Also of note, snowshoe hare is a favoured prey of several of the mammalian carnivores detected in the region, including coyote and bobcat (Patterson et al.1998; Matlack and Evans 1992). The snowshoe hare is frequently encountered in the region yet its presence at the crossing structures was relatively low (14) compared to other detected prey species, including squirrels (77) and groundhogs (41). Although information from winter tracking efforts confirmed fisher and snowshoe hare presence in the region, and along specific sections to the north or south of Highway 10 East, it would be beneficial to consider more systematic surveys within the region. We believe that surveys encompassing natural habitats abutting the monitored crossing structures and running along both the northern and southern boundaries of the road may provide valuable information on species distribution in the study area and possible causes of the limited detection of several mammal species at the study sites.

Co-use of existing crossing structures by wildlife and humans

Very low or no human co-use

While our study did not differentiate between squirrel species, red squirrels (*Sciurus vulgaris*) are rarely observed using crossing structures that experience human activity. Research in Spain found that only days with less than one human event allowed for crossings by red squirrels and rats (Mata et al. 2005). Another study evaluated wildlife use of a wildlife-designated structure and two existing crossing structures and found that red squirrels were observed crossing only through the wildlife-designated structure (Yushin et al. 2020). The results from both studies coincide with what we have observed at our crossing structures, namely that squirrel species have a very low human co-use level and were not observed crossing through a structure on days with over four human activities.

Low human co-use

In our study, American minks and snowshoe hares rarely utilized the crossing structures when daily human activity levels were above four, suggesting a low co-use to human activity. Research has shown that European hares (*Lepus europaeus*) have been observed using multi-use crossing structures three hours after use by humans (van der Ree and van der Grift 2015). Small mammals, including Eurasian hares (*Lepus capensis*) and mustelid species, pass through wildlife culverts in Poland significantly less often during months that incurred high levels of human activity (May and October) (Wazna et al. 2020). These studies indicate aversion to crossing structures for hare and mustelid species when daily human activity levels are high. Contrarily, one study conducted on woolly hares (*Lepus oiostolus*) found that human presence did not influence their use of existing crossing structures (Wang et al. 2018). However, this lack of correlation may be due to the limited range of human activity detected at the crossing structures, which mainly consisted only of occasional highway maintenance crew visits to the sites.

We found a negative correlation between American mink full crossings and human presence and a strong negative correlation between total observation events and human presence (Table 4). Out of the 78 American mink detections throughout the study period, 77 of them occurred at one of five water culvert sites, which are the structure type that exhibited the lowest overall daily human activity levels (between 0.1 and 1.3 per day). These findings suggest that American mink are less likely to be observed near crossing structures that experience more than an average of one human activity per day.

Moderate human co-use

Red foxes showed a negative correlation between successful full crossings and increasing daily human activity at the study sites. Our statistical results about red foxes suggest a negative correlation for full crossings and a marginally significant negative correlation for total detections (Table 4). Many studies have found little to no correlation between full crossings by red foxes and human presence at wildlife passages and existing crossing structures (Rodriguez et al. 1996; Mata et al. 2005; Grilo et al. 2008; Yushin et al. 2020). However, one study found a negative correlation between wildlife use and human use of wildlife passages for all species observed, which included red foxes (Wazna et al. 2020), which supports our categorization of moderate human co-use for red foxes at our study sites.

Our observation that white-tailed deer are less likely to approach crossing structures that exhibit higher human activity levels agrees with other studies. While we did not analyze the times of day at which individual species utilized the crossing structures (other than raccoon in Fig. 5), Barrueto et al. (2014) reported that white-tailed deer are prone to crossing through crossing structures more often during crepuscular and nocturnal hours, whereas daily human activity levels are high during daytime hours. Similarly, van der Ree and van der Grift (2015) found that deer species would cross through crossing structures on average three hours after human presence for sites with high daily human activity levels. Other research also found that the total number of full crossings for roe deer (*Capreolus capreolus*) and white-tailed deer was negatively correlated with an increase in human activity (Bhardwaj et al. 2020; Wazna et al. 2020).

Our statistical results on white-tailed deer and human presence do not suggest a relationship between full crossings and human presence but do show a negative relationship between total detections and human presence. While our results align with other studies (Bhardwaj et al. 2020; Wazna et al. 2020), many factors are likely to influence use of existing crossing structures by white-tailed deer (as well as for other species). Ungulate use of culverts is rare due to aversion behaviour toward spaces and structures with low openness (Foster and Humphrey 1995; Clevenger and Waltho 2005; Kintsch and Cramer 2011). Although the water culverts in our study experienced the lowest average daily human activity levels across all structure types, white-tailed deer rarely crossed through the monitored water culverts, likely due to low openness and presence of water. This general aversion behaviour toward the water culverts would influence the results obtained from the Kendall's Tau tests.

High human co-use

Our study found no correlation between coyote full crossings and level of human activity at the scale of full days, but this difference compared to other studies may be due to the different evaluation timeframes used in the studies. Coyote have been known to modify their behaviour near wildlife crossing structures to avoid human presence, preferring to cross during crepuscular and nocturnal hours (Barrueto et al. 2014). Barrueto et al. (2014) also found that coyotes tend to cross later on days with high human activity.

Groundhogs were observed to use the underpasses regardless of human activity levels. One study conducted on Himalayan marmots (*Marmota himalayana*) also found no correlation between use of crossing structures and human activity levels (Wang et al. 2018). Additionally, studies have found no correlation between use of crossing structures and levels of human activities for the domestic cat (Mata et al. 2005; Yushin et al. 2020). The results from our correlation tests on groundhog and human presence support these findings, suggesting there is no clear relationship between human presence and groundhog full crossings nor total detections (Table 4). Groundhog observations at the study sites remained relatively stable across all categories of daily human activity levels.

Very high human co-use

We found a strong positive correlation between the use of existing crossing structures by raccoon and the presence of raccoon at the structures with increasing human activity levels. This correlation may be heavily influenced by raccoon use of the gravel road underpass (site 5), which had the highest observed daily human activity levels (33.9 per day) of all study sites. Additionally, site 5 is located on a small gravel municipal road that is sparsely lined with houses and cottages, which may attract raccoons to the area for scavenging purposes. A recent study by Yushin et al. (2020) found that raccoons exhibited no preference between a wildlife passage and two existing crossing structures used by humans.

Limitations and future research needs

While our observations across eight existing crossing structures provide evidence of mammal presence and use of the structures and of a species-specific influence of human use, a larger sample size of existing crossing structures will be needed to further analyze the influence of human use on mammal behaviour and movement patterns, while controlling for other variables. There have been a few studies comparing the effects of human use at large numbers of existing crossing structures (LaPoint et al. 2003; Ng et al. 2004; Grilo et al. 2008), yet their periods of observation were limited to ranges of only 4 to 40 days, or their sites were limited to low levels of human activity (Rodriguez et al. 1997). We chose to analyze fewer underpasses in exchange for a longer observation period, as we believe the seasonal and diurnal changes in human and mammal activity levels could be an important factor to consider in future statistical analyses on this dataset to assess the effectiveness of existing underpasses for mammal use.

The detectability of mammals by motion-sensor cameras has been questioned in a recent comparison of video to infrared and motion-detection cameras showing that the cameras missed 10% of medium-sized mammals visiting culverts (Jumeau et al. 2017). As we chose to employ an equal number of cameras at each site, regardless of structure size and openness, it is possible that some mammal crossings (most likely by small- and medium-sized mammals) were not detected, at least in the larger structures. For large mammals, this is less likely, as all cameras were adjusted for maximum range detection and maximal coverage of underpass width. However, at the train underpasses or the road underpass, a few large mammals may have been missed, while detection of small mammals may have been higher in the water culverts. We would encourage future studies to use a greater diversity of angles and heights to maximise detection of species of all sizes (Meek et al. 2014). Numbers of mammal detections at all sites should be considered as a minimum activity, as true passages and presence may be higher. At the circular water culvert at site 2, the placement of cameras did not allow for the detection of ATVs and pedestrians passing by the northern end of the culvert via an adjacent bridge. The tally of human activity at this site must therefore be taken as a minimum, and the results at this site are likely incomplete. Another limitation of the use of cameras is the possibility of underrepresented species due to camera avoidance behaviour. Some predators, including red fox, detect and avoid cameras due to certain stimuli (Meek et al. 2016). Since we did not include a second method of mammal detection in our study for comparison, such as print traps, we cannot determine whether wildlife exhibited avoidance behaviour toward the cameras.

It is important to note that Kendall's Tau tests only consider overall positive or negative relationships (Laurencelle 2009), but for species that exhibit higher occurrences of full crossings or detections on days with intermediate human activity levels, the results from Kendall's Tau test would not reflect this non-linear relationship.

A final limitation of this study is the lack of robust statistical analysis, due to the limited number of sites observed, and the high variability of characteristics between sites. It is difficult to include all eight research sites into one combined statistical test due to the wide range of structural differences between the structures. For example, the culvert located at site 9, which always showed presence of water, varies greatly from the train underpass located at site 1, which always had a dry path and has a much higher openness ratio. These differences are difficult to quantify and are complex to incorporate into a comprehensive statistical test, unless a large sample of structures is monitored. Such a larger analysis would also allow for a species-specific approach to identify preferences for existing crossing structures by different species if the observation period is long enough (several years) to gather sufficient data for individual species.

Conclusion

Our results provide evidence that 21 wildlife species of small-, medium-, and large-sized mammals in the study area used one or several existing crossing structures, including water culverts, train underpasses, and a gravel road byway. We found evidence that some mammal species will use underpasses with low levels of daily human activity, suggesting co-use of existing crossing structures is possible for select species. The crossing structures that are most promising in supporting a diversity of wildlife crossings by species of particular interest for conservation (moose, black bear, bobcat, coyote, fisher) and by large mammals causing the most damage or loss of lives in WVCs (i.e., including white-tailed deer) were the two train underpasses, whereas the gravel road underpass was mostly used by raccoons, with only a moderate number of crossings by white-tailed deer and very few crossings by any other species. The water culverts were the least promising as overall, they were very rarely used by these species due to structural and environmental characteristics, including their smaller size, substrate composition, frequent presence of water, and lack of vegetation.

While our study did not consider crossing structures of higher human use, such as high-use roads or highways, the strengths of our study include the length of time during which continuous monitoring took place at the structures (up to 778 days) and the placement of four camera traps at each structure (two facing inward and two facing outward), allowing us to determine whether individuals successfully crossed through the structures or displayed avoidance behaviour.

Despite the absence of an extensive statistical analysis within our study, we have gathered an extensive number of observations spanning seasons and years around the study area and we believe the following recommendations should be considered for future research and conservation efforts. Given our knowledge of habitat fragmentation and WVCs, we recommend that to increase the use of existing underpasses by mammals, fencing should be installed along Highway 10 East to guide wildlife to the structures and to decrease road mortality. Wildlife fencing is effective at reducing road mortality, whereas measures that are less expensive than fencing, such as wildlife warning signs and reflectors, are ineffective, and wildlife passages do not reduce road mortality unless fences are present (Rytwinski et al. 2016). Continued use of cameras will then be able to determine if additional species would discover and start using the structures. Mortality reduction graphs can be applied to the area to prioritize road sections for fencing (Spanowicz et al. 2020). Based on our knowledge of the study area and species observed near the crossing structures, we believe retrofitting the existing water culverts with dry ledges might encourage small- and medium-sized mammals that were rarely observed crossing through the monitored water culverts to utilize the structures (including groundhog and red fox). Additionally, while our study does not explicitly demonstrate that designated wildlife passages are needed, the construction of such wildlife passages (e.g., in priority areas with high animal activity and in mortality hotspots where existing structures are not well used by wildlife) would very likely encourage safe wildlife crossings for species, particularly the mammal species grouped into the lower levels of human-co-use in our paper (including North American porcupine, American mink, and bobcat). To better support these considerations, we recommend that further research within the area focus on a considerably larger sample size of underpasses to allow for a comparison of the influence of structural and environmental variations between existing structures.

Acknowledgements

We extend our sincere gratitude to the Ministère des Transports du Québec (MTQ) for providing mortality data and permission to access the sites and install cameras, and Appalachian Corridor for project coordination. We warmly thank all the volunteers who helped with fieldwork and photo analysis, including Melissa Allen, Raphaël-Jonathan Beaupré, Benjamin Brunen, Grisel Calcagno, Antony Di Done, Jenny Paola Espitia Contreras, Colette Ethier, Nicolas Hamel, Eva-Maria Hanchar, Maddie Karcher, Sara Khakwani, Milan Konman, Anna Krupa, Jonathan Mercier-Leboeuf, Sabrina Mruczek, Nadege Pieters, Devin Pawluk, Clément Robidoux, Bernardo Alvarado-Rojas, Tara Angelina Hopkins Rose, Lauren Samo, Calcin Schnurr, Mehan Stanlet, Brittany Talarico, Steffy Velosa, Nancy Warnock, Vanessa Weber, as well as unconditional support from Jonathan Cole, Jaynina Deku, Jennifer Donnini, and Mehrdokht Pourali. We appreciate critical and constructive comments from J-O Helldin and an anonymous reviewer that helped improve this paper. Parts of this project were funded by a Concordia Undergraduate Student Research Award (CUSRA) to D.L. from Concordia University, and by the MTQ and the ECHO Foundation.

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Appendix 1

Table A1. Number of detections by type, species, and level of daily human activity on average over 50 days.

Number of human activities per day	**Number of days in this bin**	**Species**		**American mink *Neovison vison***	**Black bear *Ursus americanus***	**Bobcat *Lynx rufus***	**Chipmunk *Tamias striatus***	**Coyote *Canis latrans***	**Domestic cat *Felis catus***	**Fisher *Pekania pennanti***	**Groundhog *Marmota monax***
		Type of detection	Sum of detections	78	2	29	1	18	32	3	49
[0]	2767	Full crossing		0.452	0.036	0.036	-	-	0.018	-	0.108
		Aversion		0.289	-	0.036	-	0.054	0.018	0.018	0.054
		Unknown		0.560	-	-	0.018	0.108	-	0.018	-

Number of human activities per day	Number of days in this bin	Species		American mink *Neovison vison*	Black bear *Ursus americanus*	Bobcat *Lynx rufus*	Chipmunk *Tamias striatus*	Coyote *Canis latrans*	Domestic cat *Felis catus*	Fisher *Pekania pennanti*	Groundhog *Marmota monax*
		Type of detection	Sum of detections	78	2	29	1	18	32	3	49
[1]	221	Full crossing		0.226	-	-	-	-	1.131	-	0.226
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[2]	353	Full crossing		-	-	-	-	-	0.992	-	-
		Aversion		0.425	-	-	-	-	0.142	-	0.283
		Unknown		-	-	-	-	-	-	-	-
[3]	288	Full crossing		-	-	2.083	-	-	0.174	0.174	0.521
		Aversion		-	-	2.083	-	0.174	-	-	0.174
		Unknown		-	-	-	-	-	-	-	0.694
[4]	264	Full crossing		-	-	1.515	-	0.189	-	-	0.568
		Aversion		-	-	1.515	-	0.189	-	-	0.189
		Unknown		-	-	-	-	-	-	-	-
[5]	152	Full crossing		0.329	-	-	-	0.329	1.645	-	1.316
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[6]	119	Full crossing		-	-	-	-	-	-	-	1.261
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[7]	79	Full crossing		-	-	1.266	-	0.633	1.266	-	1.266
		Aversion		-	-	1.266	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[8]	56	Full crossing		-	-	-	-	-	-	-	-
		Aversion		0.893	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	0.893	-	-
[9–10]	53	Full crossing		-	-	-	-	-	-	-	0.943
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[11–13]	77	Full crossing		-	-	-	-	-	-	-	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[14–15]	50	Full crossing		-	-	-	-	-	3.000	-	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[16–19]	64	Full crossing		-	-	-	-	-	-	-	0.781
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	0.781	-	-
[20–22]	58	Full crossing		-	-	-	-	0.862	-	-	0.862
		Aversion		-	-	-	-	-	-	-	2.586
		Unknown		-	-	-	-	-	-	-	-
[23–26]	63	Full crossing		-	-	-	-	-	-	-	-
		Aversion		-	-	-	-	-	-	-	0.794
		Unknown		-	-	-	-	-	-	-	-
[27–30]	57	Full crossing		-	-	-	-	0.877	-	-	-
		Aversion		-	-	-	-	-	-	-	0.877
		Unknown		-	-	-	-	-	-	-	-
[31–35]	50	Full crossing		-	-	-	-	-	-	-	-
		Aversion		-	-	-	-	-	-	-	1.000
		Unknown		-	-	-	-	-	-	-	-
[36–44]	50	Full crossing		-	-	-	-	1.000	-	-	1.000
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-

Number of human activities per day	Number of days in this bin	Species	American mink *Neovison vison*	Black bear *Ursus americanus*	Bobcat *Lynx rufus*	Chipmunk *Tamias striatus*	Coyote *Canis latrans*	Domestic cat *Felis catus*	Fisher *Pekania pennanti*	Groundhog *Marmota monax*
		Type of detection Sum of detections	78	2	29	1	18	32	3	49
[45–67]	53	Full crossing	-	-	-	-	0.943	1.887	-	0.943
		Aversion	-	-	-	-	-	0.943	-	0.943
		Unknown	-	-	-	-	-	-	-	-
[68–120]	24	Full crossing	-	-	2.083	-	-	-	-	-
		Aversion	-	-	2.083	-	-	-	-	-
		Unknown	-	-	-	-	-	-	-	-

Table A2.

Number of human activities per day	Number of days in this bin	Species	Moose *Alces alces*	Mouse spp. *Mus* spp.	Muskrat *Ondatra zibethicus*	North American beaver *Castor canadensis*	North American porcupine *Erethizon dorsatum*	North American river otter *Lontra canadensis*	Raccoon *Procyon lotor*	Rat spp. *Rattus* spp.
		Type of detection Sum of detections	5	26	26	1	18	7	1586	20
[0]	2767	Full crossing	-	0.072	0.253	0.018	0.271	0.108	6.831	0.361
		Aversion	0.018	0.235	0.054	-	0.036	-	2.765	-
		Unknown	-	0.163	0.126	-	-	0.018	0.922	-
[1]	221	Full crossing	-	-	-	-	-	-	3.167	-
		Aversion	-	-	-	-	-	-	1.357	-
		Unknown	-	-	-	-	-	-	-	-
[2]	353	Full crossing	-	-	-	-	-	-	1.983	-
		Aversion	-	-	-	-	-	-	0.567	-
		Unknown	-	-	-	-	-	-	0.142	-
[3]	288	Full crossing	0.347	-	-	-	-	-	4.688	-
		Aversion	-	-	-	-	-	-	0.174	-
		Unknown	-	-	-	-	-	-	-	-
[4]	264	Full crossing	-	-	-	-	-	-	4.356	-
		Aversion	-	-	-	-	-	-	0.379	-
		Unknown	-	-	0.189	-	-	-	0.568	-
[5]	152	Full crossing	-	-	-	-	-	-	2.303	-
		Aversion	-	-	-	-	-	-	0.658	-
		Unknown	-	-	-	-	-	-	0.658	-
[6]	119	Full crossing	0.420	-	-	-	-	-	2.521	-
		Aversion	0.420	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	-	-
[7]	79	Full crossing	-	-	-	-	-	-	3.165	-
		Aversion	-	-	-	-	-	-	3.797	-
		Unknown	-	-	-	-	-	-	-	-
[8]	56	Full crossing	-	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	0.893	-
[9–10]	53	Full crossing	-	-	-	-	-	-	9.434	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	1.887	-
[11–13]	77	Full crossing	-	-	-	-	-	-	16.883	-
		Aversion	-	-	-	-	-	-	0.649	-
		Unknown	-	-	-	-	-	-	1.948	-
[14–15]	50	Full crossing	-	-	-	-	-	-	21.000	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	2.000	-
[16–19]	64	Full crossing	-	-	-	-	-	-	23.438	-
		Aversion	-	-	-	-	-	-	0.781	-
		Unknown	-	-	-	-	-	-	3.906	-

Number of human activities per day	Number of days in this bin	Species		Moose *Alces alces*	Mouse spp. *Mus* spp.	Muskrat *Ondatra zibethicus*	North American beaver *Castor canadensis*	North American porcupine *Erethizon dorsatum*	North American river otter *Lontra canadensis*	Raccoon *Procyon lotor*	Rat spp. *Rattus* spp.
		Type of detection	Sum of detections	5	26	26	1	18	7	1586	20
[20–22]	58	Full crossing		-	-	-	-	-	-	86.207	-
		Aversion		-	-	-	-	-	-	0.862	-
		Unknown		-	-	-	-	-	-	1.724	-
[23–26]	63	Full crossing		-	-	-	-	-	-	19.048	-
		Aversion		-	-	-	-	-	-	3.968	-
		Unknown		-	-	-	-	-	-	4.762	-
[27–30]	57	Full crossing		-	-	-	-	-	-	57.895	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	3.509	-
[31–35]	50	Full crossing		-	-	-	-	-	-	38.000	-
		Aversion		-	-	-	-	-	-	1.000	-
		Unknown		-	-	-	-	-	-	2.000	-
[36–44]	50	Full crossing		-	-	-	-	-	-	61.000	-
		Aversion		-	-	-	-	-	-	8.000	-
		Unknown		-	-	-	-	-	-	6.000	-
[45–67]	53	Full crossing		-	-	-	-	-	-	144.340	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	12.264	-
[68–120]	24	Full crossing		-	-	-	-	-	-	93.750	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	4.167	-

Table A3.

Number of human activities per day	Number of days in this bin	Species		Red fox *Vulpes vulpes*	Rodent spp.	Snowshoe hare *Lepus americanus*	Squirrel spp. *Sciurus* spp.	Striped skunk *Mephitis mephitis*	Weasel *Mustela erminea*	White-tailed deer *Odocoileus virginianus*	Unknown
		Type of detection	Sum of detections	461	9	14	86	4	2	1106	9
[0]	2767	Full crossing		2.024	-	0.036	0.217	0.072	0.018	0.632	0.018
		Aversion		3.704	0.163	0.145	1.175	-	-	7.553	0.072
		Unknown		0.434	-	-	0.072	-	-	0.253	-
[1]	221	Full crossing		1.584	-	-	-	-	-	2.941	-
		Aversion		0.226	-	-	-	-	-	7.014	-
		Unknown		0.226	-	-	-	-	-	0.679	-
[2]	353	Full crossing		1.416	-	-	0.142	-	-	6.941	0.142
		Aversion		0.425	-	0.283	0.142	-	-	10.765	-
		Unknown		0.567	-	-	-	-	-	1.558	-
[3]	288	Full crossing		2.951	-	-	-	-	0.174	5.556	-
		Aversion		-	-	-	-	-	-	3.993	-
		Unknown		0.174	-	-	-	-	-	0.694	-
[4]	264	Full crossing		3.030	-	-	-	-	-	6.818	-
		Aversion		0.189	-	0.189	-	-	-	4.356	-
		Unknown		0.189	-	-	-	-	-	0.568	-
[5]	152	Full crossing		1.316	-	0.329	-	-	-	8.553	-
		Aversion		0.658	-	-	-	-	-	5.592	0.329
		Unknown		0.329	-	-	-	-	-	2.961	-

Number of human activities per day	**Number of days in this bin**	**Species**	**Red fox *Vulpes vulpes***	**Rodent spp.**	**Snowshoe hare *Lepus americanus***	**Squirrel spp. *Sciurus* spp.**	**Striped skunk *Mephitis mephitis***	**Weasel *Mustela erminea***	**White-tailed deer *Odocoileus virginianus***	**Unknown**
		Type of detection Sum of detections	461	9	14	86	4	2	1106	9
[6]	119	Full crossing	4.202	-	-	-	-	-	2.941	-
		Aversion	1.681	-	-	0.840	-	-	2.521	-
		Unknown	0.420	-	-	-	-	-	3.361	-
[7]	79	Full crossing	6.329	-	-	-	-	-	0.633	-
		Aversion	1.266	-	-	-	-	-	5.696	-
		Unknown	-	-	-	-	-	-	3.165	-
[8]	56	Full crossing	0.893	-	-	-	-	-	0.893	-
		Aversion	-	-	-	-	-	-	14.286	-
		Unknown	-	-	-	-	-	-	-	0.893
[9–10]	53	Full crossing	0.943	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	3.774	-
		Unknown	-	-	-	-	-	-	2.830	-
[11–13]	77	Full crossing	3.247	-	-	-	-	-	1.948	-
		Aversion	-	-	-	-	-	-	2.597	-
		Unknown	0.649	-	-	-	-	-	0.649	-
[14–15]	50	Full crossing	-	-	-	-	-	-	2.000	-
		Aversion	-	-	-	-	-	-	5.000	1.000
		Unknown	-	-	-	-	-	-	1.000	-
[16–19]	64	Full crossing	-	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	1.563	-
		Unknown	-	-	-	-	-	-	0.781	-
[20–22]	58	Full crossing	-	-	-	-	-	-	3.448	-
		Aversion	-	-	-	-	-	-	2.586	-
		Unknown	-	-	-	-	-	-	1.724	-
[23–26]	63	Full crossing	0.794	-	-	-	-	-	3.175	-
		Aversion	-	-	-	-	-	-	3.968	-
		Unknown	-	-	-	-	-	-	-	-
[27–30]	57	Full crossing	-	-	-	-	-	-	-	-
		Aversion	3.509	-	-	-	-	-	1.754	-
		Unknown	-	-	-	-	-	-	2.632	-
[31–35]	50	Full crossing	1.000	-	-	-	-	-	2.000	-
		Aversion	-	-	-	-	-	-	1.000	-
		Unknown	-	-	-	-	-	-	6.000	-
[36–44]	50	Full crossing	-	-	-	-	-	-	2.000	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	1.000	-
[45–67]	53	Full crossing	-	-	-	-	-	-	2.830	-
		Aversion	0.943	-	-	-	-	-	5.660	-
		Unknown	-	-	-	-	-	-	3.774	-
[68–120]	24	Full crossing	-	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	6.250	-
		Unknown	2.083	-	-	-	-	-	-	-

Nature Conservation 47: 271–281 (2022)
doi: 10.3897/natureconservation.47.71472
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Effectiveness of wire netting fences to prevent animal access to road infrastructures: an experimental study on small mammals and amphibians

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Academic editor: Cristian Remus Papp | Received 12 July 2021 | Accepted 24 January 2022 | Published 25 March 2022

http://zoobank.org/C1001863-D6C7-47AC-B249-08D240177378

Citation: Conan A, Fleitz J, Garnier L, Le Brishoual M, Handrich Y, Jumeau J (2022) Effectiveness of wire netting fences to prevent animal access to road infrastructures: an experimental study on small mammals and amphibians. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 271–281. https://doi.org/10.3897/natureconservation.47.71472

Abstract

Transport infrastructures, such as highways, disrupt animal migrations and cause roadkill. To mitigate the latter problem, fences have been built but their effectiveness has rarely been tested under controlled conditions. Here, we tested the effectiveness of the most commonly used fence in France and probably in Europe (wire netting fence) to block animals. We tested the wire netting fence, with and without a structural modification (i.e. an overhang), with three small mammalian species (the European hamster: *Cricetus cricetus* Linnaeus, 1758; the common vole: *Microtus arvalis* Pallas, 1778 & the wood mouse: *Apodemus sylvaticus* Linnaeus, 1758) and two amphibian species (the marsh frog: *Pelophylax ridibundus* Pallas, 1771 & the European green toad: *Bufotes viridis* Laurenti, 1768). During testing, all small vertebrate species tested were placed into an arena, from which they could only escape by crossing the wire netting fence. Without an overhang, almost all adult individuals of all tested species were able to climb over a 30 to 40 cm high wire netting fence. Furthermore, the addition of an 8 cm long overhang at the top of the fence stopped the amphibian species tested but not the most agile mammalian species, such as the hamster and the wood mouse. Based on these results, we do not support the construction of wire netting fences along roads as a measure to stop small animals from crossing. We recommend the use of more effective and durable fences, which, in addition, can be associated with wildlife passages to reconnect isolated populations.

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* These authors contributed equally and are co-last authors.

Keywords
Amphibians, fences, roadkill, small mammals

Introduction

Millions of animals around the world are killed daily by wildlife-vehicle collisions, affecting populations of most taxa (Bruinderink and Hazebroek 1996; Laist et al. 2001; Rao and Girish 2007). Even on roads with only moderate traffic, roadkill can severely impact population viability (Eigenbrod et al. 2007). These impacts can be accentuated in highly modified landscapes, when terrestrial fauna has to cross roads on a daily basis and/or during dispersion and migration movements (Billeter et al. 2008; Bissonnette and Rosa 2009). To limit roadkill, different mitigation measures, such as the construction of fences and wildlife passages, have been implemented, especially in industrialized regions (e.g. Australia, Western Europe and North America). Initially installed to limit vehicle collisions with large mammal species, like ungulates (e.g. deer, wild boar), the primary aim of fence construction concerned human safety and the limitation of economic losses associated with these collisions (Romin and Bissonette 1996; Schwabe et al. 2002; Forman et al. 2003; Bouffard et al. 2012). The installation of fences on both sides of the road or along railways is not mandatory but global recommendations advise such measures, if the risk of collision and/or wildlife mortality is high (Iuell et al. 2003). Large-fauna fences or wire netting must be tall enough to prevent animals from jumping over it (i.e. >1.8 m, Iuell et al. 2003; Morand and Carsignol et al. 2019), while mesh size of such fences is typically relatively large (in general greater than 60×60 mm).

When research demonstrated the major role that roads play in habitat fragmentation and its negative impact on the populations of many species (and not only large mammals), further mitigation measures were implemented. These mitigation measures are designed to reduce roadkill (i.e. fences) and restore population connectivity (i.e. wildlife passages) to allow safe movements on different parts of the habitats separated by the road for various small fauna, such as reptilian (turtle), amphibian (frog and toad), small (shrew) and medium-sized mammalian species (hares, foxes, badgers, etc.) (Aresco 2003; Glista et al. 2009; Klar et al. 2009; Jarvis et al. 2019; Plante et al. 2019). For these species, different fences (made from wire netting, concrete, PVC or metal) were designed and often installed alongside the large-fauna fences. In Western Europe, wire netting fences (with a typical mesh size of 6.5×6.5 mm and a height of 40 to 60 cm) are most often used to block small fauna, and are usually attached to the large-fauna fences (Iuell et al. 2003; Puky 2003; Beebee 2013; Morand and Carsignol et al. 2019). Similar to the large-fauna fences, these small-fauna fences coupled with a wildlife passage are needed to manage the reconnection of populations in areas of high biodiversity (Clevenger et al. 2001; Iuell et al. 2003; Beebee 2013; Testud and Miaud 2018).

Some species are more sensitive than others and require special attention during the planning of infrastructure, such as roads. For example, amphibians are particularly vulnerable to roadkill due to their mass migration strategy (Joly 2019; Cayuela et al. 2020) and their immobility when facing motor vehicles (Gibbs and Shriver 2005; Mazerolle et al. 2005). Amphibians are of particular concern, since globally 41% of all amphibian species are threatened with extinction (IUCN 2021). Small mammals are also of concern, since they often use the side of roads as refuge, especially in a highly modified landscape (Ruiz-Capillas et al. 2013; Jumeau 2017). While the impact of road mortality on populations of these small mammalian species may not appear problematic, because their population densities are generally high, this is not always the case. Studies show that some of these species are declining at an alarming rate and are now considered endangered, like the garden dormouse (*Eliomys quercinus*) or the European hamster (*Cricetus cricetus*) (Surov et al. 2016; Bertolino 2017). Hence, roadkill of wildlife is an important issue that has to be addressed in an overall conservation strategy (O'Brien 2015; Pinot et al. 2016).

Research objectives

To avoid roadkill of various small-fauna species, such as amphibian and small mammalian species, road managers in Western Europe frequently install wire netting fences alongside roads. Because of their low costs and easy installation, they may seem an attractive measure in roadkill prevention. However, to the best of our knowledge, the effectiveness of such fences to stop amphibian and small mammalian species from entering the road has rarely been tested under controlled conditions (Dodd et al. 2004; Woltz et al. 2008; Brehme et al. 2021). The goal of our study was to experimentally test the effectiveness of wire netting fences to block small fauna, preventing passage into roads. We hypothesized that a wire netting fence will not be appropriate for "agile" species, which might be able to climb the fence (e.g. mice) or jump over it (e.g. frogs), while it will be effective for other species (e.g. hamsters, voles). We further hypothesized that the inclusion of an overhang (i.e. back-bending the top wire netting) will improve its effectiveness. Finally, our study focused on the effectiveness of fences to stop animal road crossing, while studies investigating the effectiveness of such fences in guiding animals towards wildlife passages are lacking and should be encouraged.

Materials and methods

Protocol

This study presents the combined results from four independent experiments that were conducted between 2015 and 2020. While the individual protocols and the group of individuals used (adults/juveniles) differed to some degree between studies, they all shared the same general principle. In each study, individuals were placed in an arena for a pre-determined duration, from which they could only exit by crossing the fence under investigation. During that period, animals were monitored continuously with an infrared video-camera, so that individual behaviour and the success or failure of passage could be determined.

All studies used a wire netting fence with a mesh size of 6.5×6.5 mm. However, studies differed with respect to fence height (30 or 40 cm, which corresponds to the height typically found along roads in Alsace), the presence or absence of an overhang and its length (from 2 to 15 cm), the tested species, the number of individuals used per test, and the time given to individuals to escape the arena (30 min, 10 or 12 hours). The latter was due to behavioural differences between species and the requirements imposed by the various capture and ethical permits. (Table 1; see Suppl. material 1, for the exact protocol of each study). With the exception of the study concerning the European hamster, the length of the overhang was varied to test its effect on passage success. The greatest length of the overhang was tested first (15 cm or 10 cm, depending on the study) and decreased gradually in subsequent trials, once all individuals had been tested for a given length. Given the nocturnal activity patterns of the tested species, all experiments were conducted during the night, spanning the summers from 2015 to 2020.

Species were selected according to their mode of locomotion. The following species were tested (Table 1): (1) two small mammalian species, considered to be 'non-agile', the European hamster and the common vole, both of which are good runners but have limited jumping abilities; (2) one 'agile' small mammal, the wood mouse, which has good climbing and jumping abilities; (3) one 'agile' amphibian species, the marsh frog, with good jumping abilities; and, lastly, (4) one 'non-agile' amphibian species, the European green toad, which has limited jumping abilities. All tested individuals were captured from the wild for the purpose of the concerned study, except hamsters, which came from a local breeding centre. However, only European green toads were maintained in captivity after capture (for 3 and 15 days for juveniles and adults, respectively, since they participated in a further study). All other captured species were released immediately after the end

Table 1. Summary of the species tested and experimental set-up (for more details, see SM).

Species	Origin of animals	N	Height of netting fence tested (cm)	Length of the overhang (cm)	Body length (mean±SEM) cm	Duration of experiment	Number of animals tested simultaneously
European hamster	Laboratory	26 (5♀ adults 8♂ adults & 13 juveniles)	40	8	25.17±2.00 (adults) 19.88±1.37 (juveniles)	12 h per individual	1
Common vole	Wild	40 adults of each species (8 for each overhang length)	30	0, 2, 5, 10, 15	9.16±0.68	30 minutes per individual	1
Wood mouse	Wild	40 adults (8 for each overhang length)	30	0, 2, 5, 10, 15	9.48±0.70	30 minutes per individual	1
Marsh frog	Wild	40 adults (8 for each overhang length)	30	0, 2, 5, 10, 15	No data.	30 minutes per group	8 adults
European green toad	Wild	39 (9♂ adults & 20 juveniles), the same for both the 0 or 10 cm overhang	40	0 or 10 (only for adults)	5.94±0.67 (adults) ~ 1 cm (juveniles)	10 hours per group	9 for adults & 20 for juveniles

of testing. The total number of individuals that could be used for experimentation was limited by capture/ethical permits. Before experimentation, individuals were measured and weighed, and sex was determined in all species tested, except marsh frogs. The capture and housing protocols are detailed in the Suppl. material 1. All manipulations were carried out after obtaining the legal authorizations for capture and transport, and the approval of the different protocols by the Ethical Committee (see Suppl. material 1).

Methods

Each time an individual was placed in the arena, alone or with conspecifics, the result of the passage test was recorded either as success (if the individual successfully crossed the fence by climbing or jumping over it) or as failure (if the fence was not crossed). For each overhang length tested, the proportion of crossing success (mean±SEM) was calculated for all individuals tested at that specific overhang length. In the case of the European hamsters and European green toads, test results from adult and juvenile animals were kept separate. For both amphibian species, animals were tested as groups, which prevented to recognize the crossing success of individuals. Given the differences in the experimental protocol of the various species (i.e. individual/group testing, presence/absence and dimensions of the overhang), we present results from all experiments without statistical testing. Nevertheless, we believe that the results are explicit, even in the absence of statistical analysis.

Results

Effectiveness of wire netting fences

Without an overhang, all species were able to cross the fence. The crossing success rate varied between 45% for juvenile green toads and 100% for wood mice, marsh frogs and adult green toads (Table 2). Hamsters were not tested without an overhang. Since crossing success rate of juvenile hamsters was 100% for a fence with a 10 cm overhang

Table 2. Crossing success rates for wire netting fences.

Species	Locomotion type	Status	Fence height	Crossing success without overhang	Crossing success with an 8/10 cm overhang
European hamster	Running+	Adult	40 cm	NA	80%
	Running-	Juvenile	40 cm	NA	100%
Common vole	Running-	Adult	30 cm	87.5%	0% (25% at 15 cm)
Wood mouse	Climbing+/Jumping+	Adult	30 cm	100%	75% (100% at 15 cm)
European green toad	Jumping-	Adult	40 cm	100%	0%
	Jumping-	Juvenile	40 cm	45%	NA
Marsh frog	Jumping+	Adult	30 cm	100%	0%

Without overhang, wire netting fences of 40 cm are not effective to stop the tested small mammals and amphibians. With a 10 cm overhang, the European hamster, Common vole and the Wood mouse can still climb over these fences. The '+' and '-' signs indicate the capabilities of the species, with the '+' sign indicating better performance than the '-' sign.

(and 80% for adult hamsters; Table 2), it is likely that both juvenile and adult hamsters would have crossed the fence lacking an overhang without problems. For the other species, the presence of an 8–10 cm overhang decreased the crossing success rate to 0% for green toads and common voles, but only to 75% for wood mice (Table 2).

In marsh frogs, crossing success dropped (from 100% to 12.5%) when the overhang reached a length of 5 cm and became zero at a 10 cm overhang. For the common vole, the introduction of an overhang reduced the crossing success substantially but some individuals were still able to cross the fence with a 15 cm overhang. The length of the overhang had little effect on the crossing rate of wood mice, which passed even at the greatest length tested.

How animals crossed the fence

Seven of the 20 juvenile green toads tested were able to pass through the 6.5 mm mesh of the wire netting. All other individuals of this species and all individuals of the other species tested that managed to pass the fence, did so by climbing it and not by jumping over it. European hamsters (the largest species tested) were able to pull themselves up onto the overhang by grabbing the end of the overhang and pulling themselves up using their front legs (i.e. without climbing along the overhang), once they reached the top of the fence. The same occurred in wood mice up to an overhang length of ~10 cm. For longer overhangs, wood mice climbed along the overhang, upside down, until they reached its far end, where they passed. The same behaviour was occasionally observed in juvenile hamsters.

Discussion

Our study, which experimentally investigated the effectiveness of wire netting fence to stop small terrestrial vertebrates (five species of small mammals and amphibians) from entering into road infrastructures, clearly demonstrates the limitations of such structures.

Without an overhang at the top of the wire netting fence, individuals of all tested species, adults and juveniles, were able to pass the structure. Clearly, wire netting fences without overhang should be avoided in future constructions. Furthermore, even the addition of an overhang only marginally increased the effectiveness of the wire netting fence in blocking the tested mammalian species. Individuals of all small mammal species tested were still able to cross the fence, including the common vole despite some difficulties, even with a long, 15 cm overhang. For example, hamsters were sufficiently large to reach the far end of the overhang, so that they could pull themselves up and cross the fence. However, some adult individuals were unable to cross the fence, which was likely explained by their body condition (i.e. these were the largest and heaviest adult hamsters). Since the hamsters tested were captive individuals from a breeding center, they were presumably fatter and less agile than wild hamsters. Wood mice were able to reach the far end of the overhang by climbing along the mesh, upside down. However, changes in the design of the overhang structure, like the use of a solid structure (e.g. a metal plate), without gripping possibility, might prevent such small/agile species from crossing. Nevertheless, structures similar to the ones used in our study should be avoided, at least for small mammals.

By contrast, for amphibians, the tested wire netting fence might prove effective when combined with a 10 cm overhang. Adult individuals of European green toads and marsh frogs were unable to pass such a structure during our tests. However, since juvenile frogs were able to pass through the mesh of wire netting fences, even at a relatively small mesh size, their use should be avoided at the proximity of ponds. They should also be avoided when more "agile" amphibians, such as achieved jumping (i.e. Agile frog, *Rana dalmatina*) or climbing species (i.e. European tree frog, *Hyla arborea* or newts) are present. These species were not tested in our study but have been shown to easily cross a 40 cm concrete fence (Conan et al. 2021).

Given our current test results, we suggest to avoid the use of wire netting fence along motorways. In eastern France, 70.4% of overhangs of wire netting fences along motorways inspected by Jumeau (2017) had a length of less than 9 cm, which is lower than the 10 cm overhangs that proofed effective for the tested amphibians in our study. The author explained this situation by a lack of information/communication on behalf of the work crews installing these fences along the roads. If during construction the fences were buried a few centimetres too deep, while fence height above ground was maintained, bending the top of the fence resulted in a too short overhang. In addition, the author reported that 78.2% of inspected fences, even recently built fences, showed signs of deterioration, such as broken mesh, too high vegetation (allowing animals to climb over the fence; Arntzen et al. 1995), as well as deteriorated or absent overhang. These results are especially troubling, since such a state will also reduce the effectiveness of fences for their second role, namely to guide animals to wildlife passages (Clevenger et al. 2001; Beebee 2013; Testud and Miaud 2018).

For several years, studies have highlighted the ineffectiveness of wire netting fences in excluding animals from road infrastructures, especially for amphibians (Schmidt et al. 2008; Testud 2020). Nevertheless, these fences are still being used along newly built roads, even when they are located in the dispersal corridors of endangered species (e.g. green toad and European hamster in Alsace, France). Therefore, we recommend that these fences should be replaced by viable alternatives. Opaque fences, for example, may be more effective in guiding small animals to the wildlife passages, and experimental tests to confirm this are urgently needed. It is, however, important to note that effective fences can impact the movement of individuals on both sides of a road and consequently lead to a decrease in gene flow if individuals are unable to reach wildlife passages (e.g. newt; Matos et al. 2018). In this context, testing the effectiveness of structures to guide animals to wildlife passages is needed in controlled and field conditions while an increase in the number of wildlife passages might also be necessary.

Conclusions

Wire netting fence between 30 and 60 cm is a commonly used mitigation device to prevent small vertebrate species from entering/crossing roads and reduce roadkill. This study showed that its effectiveness is very limited. Accordingly, we suggest that this device should be avoided and replaced by more effective and durable fences.

Ethics approval

All manipulations were carried out after obtaining the legal authorizations for capture and transport (2019-DREAL-EBP-0031) and a certificate permitting the detention of wildlife species in captivity (DDPP67-SPAE-FSC-2019-04). The experimental protocol was approved by the ethics committee (CREMEAS and Ministry) under the agreement number (#18546-2019011810282677 v7).

Acknowledgements

We thank all the students who participated in this study and anonymous reviewers for their valuable comments. We thank Manfred Enstipp for the English editing. Special thanks to Frederic Voegel and Laurence Feltmann. This study was funded by the French Minister of Ecology (DREAL Grand-Est), the Région Grand-Est, and the Collectivité européenne d'Alsace (CeA). They had no role in the study design, writing, collection, analysis and interpretation of data. They agree to the publication of this study.

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Supplementary material 1

Supplementary materials and methods

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Data type: docx. file

Explanation note: In the following we provide details for the four separate studies conducted. Each study used a different experimental set up, which was adapted to the species tested.

Link: https://doi.org/10.3897/natureconservation.47.71472.suppl1

Nature Conservation 47: 283–302 (2022)
doi: 10.3897/natureconservation.47.72321
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Implementing wildlife fences along highways at the appropriate spatial scale: A case study of reducing road mortality of Florida Key deer

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Academic editor: Clara Grilo | Received 29 July 2021 | Accepted 13 November 2021 | Published 25 March 2022

http://zoobank.org/421DFC9F-3DB2-4A09-AD05-43F1E225F3F8

Citation: Huijser MP, Begley JS (2022) Implementing wildlife fences along highways at the appropriate spatial scale: A case study of reducing road mortality of Florida Key deer. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 283–302. https://doi.org/10.3897/natureconservation.47.72321

Abstract

Florida Key deer mortality data (1966–2017) showed that about 75% of all reported deer mortalities were related to collisions with vehicles. In 2001–2002, the eastern section of US Hwy 1 on Big Pine Key (Florida, USA) was mitigated with a wildlife fence, 2 underpasses, and 4 deer guards. After mitigation, the number of reported Key deer road mortalities reduced substantially in the mitigated section, but this was negated by an increase in collisions along the unmitigated section of US Hwy 1 on Big Pine Key, both in absolute numbers and expressed as a percentage of the total deer population size. The data also showed that the increase in Key deer collisions along the unmitigated highway section on the island could not be explained through an increase in Key deer population size, or by a potential increase in traffic volume. The overall Key deer road mortality along US Hwy 1 was not reduced but was moved from the mitigated section to the nearby unmitigated section. Thus, there was no net benefit of the fence in reducing collisions. After mitigation, a significant hotspot of Key deer-vehicle collisions appeared at the western fence-end, and additional hotspots occurred further west along the unmitigated highway. Exploratory spatial analyses led us to reject the unmitigated highway section on Big Pine Key as a suitable control for a Before-After-Control-Impact (BACI) analysis into the effectiveness of the mitigation measures in reducing deer-vehicle collisions. Instead, we selected highway sections west and east of Big Pine Key as a control. The BACI analysis showed that the wildlife fence and associated mitigation measures were highly effective (95%) in reducing deer-vehicle collisions along the mitigated highway section. Nonetheless, in order to reduce the overall number of deer-vehicle collisions along US Hwy 1, the entire highway section on Big Pine Key would need to be mitigated. However, further mitigation is complicated because of the many buildings and access roads for businesses and residences. This case study illustrates that while fences and associated measures can be very effective in reducing collisions, wildlife fences that are too short may result in an increase in collisions in nearby unmitigated road sections, especially near fence-ends. Therefore it is important to carefully consider the appropriate spatial scale over which highway mitigation measures are implemented and evaluated.

Keywords
Collisions, fences, fence-end, key deer, mitigation, net benefit, road ecology, roadkill

Introduction

Most wildlife mitigation measures along highways are aimed at improving human safety, reducing direct wildlife mortality, and providing safe crossing opportunities for wildlife (e.g. Ford et al. 2009; van der Grift et al. 2017). Fences that are designed for large mammals, that are carefully installed and maintained, and that are implemented over at least several miles of road length, can reliably reduce collisions by at least 80% (Huijser et al. 2016a; Rytwinski et al. 2016). Since fences alone would result in a near absolute linear barrier for the target species, fences are often combined with wildlife crossing structures under or over the road. These underpasses and overpasses allow wildlife to safely cross to the other side of the road, and, in general, their use increases when they are connected to wildlife fences that help guide the animals towards the structures (Dodd et al. 2007; Gagnon et al. 2010). The suitability of the different types of crossing structures (e.g. underpasses vs. overpasses) and their dimensions (height, width, length), depend on the species (e.g. Sawyer et al. 2016), and sometimes also the sex and age of the individuals (e.g. Ford et al. 2017). Nonetheless, use of wildlife crossing structures can be considered substantial and can increase over time, presumably because the animals learn about the location of the structures and that they are safe to use (Clevenger and Barrueto 2014; Huijser et al. 2016b).

While a combination of fences and crossing structures is probably the most reliable and robust measure to improve human safety, reduce direct wildlife mortality, and provide safe crossing opportunities for wildlife, there is still much to learn on how to both make fences and crossing structures more effective and have the structures more readily accepted by different species (e.g. Huijser et al. 2015a; Rytwinski et al. 2016; Denneboom et al. 2021). One of the factors that affects the effectiveness of wildlife fences in reducing collisions is the scale at which the fence is implemented. For large mammals, at least 5 kilometers (3 miles) of road length needs to be fenced to reliably reduce collisions by 80% or more (Huijser et al. 2016a). Collisions that still occur within the fenced road sections tend to be concentrated near the fence-ends (Huijser et al. 2016b; Plante et al. 2019). Embedding barriers (e.g. wildlife guards or electrified barriers) in the travel lanes at fence-ends, can reduce intrusions into the fenced road corridor (Peterson et al. 2003; Gagnon et al. 2010). However, collisions can also be concentrated just beyond the fence-ends in the adjacent unmitigated road sections (Huijser et al. 2016b). On a larger spatial scale, there are also some cases where collisions may have been moved further into the adjacent unmitigated road sections (van der Grift and Seiler 2016) and where there is no evidence that there was a net benefit of wildlife fences. Therefore, it is important to install fences of sufficient length and to choose the locations for fence-ends carefully. Fenced road sections should include a buffer zone that extends well beyond the known hotspots for wildlife-vehicle collisions (Huijser et al. 2015a). Additional considerations such as habitat and topography can also help identify suitable locations for fence-ends.

Here we investigate the effectiveness of a wildlife fence and associated measures in reducing collisions with an endangered species, the Florida Key deer (*Odocoileus virginianus clavium*), on Big Pine Key, Florida, USA. We first explored the absolute Key deer road mortality numbers over the years and evaluated the spatial pattern in reported collisions with Key deer before and after the fence was constructed. Then we corrected the number of reported collisions for the Key deer population size for both the mitigated highway section and different potential control road sections for a Before-After-Control-Impact (BACI) analysis through which we evaluated the effectiveness of the fence. We also investigated potential differences in traffic volume between the mitigated and unmitigated highway section on Big Pine Key, and how traffic volume may have affected Key deer collisions along the unmitigated highway section. These exploratory analyses allowed us to find a suitable control for the BACI analysis. The careful consideration of different potential control road sections also allowed us to explore the net benefit of the wildlife fence on a larger spatial scale. The results help us to be more effective when designing wildlife mitigation measures along highways and to be more accurate when evaluating their effectiveness.

Methods

Study area and mitigation measures

In 1957, the National Key Deer Refuge was established in the Lower Florida Keys, Florida, USA. It is one of four national wildlife refuges in the area. The refuges were established to protect the endangered Key deer along with other endangered species and the habitat they depend on. At the time, hunting had reduced the Key deer population to fewer than 50 individuals (Hardin et al. 1984). Since then, the Key deer population has increased to an estimated 1,050 individuals in 2017 (U.S. Fish and Wildlife Service 2019). Most of the deer are found from Sugarloaf Key (west) to Big Pine Key and No Name Key (east), partially aided by reintroduction on some islands (Parker et al. 2008). An estimated 85% of the Key deer occur on Big Pine Key and No Name Key (U.S. Fish and Wildlife Service 2019). Parts of the islands have been urbanized, resulting in a mosaic of natural habitat (pine rocklands, freshwater marshes, tropical hard-wood hammocks, transitional buttonwood mangroves, mixed mangrove forests, and beach berm communities), residential areas, and commercial lots. This development has especially occurred on Big Pine Key. Additionally, tourism has increased substantially over the last several decades (peak season November-April) (Rockport Analytics 2019; Braden et al. 2020; Key West Travel Guide 2021). This has resulted in more than five million visitors per year to the Florida Keys (Rockport Analytics 2019), many of whom travel on US Hwy 1 from the mainland of peninsular Florida towards Key West. The Average Annual Daily Traffic (AADT) for US Hwy 1 on Big Pine Key was about 18,000 vehicles in 2016 (Consulting KBP Inc. 2017). Since there are no natural predators for key deer, conflicts with humans, including vehicle collisions, are now the most important causes of mortality for the deer (U.S. Fish and Wildlife Service 2019). Since 1966, wildlife refuge staff and Florida Fish and Wildlife Conservation Commission law enforcement staff, aided by other law enforcement staff and the public, have recorded Key deer mortalities, including road mortality. Although there is no standardized monitoring effort for Key deer struck by vehicles, there is high reporting effort because of their endangered status and because of the public concern about the species. The historic road mortality data showed that most direct road mortality occurred along US Hwy 1 on Big Pine Key (Parker 2006), especially in the early morning and early evening (Braden et al. 2020). Note that not every dead Key deer and cause of death is reported and recorded in the database. This means that there are inherent biases in the data; for example, a roadkilled Key deer is more likely to be found and recorded than a drowned Key deer.

In 2001–2002 a 1.64 mi (2.64 km) section of US Hwy 1 on the east side of Big Pine Key was mitigated with a 2.4 m (8 ft) high fence, 2 underpasses, and 4 deer guards (similar to cattle guards) (Braden et al. 2008; Parker et al. 2011) (Fig. 1). US Hwy 1 on the west side of the island was left unmitigated because of the access to businesses and residential areas (Parker et al. 2008). The mitigated highway section is largely situated within natural habitat with only a few access points for side roads. The western fence-end and the three side roads all have a deer guard embedded in the travel lanes. The eastern fence-end end at the Spanish Harbor Channel Bridge does not have a deer guard. Based on a Before-After comparison in a previous study, the mitigation measures along US Hwy 1 reduced Key deer collisions by about 90% in the mitigated road section (Parker et al. 2011). Furthermore, Key deer use the two underpasses, and the use has been increasing with the age of the structures (Braden et al. 2008; Parker et al. 2011). However, Key deer collisions continued to increase overall, i.e. on other unmitigated road sections (Parker et al. 2011). The continued increase in Key deer-vehicle collisions was attributed to the growing Key deer population size and traffic volume, especially on Big Pine Key and US Hwy 1 (Parker et al. 2011). While hurricane Irma blew over large sections of the wildlife fence along US Hwy 1 in September 2017, this did not affect our study as we only included Key deer mortality data through 2016 for our evaluation of the effectiveness on the measures in reducing collisions (see later). Other mitigation measures aiming at reducing collisions with Key deer along both the mitigated and unmitigated section of US Hwy 1 on Big Pine Key include low maximum posted speed limits (daytime 45 MPH;

Figure 1. The mitigated section of US Hwy 1 on Big Pine Key.

nighttime 35 MPH), mobile speed radar units informing drivers of the speed of their vehicle, parked police cars (no law enforcement personnel present), and a variety of warning and informational signs.

Key deer road mortality numbers and spatial patterns

We used the existing database on Key deer mortalities between 1966 (first record 9 March 1966) through partway 2017 (last record 9 November 2017) to assess road mortalities versus mortality from other causes. We calculated the absolute number of Key deer road mortalities along all roads combined (1966–2016) and in the ten years before mitigation (1991–2000) and in the fourteen years after mitigation (2003–2016) along both the mitigated and unmitigated highway section on Big Pine Key. We also explored where Key deer collisions occurred before and after the mitigation measures were implemented. Exploration of the spatial pattern of Key deer road mortalities after the mitigation measures were implemented allowed us to identify locations where further efforts to reduce Key deer-vehicle collisions should be directed, should one choose to do so. In addition, the spatial patterns in Key deer collisions before and after the mitigation measures were implemented provided the first step in identifying a suitable control for a BACI analysis to calculate the effectiveness of the fence and associated measures.

We investigated where the highest greatest concentrations of Key deer roadkill were after the eastern section of US Hwy 1 was mitigated. For this hotspot analysis, we only selected roadkill records of Key deer for the most recent 10-year period (2007 through 2016, n=1,182), regardless of where they occurred i.e. both on and off Big Pine Key, both inside and outside the mitigated section of US Hwy 1. We chose to use this subset of records as a balance between having recent data that identify current hotspots, and having a robust sample size. To identify hotspots, we conducted a Kernel density analysis using ArcGIS 10.6.1 (ESRI 2018a) for point features of Key deer-vehicle collision locations using a 25 m cell size (82 ft × 82 ft). A 25 m cell size is relatively fine scale but still accommodates for some spatial inaccuracies in GPS coordinates. The Kernel density analysis calculates the density of roadkills in a neighborhood around each cell and is based on the quartic kernel function described by Silverman (1986). Consistent with Gomes et al. (2009) we set the neighborhood search radius at 500 m (0.31 mi). On a straight road this means that Key deer roadkill that are up to about 500 m away are included in the density analysis for each cell. To help interpret the results of the Kernel density analyses and identify hotspots, we displayed the raster output using a heat map classification with varying densities of Key deer collisions. We used percentage breaks to create five categories (<5%, 5-<25%, 25-<50%, 50-<75%, and 75–100%) that display the areas with the highest densities of Key deer collisions (<5%) to areas with the lowest densities (75–100%).

Wherever a fence ends, there is a possibility of a concentration of collisions just beyond the fence end; the “fence-end effect”. For example, after implementation of the fence, some Key deer may have walked alongside the fence until they reached one of the two fence-ends. They could then cross the highway at-grade at the fence-end where they are exposed to potential collisions with vehicles. If such fence-end effects are indeed present, and if such road sections would be included in the control, it would result in an overestimation of the collisions in the control section and, through the BACI analysis, it would then also overestimate the effectiveness of the mitigated road section. Therefore, for a control to be suitable, it should not be influenced by the mitigation measures, and potential fence-end effects should be excluded from the control. We explored the potential presence of a concentration of Key deer road mortality near the western and the eastern fence-ends through an optimal hot spot analysis (Getis-Ord Gi*) in ArcGIS 10.6.1 (ESRI 2018b). This analysis identifies statistically significant spatial clusters of hotspots and cold spots of Key deer road mortalities. We selected Key deer road mortality observations along US Hwy 1 on Big Pine Key, both along the mitigated and unmitigated road section, before and after mitigation, up to 50 m from the highway. We then created a bounding polygon around the highway (50 m buffer from approximately the center of the highway) to allow for some spatial imprecision in the original data. We conducted separate analyses for the “before” (1991–2000; 331 observations, 5 outliers) and “after” data (2003–2016; 795 observations, 11 outliers). Within the optimal hot spot analysis (Getis-Ord Gi*) procedure, an outlier is defined as a location that is more than a three standard deviation distance away from its closest noncoincident neighbor. For the “before” data, the optimal grid size was 43 m, and the optimal fixed distance band was 302 m. For the “after” data, the optimal grid size was 44 m, and the optimal fixed distance band was 164 m.

Key deer road mortality in relation to population size

We investigated the net benefit of the mitigation measures by calculating Key deer road mortality as a percentage of the Key deer population size for all roads combined, US Hwy 1 on Big Pine Key (mitigated and unmitigated sections combined), and the mitigated road section of US Hwy 1 on Big Pine Key. We conducted the same analysis for different sections of unmitigated road sections of US Hwy 1 to identify a suitable control for the BACI analysis. The potential control sections that were evaluated included the unmitigated road section of US Hwy 1 on Big Pine Key up to the fence-end, the unmitigated road section of US Hwy 1 on Big Pine Key excluding a potential fence-end effect (see previous section), and the unmitigated road sections of US Hwy 1 west and east of Big Pine Key. This allowed for a second step in finding a suitable control for the BACI analysis as the analyses described above can detect evenly distributed increases in road mortality in different potential control road sections that are associated with the implementation of the mitigation measures.

To express Key deer road mortality as a percentage of the Key deer population size, we relied on historical population estimates. Unfortunately, total Key deer population size estimates were only available for certain years (Appendix 1). The respective authors usually presented both a minimum and maximum population estimate. Therefore, we calculated the average population size for each of the available minimum and maximum population estimates. We then fitted an exponential growth curve through the available population size estimates, allowing us to calculate the associated population size estimate for each calendar year before (1991 through 2000) and after mitigation (2003 through 2014). Note that we did not calculate population estimates after 2014, the last year the population was estimated based on field work, as we did not want to extrapolate beyond the data collection period. We tested for potential differences between the percentage of roadkilled Key deer of the total population size in the years before and after the mitigation measures were implemented (Kruskal-Wallis One-Way ANOVA on Ranks).

Traffic volume

To investigate if traffic volume may have played a role in the increase in Key deer road mortality along the unmitigated section of US Hwy 1 on Big Pine Key after the mitigation measures were implemented, we summarized traffic volume on US Hwy 1 on Big Pine Key between 1994–2017 based on traffic counter data (URS 2017; FDOT 2018). We tested for a potential difference in traffic volume before (1994–2000) and after (2003–2017) implementation of the fence and associated mitigation measures (two-sided t-test).

Effectiveness of the mitigation measures

We investigated the effectiveness of the mitigation measures in reducing collisions with Key deer through a BACI analysis. We selected roadkill records of Key deer; 10 years before the implementation of the mitigation measures (1991 through 2000), and 14 years after the implementation of the mitigation measures (2003 through 2016). We searched for a suitable control section of US Hwy 1 through the analyses described in the sections above. The unmitigated section of US Hwy 1 on Big Pine Key, starting immediately adjacent to the fence-end, was not suitable due to a concentration of collisions just beyond the fence-end. Excluding the fence-end effect still did not result in a suitable control as Key deer road mortality expressed as a percentage of the Key deer population size was still elevated, presumably because of the nearby mitigated road section. However, the combined unmitigated road sections US Hwy 1 west (11.7 mi; 18.8 km) and east (2.7 mi; 4.3 km) of Big Pine Key seemed unaffected by the implementation of the mitigation measures on Big Pine Key. Therefore, we selected these road sections as the control for the BACI analysis (total length for the control was 14.4 mi; 23.2 km) (Fig. 2). Since there was some spatial imprecision in the original data, we included observations of roadkilled Key deer that were up to 50 m from either side

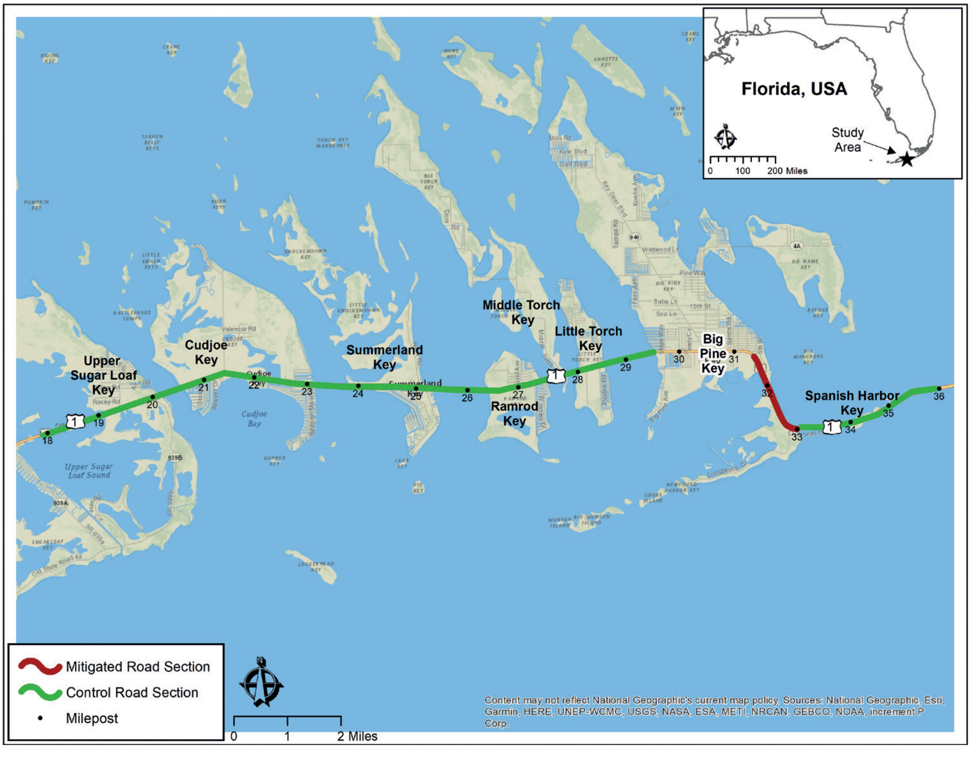

Figure 2. The mitigated section of US Hwy 1 on Big Pine Key and the two highway sections west and east of Big Pine Key that served as the control in the BACI analysis.

of US Hwy 1. For the BACI analysis, we calculated the number of Key deer roadkill records per mile for each calendar year for the control (unmitigated) and the impact (mitigated) road section. We calculated the BACI effect based on the mean number of roadkilled Key deer per mile per year (μ) in the impact road section and the control road section before and after the measures were implemented according to ($\mu_{control,after}$ - $\mu_{control,before}$) - ($\mu_{impact,after}$ - $\mu_{impact,before}$). In addition, the Key deer roadkills per mile per year were transformed (ln(x+0.1)) to make the count variable resemble a normal distribution. This allowed for the investigation of a potential interaction of the before-after and control-impact parameters through an ANOVA. Should there be an effect of the treatment (i.e. the wildlife fence and the associated mitigation measures), we expected the effect to result in fewer collisions rather than more. Hence our ANOVA was a one-sided test.

Results

Key deer road mortality numbers and spatial patterns

There were 4,753 recorded mortalities of Key deer from 1966–2017. Overall, roadkill was the most common recorded cause of mortality (*N*=3,412, 71.8%), followed by "undetermined" (*N*=681, 14.3%), and disease (*N*=276, 5.8%). Drowning, predation by dogs, entanglement, intraspecies combat, poaching, humans (various causes), and physical impact of hurricanes each represented less than 5% of the recorded mortalities. Road mortality has consistently been the leading known cause of mortality since record keeping began in 1966. The average percentage of Key deer road mortalities out of all recorded Key deer mortalities for each year (1966–2016) per year was 75.5% (SD=10.2). While the absolute number of recorded Key deer road mortalities dropped substantially in the mitigated road section after the mitigation measures were implemented in 2001–2002, the number of Key deer road mortalities for all roads combined and for the unmitigated section of US Hwy 1 on Big Pine Key continued to increase (Fig. 3).

After the mitigation measures were implemented, Key deer road mortality was concentrated along the unmitigated western section of US Hwy 1 on Big Pine Key (Fig. 4). There were two main hotspots; one on the west side of Big Pine Key (opposite of the canals (W. Cahill Ct.) until Deer Run Tr.), and one at the west end of the wildlife fence (opposite of the St. Peter Catholic Church), extending further west till Cunningham Ln. Post-mitigation, there were 575 reported Key deer road mortalities in the unmitigated section of US Hwy 1, and 25 in the fenced section.

Before the eastern section of US Hwy 1 was mitigated, there was a significant concentration of Key deer-vehicle collisions at the eastern edge of Big Pine Key (Fig. 5a). This hotspot disappeared after the implementation of the mitigation measures, and almost the entire length of the mitigated road section turned into a significant cold spot (Fig. 5b). However, after mitigation, a significant hotspot appeared at the western fence-end, extending for about 300 m (984 ft) into the unmitigated high-

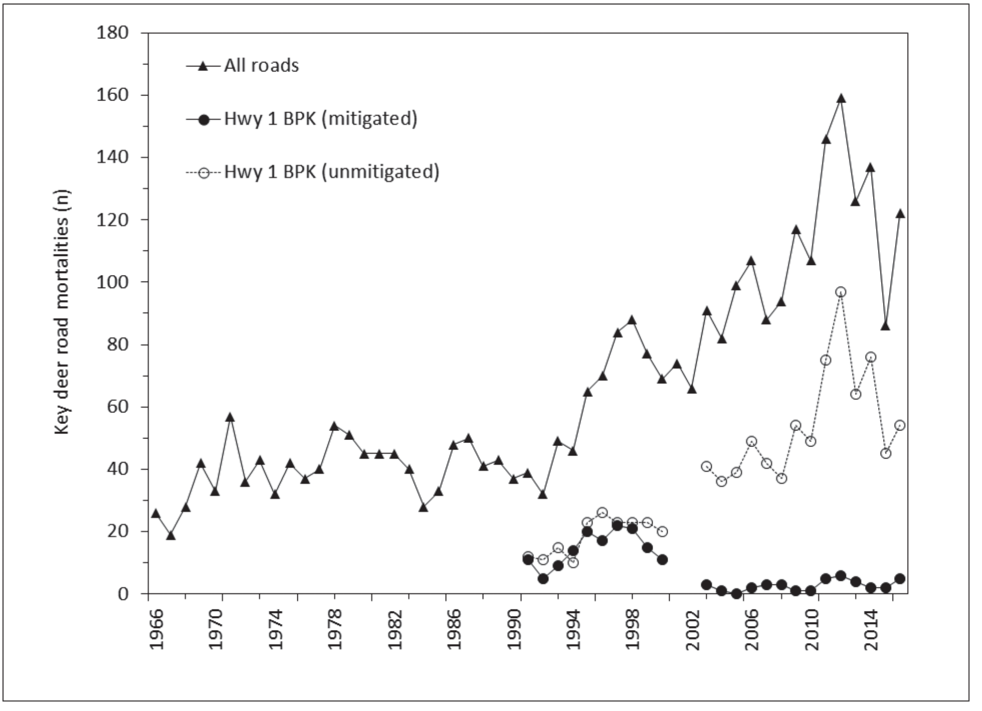

Figure 3. The number of Key deer road mortalities per year along all roads combined (1966–2016) and during the ten years before (1991–2000) and the fourteen years after mitigation (2003–2016) along both the mitigated and unmitigated section of US Hwy 1 on Big Pine Key (BPK).

way section (Fig. 5b). Other significant hotspots were present further west along the unmitigated section of US Hwy 1. The 90% confidence hotspot extended about 325 m (1,066 ft) from the western fence-end (142 records from 2003–2016; 18.7% of the Key deer road mortalities on the unmitigated highway section on Big Pine Key). There were 617 records (81.3%) outside this hotspot along the unmitigated highway section on Big Pine Key. The 95% confidence hotspot (119 records from 2003–2016; 15.7% of the Key deer road mortalities on the unmitigated highway section on Big Pine Key) extended about 280 meters (919 ft) from the western fence-end. There were 640 records (84.3%) outside this hotspot along the unmitigated highway section on Big Pine Key.

Key deer road mortality in relation to population size

Key deer population size has grown exponentially since the 1940s (Fig. 6). While there were only seven population size estimates available in total, the population may have been stable or experienced a slight decline between 1974 and 1990. Nonetheless, in general, and specifically since the mitigation measures were implemented in 2001–2002, the population size has grown exponentially.

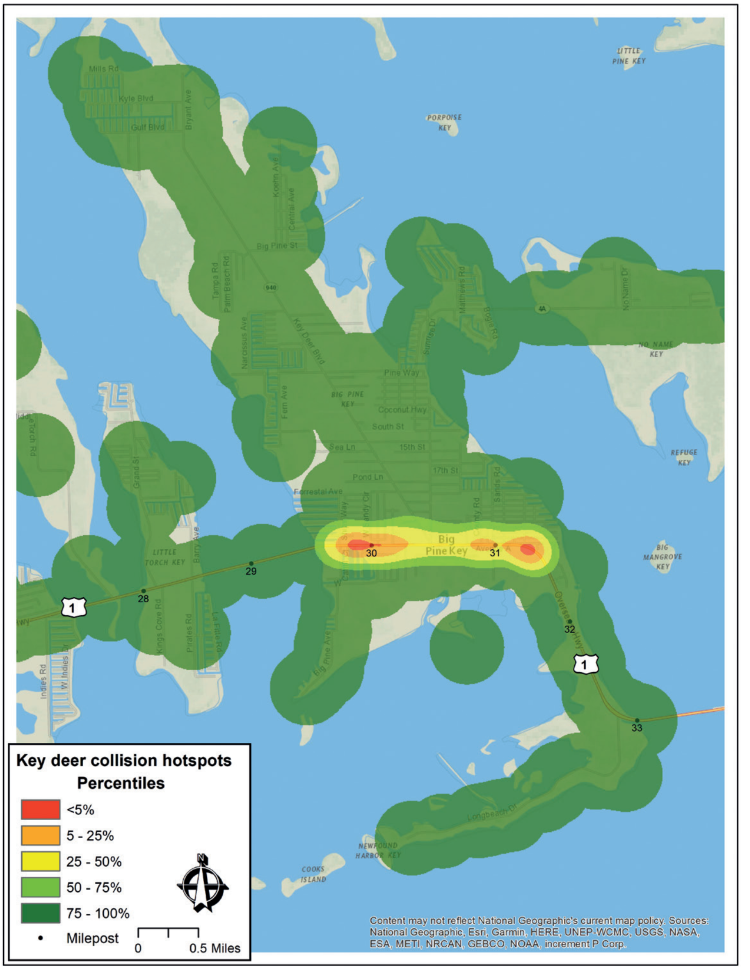

Figure 4. Kernel density hotspot map using percentiles for Key deer-vehicle collisions (2007–2016).

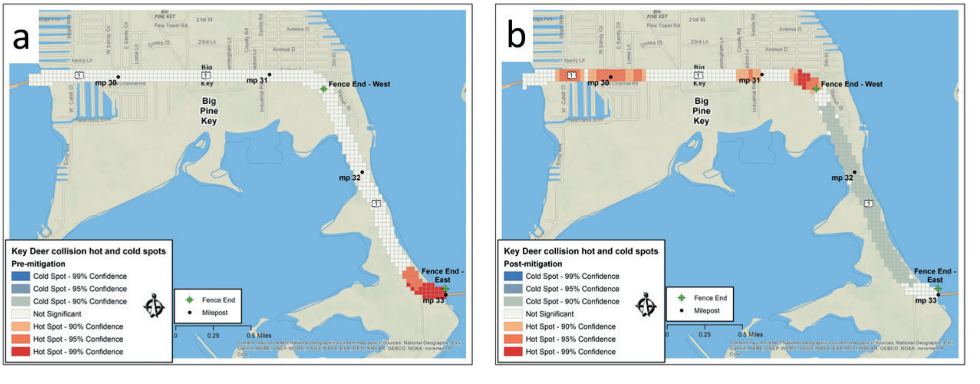

Figure 5. Significant hotspots and cold spots for Key deer-vehicle collisions along US Hwy 1 before (**a**) and after (**b**) mitigation. Numbers represent the mile reference posts.

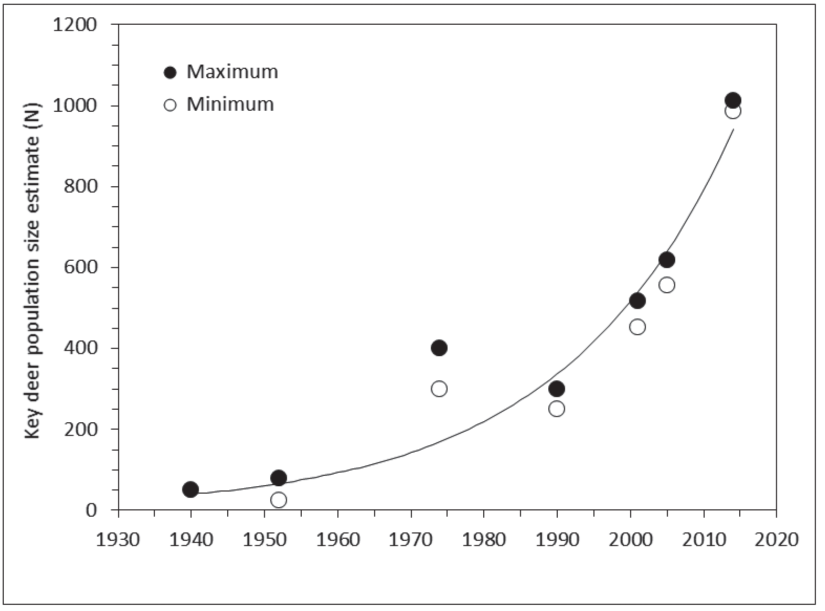

Figure 6. Estimated Key deer population size. An exponential growth curve ($y=e^{(0.04279*((year)-1853.976)}$; R^2 = 0.93) was fitted through data obtained from the literature (see Appendix 1).

The percentage of roadkilled Key deer of the total population size for all roads combined was similar before (average 14.2%, SD=3.2) and after (average 14.9%, SD=1.8) the fence and associated mitigation measures were implemented along the eastern section of US Hwy 1 (Kruskal-Wallis One-Way ANOVA on Ranks, Chi^2 = 0.109, p = 0.742) (Fig. 7). The percentage of roadkilled Key deer of the total population size for US Hwy 1 on Big Pine Key was also similar before (7.6%, SD=2.1) and after (7.5%, SD=1.8) mitigation (Chi^2 = 0.017, p = 0.895). However, there was a substantial decrease (90.0%) in the mitigated section (before (3.3%, SD=1.2), after (0.3%, SD=0.2)) (Chi^2 = 15.652, p < 0.001). At the same time, there was a substantial increase (68%) in the unmitigated section on Big Pine Key (before (4.3%, SD=1.1), after (7.2%, SD=1.7)) (Chi^2 = 14.126, p < 0.001). There was still an increase in the unmitigated section (65%) on Big Pine Key when the 90% confidence hotspot at the fence-end was excluded (before (3.5%, SD=0.9), after (5.8%, SD=1.5)) (Chi^2 = 12.678, p < 0.001). For the unmitigated highway section west and east of Big Pine Key there was no significant difference before (1.2%, SD=0.6) and after (1.4%, SD=0.6) mitigation (Chi^2 = 0.626, p = 0.429).

Traffic volume

In 2017, US Hwy 1 on Big Pine Key had an Annual Average Daily Traffic Volume (AADT) of 18,590–19,600 vehicles per day depending on the location of the traffic counter (FDOT 2018). The vast majority were passenger cars (92.2%) and 7.8% of the vehicles were trucks (single unit, combination trailer, and multi-trailer trucks com-

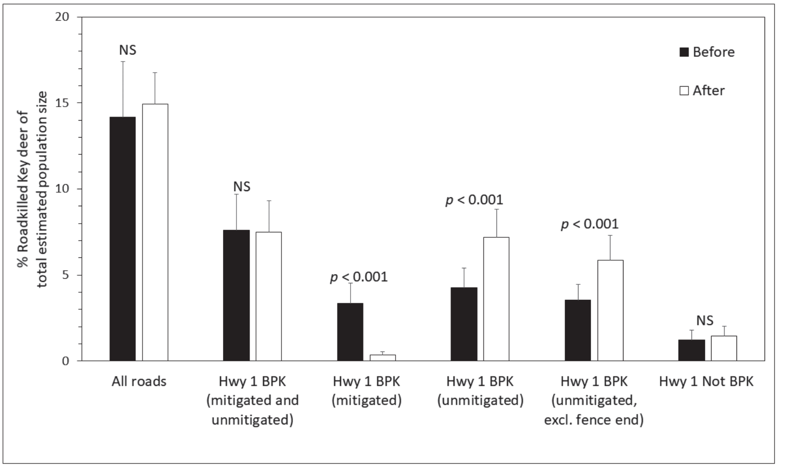

Figure 7. The average percentage (and SD) of roadkilled Key deer of the total estimated population size in the years before and after implementation of the mitigation measures along the eastern section of US Hwy 1 on Big Pine Key (BPK).

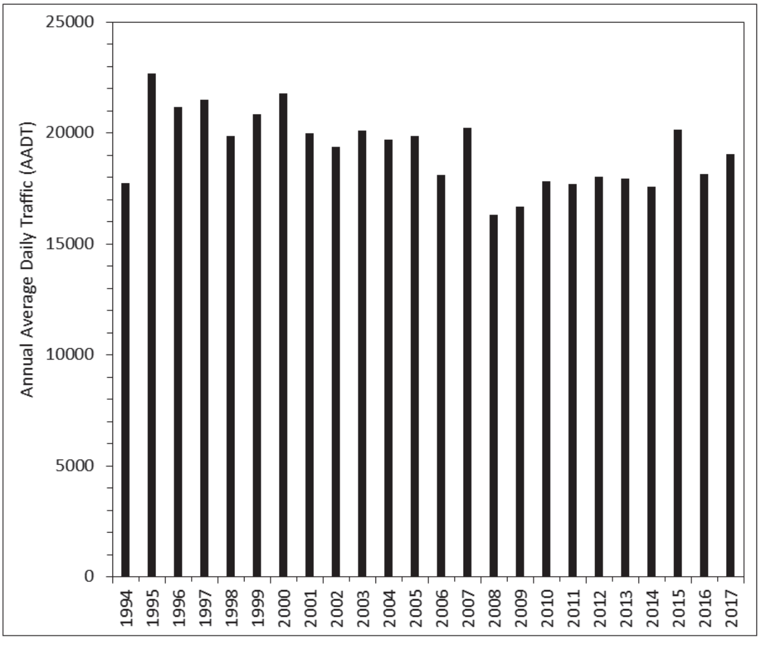

Figure 8. Annual Average Daily Traffic (AADT) on US Hwy 1, Big Pine Key (URS 2017; FDOT 2018).

bined) (FDOT 2018). The average and median AADT before mitigation (1994–2000) was higher (mean = 20,799; median = 21,186; SD = 1,600) than after mitigation (2003–2016) (mean = 18,450; median = 18,053; SD = 1,310) (two-sided t-test $t(19) = -3.6035$, $p = 0.002$) (Fig. 8).

Effectiveness of the mitigation measures

Before the mitigation measures were implemented, the average number of Key deer roadkill per mile per year was 8.4 for the mitigated road section, and 0.4 for the control section (Fig. 9). After the implementation of the mitigation measures, Key deer roadkill decreased by 95.0% in the mitigated road section to 0.5 Key deer roadkilled per mile per year. After the implementation of the mitigation measures Key deer roadkill increased by 112.0% in the control section to 0.8 Key deer roadkilled per mile per year. The BACI effect was 8.8; there were nearly 9 fewer roadkilled Key deer per mile per year in the mitigated road section when corrected for what happened in the control section. In the context of the BACI analysis, the percentage reduction in Key deer-vehicle collisions in the mitigated road section was 94.8%. The interaction of the before-after and control-impact parameters was significant (one-sided ANOVA $F_{1,44}$=46.63, p < 0.001). This meant that the effect of time (before-after) on the number of roadkilled Key deer indeed depended on the implemented mitigation measures.

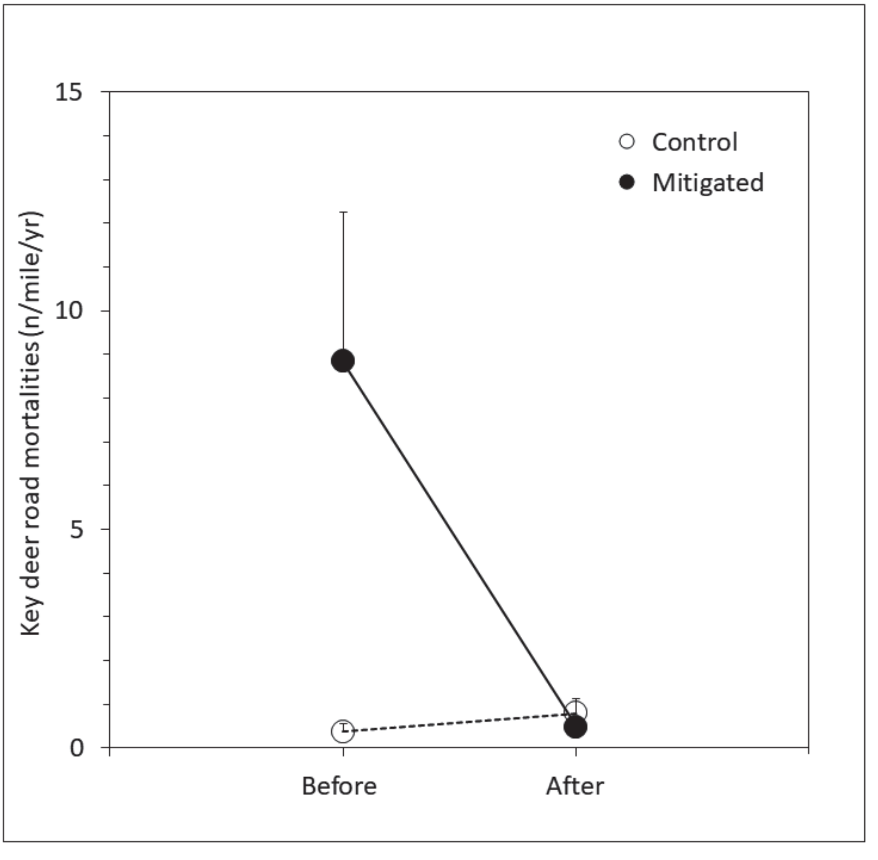

Figure 9. The average number (and SD) of Key deer-vehicle collisions per mile per year in the control and mitigated road section before and after the mitigation measures were implemented.

Discussion

Key deer road mortality and spatial patterns

Direct road mortality has consistently been the most common recorded cause of mortality for Key deer since record keeping began. Therefore, if the objective is to reduce unnatural mortality for Key deer, reducing direct road mortality should be explored first. After the mitigation measures were implemented, Key deer road mortality was concentrated along the unmitigated western section of US Hwy 1 on Big Pine Key. Therefore, this is the road section that should be prioritized if the objective is to reduce direct road mortality of Key deer.

Effectiveness of the mitigation measures

Based on the BACI analysis, the wildlife fence and associated mitigation measures along the eastern section of US Hwy 1 on Big Pine Key were highly effective (94.8%) in reducing Key deer-vehicle collisions along the mitigated road section. However, when corrected for the population size, Key deer road mortality was similar before and after highway mitigation for all roads combined as well as for US Hwy 1 on Big Pine Key (mitigated and unmitigated section combined). Similar to the absolute numbers, the percentage of roadkilled Key deer in relation to the population size sharply decreased by 90.0% in the mitigated section of US Hwy 1 but substantially increased by 68% in the unmitigated section of US Hwy 1 and by 65% when the fence-end effect was excluded. The hypothesis that the continuing increase in Key deer-vehicle collisions after the mitigation measures were implemented may have been associated with an increase in Key deer population size must be rejected. Similarly, traffic volume can also not explain the increase in collisions. Traffic volume was, on average, lower after the implementation of the fence and associated mitigation measures, likely because of the lead-up to the economic crisis in 2008 and the gradual recovery afterwards. However, in general, higher traffic during certain hours of the night is positively correlated with an increase in collisions with Key deer (Braden et al. 2020). Our data suggest that while the mitigation measures reduced collisions substantially in the mitigated road section, the overall Key deer road mortality on US Hwy 1 on Big Pine Key was not reduced. Instead, it was moved from the mitigated section to the unmitigated section of US Hwy 1, especially just beyond the fence-end. After mitigation, a significant hotspot of Key deer-vehicle collisions appeared at the western fence-end of the mitigated section of US Hwy 1, likely as a result of some Key deer following the fence and crossing at-grade in higher than average numbers at the fence-end. This is similar to what has been observed for other species (Clevenger et al. 2001; van der Grift and Seiler 2016; Plante et al. 2019). Other significant Key deer-vehicle collision hotspots after mitigation occurred further west along the unmitigated highway section on Big Pine Key.

The increase in Key deer road mortality along the unmitigated section of US Hwy 1 on Big Pine Key can be seen as a form of environmental leakage as the "extraction" was moved from a now protected area to a non-protected area rather than reduced (Bode et al. 2015). In other words, there was no "net benefit" of the mitigation if the "net benefit" is defined as the gains made in reducing collisions in the fenced road section minus the adverse impacts caused by this mitigation, including an increase in collisions in the adjacent unmitigated road section (Efroymson et al. 2014).

It is important to bear in mind that the overall number of collisions is just one parameter associated with the presence of the mitigation measures along the eastern section of US Hwy 1. For example, even though the overall number of key-deer vehicle collisions along US Hwy 1 was not reduced after mitigation, the remaining collisions mostly occur along the section where the design speed and surroundings (side roads, entrances to businesses, pedestrians, cyclists) may encourage drivers to have lower operating speed and pay more attention to their surroundings compared to the mitigated section of US Hwy 1 (very few side roads, no buildings adjacent to the highway, wide right-of-way). Thus, there may be a lower likelihood of human injuries and human fatalities when hitting a Key deer in the western section of US Hwy 1. Another benefit of the mitigation measures is that the mitigated section of US Hwy 1 also provides safe crossing opportunities for Key deer through the underpasses (Braden et al. 2008; Parker et al. 2011).

Management implications

While the mitigation measures along the eastern section of US Hwy 1 on Big Pine Key were highly effective in reducing Key deer-vehicle collisions, the data indicate that there was no "net benefit" of the wildlife fence in reducing collisions with Key deer along the entire section of US Hwy 1 on the island (mitigated and unmitigated road section combined). Measures that could be considered for the currently unmitigated western road section on the island include erecting a fence behind the businesses and residential properties that are adjacent to US Hwy 1. This would mean that the "first row" or "first block" of buildings would be included in the fenced road corridor, resulting in unhindered access to these buildings from US Hwy 1. A limited number of gaps in the fence, with wildlife guards, would allow for access to areas beyond the first row or block of buildings. In places where natural habitat remains adjacent to US Hwy 1, fenced corridors leading up to US Hwy 1 may be considered for wildlife, including Key deer. The fenced corridors would lead to underpasses (similar to the ones in the eastern mitigated road section) or at-grade crossing opportunities with wildlife guards or electrified barriers embedded in the travel lanes that encourage Key deer to cross the highway straight and to keep them from wandering off to the sides into the fenced road corridor. This measure can be expected to result in a reduction in Key deer collisions of about 95% (with underpasses, see this article) or 40% (with at-grade crossing opportunities, see Lehnert and Bissonette 1997) along the currently unmitigated section of US Hwy 1. Alternatively, an animal detection system may be considered, especially at the western fence-end. The effectivenes of animal detection systems in reducing collisions with large wild animals is extremely variable (33–97%), presumably due to different detection technologies, different target species, different types of warning and speed limit reduction signs, and driving culture (see review in Huijser et al. 2015b). Nonetheless, an animal detection system along the full length of the 90% probability hotspot at the western fence-end would affect 18.7% of the remaining collisions with Key deer along US Hwy 1 on Big Pine Key. The fences with two types of crossing opportunities (underpasses, at-grade crossings) and the animal detection system at the western fence end, can, depending on the road length along which they are implemented and dependent on the spatial distribution of Key deer collisions, all be expected to change the current "no net benefit" to a "net benefit" for reducing collisions with Key deer.

Conclusion

In order to substantially reduce the overall number of deer-vehicle collisions along US Hwy 1 on Big Pine Key, the entire highway section on Big Pine Key would need to be mitigated. However, the section of US Hwy 1 that remains unfenced has many buildings and access roads to businesses and residences. This means that there are many competing interests; implementing mitigation measures that are effective in reducing Key deer-vehicle collisions and that also provide safe crossing opportunities for Key deer and other wildlife species will affect other interests on and along US Hwy 1. This case study also illustrates that while fences and associated mitigation measures can be very effective in reducing collisions in the mitigated road section, wildlife-vehicle collisions in the larger area may not be reduced because the collisions can move to nearby unmitigated road sections, especially just beyond fence-ends. This phenomenon is not an indication that wildlife fences do not reduce wildlife-vehicle collisions. Instead, it is an indication that the fenced road section is too short. Therefore it is important to carefully consider the appropriate spatial scale over which highway mitigation measures are implemented and evaluated.

Acknowledgements

We thank the U.S. Fish & Wildlife Service for funding this project. Special thanks are due to Daniel Clark, Christine Ogura, and Kate Watts (all U.S. Fish & Wildlife Service) and to Fernando Ascensão, Edgar van der Grift, Clara Grilo, and Bethanie Walder for their help and review of different versions of this manuscript.

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Appendix 1

Table 1A. Key deer population size estimates.

Year	Minimum (n)	Maximum (n)	Average (min-max) (n)	Source
1940	?	50	50	Hardin et al. (1984)
1952	25	80	52.5	Dickson (1955)
1974	300	400	350	Klimstra et al. (1974)
1990	250	300	275	Seal and Lacy (1990)
2001	453	517	485	Lopez (2001)
2005	555	619	587	Roberts (2005)
2014	987	1012	999.5	Villanova et al. (2017)

Nature Conservation 47: 303–316 (2022)
doi: 10.3897/natureconservation.47.73052
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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A test of wildlife warning reflectors as a way to reduce risk of wildlife-train collisions

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Academic editor: Manisha Bhardwaj | Received 15 August 2021 | Accepted 2 December 2021 | Published 25 March 2022

http://zoobank.org/C4ABF2A8-3F91-4017-B1E7-973FDA753262

Citation: Jasińska KD, Babińska-Werka J, Krauze-Gryz D (2022) A test of wildlife warning reflectors as a way to reduce risk of wildlife-train collisions. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 303–316. https://doi.org/10.3897/natureconservation.47.73052

Abstract

Looking for an effective method to reduce risk of animal-train collisions, we tested the system of wildlife warning reflectors, a method usually used on roads. The research was conducted in central Poland, along a 2.1 km stretch of the E65 railway line near Warsaw, during eight months, in the years 2010–2011. For six months of a test period, the reflectors were uncovered (active) and, for the next two months of the control period, they were covered (non-active). Digital cameras were used to register animal reactions to trains 24-hours per day. We compared the probability of escape (escape = 1; no reaction = 0) from an oncoming train during test and control periods of the research, in different parts of a day (i.e. day vs. night) and compared escape time of roe deer between day and night and with reflectors covered and uncovered. Roe deer (*Capreolus capreolus*), red fox (*Vulpes vulpes*) and brown hare (*Lepus europaeus*) were observed most often (702 observations in total). The status of reflectors (covered/uncovered) did not influence the probability of animals' escape from an oncoming train. The only factors that affected the probability of escape were animal species and time of a day. Of the three species, roe deer was most likely to escape from an oncoming train (89% of probability at day and 52% during night, pooled data for covered and uncovered reflectors). Timing of roe deer escape from an oncoming train did not differ between day (6.4 seconds) and night, with either reflectors covered (7.5 seconds) or uncovered (4.6 seconds). The results indicated that wildlife warning reflectors were not effective to modify animal behaviour and to reduce risk of animal-train collisions.

Keywords

Animal-train collisions, mitigation measures, railway lines, roe deer, wildlife warning reflectors

Introduction

Transportation infrastructure, namely roads and railways, is one of the most widespread threats to wildlife. Transportation infrastructure fragments habitats by cutting through the individual territories and migration corridors of wildlife (Cain et al. 2003; Di Giulio et al. 2009; Ito et al. 2013; Borda-de-Água et al. 2017). As transportation networks continue to expand, the frequency of collisions between wildlife and vehicles increases (Jasińska et al. 2019). Loss of individuals to wildlife-train collisions can have large impacts on mammal populations, particularly for species that are endangered, have low population densities, have large home ranges and low reproductive rate (van der Grift 1999). For example, in a vulnerable population of grizzly bears (*Ursus arctos*) in Canada, train strikes have become a major cause of mortality (St. Clair et al. 2019). The number of wildlife-train collisions is much lower than wildlife-vehicle collisions recorded on roads (Cserkész and Farkas 2015) and research on collisions between trains and wildlife have so far focussed mainly on medium or large mammals (Kušta et al. 2011; review in: Steiner et al. 2014; Krauze-Gryz et al. 2017; Pollock et al. 2019), with moose *Alces alces* being the focal species in most papers (Andersen et al. 1991; Child et al. 1991; Jaren et al. 1991; Modafferi 1991; Gundersen et al. 1998; Hamr et al. 2019). Although risk of human injuries is usually low in train collisions, they cause significant delays to train traffic, considerable costs regarding material damage and other costs related to handling of animal carcasses or injured animals and administration of accidents (Child and Stuart 1987; Seiler and Olsson 2017).

To reduce wildlife-vehicle collisions, many methods can be used. On roads, over forty mitigating measures have been described, influencing either the driver behaviour (e.g. warning signs, animal detection systems) or animal behaviour (mostly by deterring animals from roads) (review in: Glista et al. 2009; Langbein et al. 2011; Rytwinski et al. 2016). Railway transportation is different from road transportation; for example, train traffic volume is lower, with long traffic-free intervals (Barrientos et al. 2019), thus mitigation methods used on railways should be different from those used on roads. Although fencing is considered to be the most effective measure to restrict wildlife access to railways (Ito et al. 2013), it causes serious fragmentation, so measures to maintain ecological connectivity are necessary (Carvalho et al. 2017). Moreover, because railways themselves are considered as a barrier for wildlife movement (Ito et al. 2013; Ito et al. 2017), the use of additional barriers along railway tracks should be discouraged (Carvalho et al. 2017). Thus, the mitigation measures used on the railway should focus on changing animal behaviour and forcing animals to escape when the train approaches rather than preventing animals from crossing the tracks at all (e.g. Babińska-Werka et al. 2015; Seiler and Olsson 2017).

One of the methods designed for roads and to mitigate wildlife mortality is the use of wildlife warning reflectors and mirrors (Rytwinski et al. 2016). This mitigation method has been developed to increase wildlife vigilance and awareness of oncoming vehicles (D'Angelo et al. 2006). Reflectors are mounted along the road on series of roadside posts orientated towards the road verge. At night, vehicle headlights illuminate the warning reflectors, which reflect light towards the road verge to create a "fence of light". The intent is that an animal will notice the reflected light and halt or flee away from the road until the vehicle had passed and then cross safely (D'Angelo et al. 2006; Benten et al. 2018a). Findings of different studies on the effectiveness of wildlife reflectors along roads are contradictory (Brieger et al. 2016; Benten et al. 2018a). Some of them pointed to the effectiveness of wildlife warning reflectors in reducing the number of wildlife-vehicle collisions (e.g. Schafer et al. 1985), while another showed no such evidence (e.g. D'Angelo et al. 2006). On the other hand, nothing is known about the effectiveness of relectors implemented along rail tracks.

The aim of the study was to determine the effectiveness of wildlife warning reflectors installed along the railway tracks, i.e. the likelihood of animals' escape from an oncoming train. We compared the reaction of animals to oncoming trains during nights and days, assuming that, at night, animal behaviour should be modified by the reflectors, while at day, their influence should be negligible (Benten et al. 2018a). We also compared reactions of animals to oncoming trains at night, with reflectors active (uncovered) and non-active (covered), assuming that, in the second case, animals would escape from an oncoming train less often and slower.

Methods

Study area and installation of reflectors

The research was conducted in central Poland, along the stretch of E65 railway line, between Warszawa Choszczówka and Legionowo (52°39'N, 20°96'E). This section of tracks is surrounded by a small forest complex (around 1300 ha) (Fig. 1), located in the vicinity of field and forest mosaic as well as urban area. On a given stretch of railway, three tracks were located. Trains run almost all day with a break between 0:00–4:00 a.m. On average, 90 trains run daily through the study area with 100–120 km/h speed (Polskie Koleje Państwowe 2014). The study area was characterised by the presence of ungulates – moose, roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), as well as medium-sized mammals, such as brown hare (*Lepus europaeus*), red fox (*Vulpes vulpes*) and martens (*Martes* spp.) (Nadleśnictwo Jabłonna 2013).

In 2009, 478 poles with red wildlife warning reflectors (patented by Swareflex company, Swareflex GmbH, Vomp, Austria) were mounted along the monitored stretch of railway tracks. The poles were installed every 16 m on both sides of tracks, at distance of three metres from tracks. The height of poles was 1.50 m above the top of the tracks and 2.15 m above the ground. The red Swareflex wildlife warning reflectors (two-sided) were mounted on the top of each pole and turned to the railway-side (Fig. 2). They were supposed to reflect the light of headlights of a passing train away from the railway tracks at night.

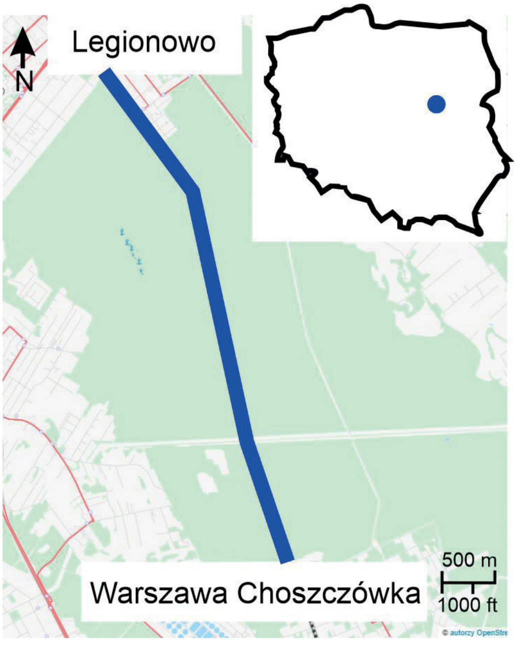

Figure 1. The stretch of E65 railway line (blue line) between Warszawa Choszczówka and Legionowo, where wildlife warning reflectors were installed and the monitoring conducted, and the placement of the study area (blue dot) on a contour map of Poland (source OpenStreetMap, modified).

Figure 2. One of the poles with red wildlife warning reflector installed along stretch of E65 railway line to mitigate animal–train collisions.

Materials ans methods

Data collection

Over the length of 2.1 km railway tracks, we monitored the reactions of animals to the trains, from August 2010 till March 2011, using ten sets of VIVOTEK digital video cameras of two megapixel resolution, equipped with motion-sensors (i.e. each case of presence of an animal on the side of the tracks triggered the video recording) and additional two infra-red illuminators. Each set (the video camera, with infra-red illuminators) was mounted on a power-line pole, two sets approx. 210 m apart from each other (Fig. 3). At half the distance between them, an additional illuminator was mounted. The cameras were turned to one direction. To ensure that the whole stretch was monitored, the view range of each digital camera was as long as 250 m (i.e. approx. 40 m longer than the distance between the two cameras), thus a video from the camera showed the next camera pole (Fig. 4). Therefore, we assigned each observation to the nearest camera, so even if an animal could be potentially registered by two cameras, only one record was taken into account. Additionally, it was possible to monitor the immediate vicinity of the rail line up to approximately 15 m from the tracks on both sides. Recorded videos were analysed using the Milestone XProtect Viewer programme.

We collected data between 1 August 2010 and 30 March 2011. From 1 August 2010 to 8 February 2011, reflectors were active (uncovered). Then, for the control period, we covered them with black plastic for the next two months (9 February – 30

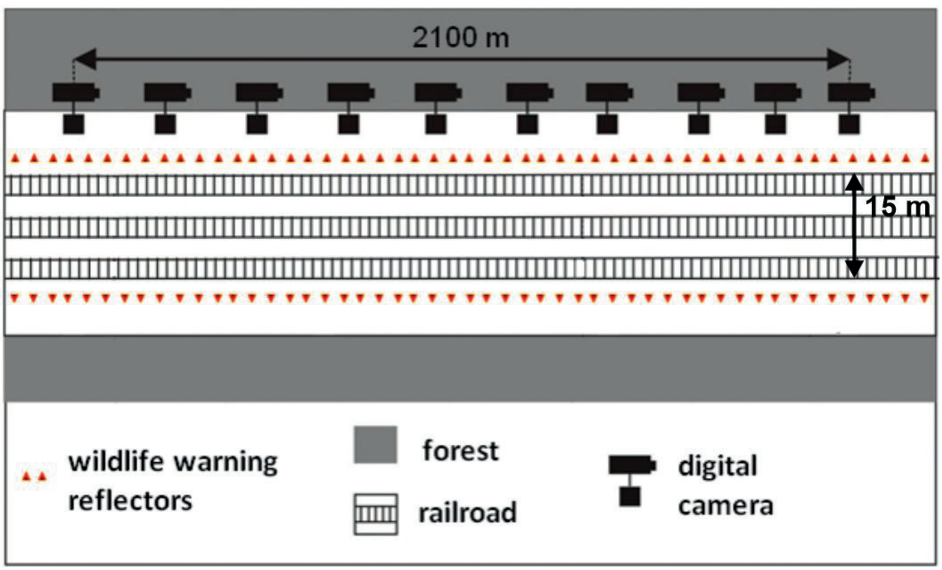

Figure 3. Deployment of the array of digital cameras along the studied E65 rail line, where wildlife warning reflectors where tested.

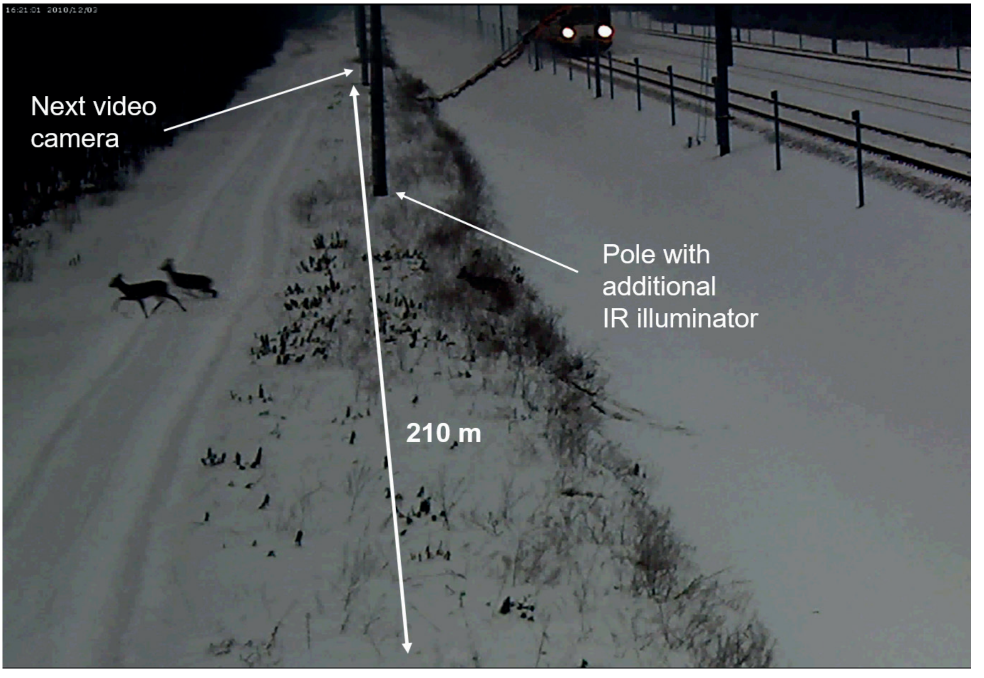

Figure 4. View from a digital camera set at the monitored stretch of E65 railway line, where wildlife warning reflectors were tested: an escape of two roe deer before an oncoming train is shown. The view from one camera extends beyond the pole with the next video camera to ensure that the whole stretch (marked with the white two-arrow line) is monitored.

March 2011), to simulate "non-active" reflectors. We registered all wildlife and train interactions (i.e. cases of animal presence near the railway tracks associated with a train passage). Animals were not marked. Each recorded sighting was counted as the presence of a single specimen or a group of animals of a given species. We differentiated two reactions of animals to a passing train: (1) escape from the track into the forest; (2) no reaction – continued foraging, a break in foraging activity or raised head. We calculated an escape time from an oncoming train as the number of seconds between the moment when an animal started to escape and the moment when a train passed the place where the animal had been standing.

For each record, we distinguished time of a day – day or night – where day was the time between sunrise and sunset and night was the time between sunset and sunrise.

Data analysis

We explored the probability of escape from an oncoming train, modelled as a logistic regression, using the reaction to the train (escape = 1, no reaction = 0) as the binary response variable. We used species, time of a day, status of reflectors (covered/uncovered) and interaction between species and time of a day and interaction between species and status of reflectors as explanatory variables. We used camera_ID as a random effect. We used Akaike Information Criterion (AIC) to evaluate the fit of models.

Then we used linear mixed-effects models to find factors affecting time of escape to an oncoming train. We used, as an exploratory variable, a combination of time of a day and status of reflectors, with three categories: (1) day (regardless of whether reflectors were covered or uncovered), (2) night with uncovered reflectors and (3) night with covered reflectors. Again camera_ID was used as a random effect. Observations for the day time were pooled together when reflectors were covered and uncovered because wildlife warning reflectors are only effective during the night, when the reflection from the train lights is visible in contrast to the dark surroundings (Benten et al. 2018a; Werka, unpubl. data).

All analyses were performed using R (v.4.1.1, R Core Team 2021) and 'lme4' package (Bates et al. 2015). Logistic regression models were fitted using the 'glmer' function with a binomial error. The linear mixed-effect model was fitted using 'lmer' function.

Results

In total, 729 observations of wildlife and train interactions were registered. A majority of these observations were recorded at night (n = 539). We recorded presence of four wild species (i.e. roe deer, brown hare, red fox and wild boar), as well as domestic cat (*Felis catus*) and domestic dog (*Canis familiaris*) and some unrecognised species (Table 1). Roe deer, red foxes and brown hares were observed most frequently, i.e. 463, 122 and 117 cases, respectively and we did further analysis only for those three species.

Probability of escape

Amongst four built models (including the null model), the one that included species, status of reflectors and interaction between species and status of reflectors was the weakest, i.e. had the highest Akaike Information Criterion (Table 2). This means that the status of reflectors (covered/uncovered) was not important in the explanation of changes in reaction of the investigated three species to an oncoming train. The inclusion of time of a day as another variable improved the fit of a model. The model selection procedure showed that the model, including species, time of a day, status of reflectors and interactions between species and status of reflectors and between species and time of a day, with camera_ID as a random effect, had the lowest Akaike Information Criterion (Table 2) and was selected as an optimal model.

The reactions of red fox and roe deer to an oncoming train were compared to reactions of brown hare. The probability of brown hare and red fox escaping from an oncoming train during day and night was similar when the reflectors were covered and uncovered (Table 3). The probability of escape of brown hare from an oncoming train equalled 59% (reflectors covered) and 54% (uncovered) during day and 69% (covered)

Table 1. Animal species registered at the stretch of E65 railway line monitored with digital cameras, between 1 August 2010 and 30 March 2011 and in times of different wildlife warning reflector status (i.e. active – uncovered and non-active – uncovered).

	Reflectors		
	Covered	Uncovered	In total
Roe deer (*Capreolus capreolus*)	33	430	463
Brown hare (*Lepus eauropaeus*)	13	109	122
Red fox (*Vulpes vulpes*)	11	106	117
Wild boar (*Sus scrofa*)	3	4	7
Domestic cat (*Felis catus*)		7	7
Domestic dog (*Canis lupus familiaris*)	3		3
Unrecognised species		10	10
	63	666	729

Table 2. Akaike Information Criterion (AIC) for models.

Model	AIC
species + time of a day + status of reflectors + species*time of a day + species*status of reflectors	890.02
species + time of a day + status of reflectors + species*status of reflectors	910.07
null model (with camera ID as a random effect)	932.96
species + status of reflectors + species * status of reflectors	935.87

Table 3. Model output for the probability of animal escape from an oncoming train. The intercept stands for brown hare reaction to an oncoming train during the day.

	Estimate	Std. Error	z value	P value
Intercept (brown hare, day, covered reflectors)	0.357	0.881	0.405	0.69
Red fox	-0.374	1.075	-0.348	0.73
Roe deer	1.727	1.003	1.722	0.09
Night	0.450	0.716	0.629	0.53
Uncovered reflectors	-0.217	0.684	-0.317	0.75
Red fox*night	-0.248	0.816	-0.305	0.76
Roe deer*night	-2.448	0.784	-3.123	0.002
Red fox*uncovered reflectors	0.015	0.961	0.015	0.99
Roe deer*uncovered reflectors	0.194	0.802	0.242	0.81

and 64% (uncovered) during night. The likelihood that red fox escaped from an oncoming train equalled 50% (reflectors covered) and 45% (uncovered) during day and 54% (covered) and 50% (uncovered) during night. Only the roe deer model output showed differences between probability of escaping from an oncoming train during day (89%) and night (52%), regardless of reflectors were covered and uncovered (Table 3).

Time to escape

We collected enough data only for roe deer to compare the time of escape from oncoming trains. Neither time of a day nor status of reflectors affected time of escape of roe deer from an oncoming train. The mean time of roe deer reaction to an oncoming train during a day (intercept) was 6.4 seconds before train arrival and this did not

Table 4. Model output for the timing of roe deer escape from an oncoming train. The intercept stands for roe deer timing of escape during day (for covered and uncovered wildlife warning reflectors).

	Estimate	Std. Error	t value	P value
Intercept (day)	-6.438	1.123	-5.733	< 0.0001
Night - covered reflectors	-1.118	3.198	-0.350	0.73
Night - uncovered reflectors	1.806	1.430	1.263	0.21

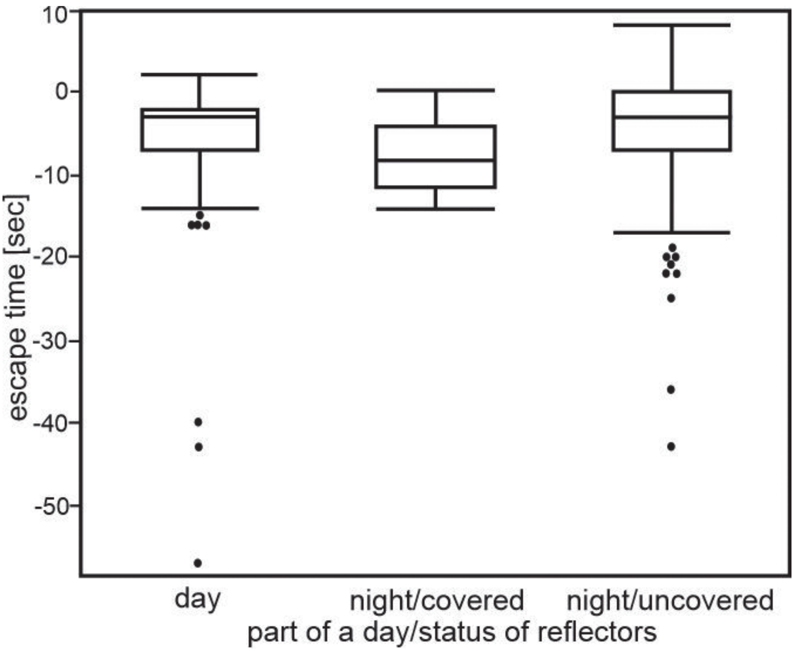

Figure 5. Time of roe deer escape from an oncoming train during day and at night when reflectors were either covered or uncovered. Negative values show that an animal escaped before a train arrived, "0" is the moment when the train passed the animal position and positive values refer to cases when animals escaped after the train had passed the place where they had been standing.

differ from time of roe deer escape during night when reflectors were either covered (mean 7.5 seconds before train arrival) or uncovered (mean 4.6 seconds before train arrival) (Table 4, Fig. 5).

Discussion

Although wildlife warning reflectors were designed primarily to reduce ungulate-vehicle collisions, they are also implemented worldwide to reduce risk of vehicle collisions with other wildlife (for example, see Ramp and Croft 2006). In our study on the effectiveness of the reflectors, we investigated reaction of three mammal species, brown hare, red fox and roe deer, to an oncoming train. According to our findings, roe deer tended to escape from an oncoming train more often than brown hares and red foxes. Nevertheless, the influence of reflectors on reaction of animals to an oncoming train was not confirmed. Time of a day was more meaningful; however, the probability of escape from an oncoming train at night (i.e. at times when reflectors were supposed to work) was not different from that recorded during a day in the case of red fox and brown hare, while it was even lower than during a day in the case of roe deer. We also compared the time of roe deer escape from an oncoming train during days (pooled data for reflectors covered and uncovered) and nights when the reflectors were either covered or uncovered. Again, the analysis did not prove that wildlife warning reflectors modified roe deer behaviour near railways. The mean time of escape of roe deer from the train ranged from approximately 4 to 7 seconds and did not differ at day and night or when reflectors were either active or non-active.

Our findings stand in line with other research conducted on roads, which did not show the clear effect of warning reflectors on the number of wildlife-vehicle collisions (e.g. Zacks 1986; Waring et al. 1991; Brieger et al. 2017; Kämmerle et al. 2017; Benten et al. 2018a; Riginos et al. 2018) or their potential to modify animal behaviour (e.g. Waring et al. 1991; D'Angelo et al. 2006; Benten et al. 2019). On the other hand, Ujvári et al. (1998) found some flight response by deer to warning reflectors, which decreased after a few days, probably due to familiarisation by the animals. Similar findings were presented by Benten et al. (2019), showing that ungulates were more likely to leave the roadside when warning reflectors were present, but the effect of reflectors expired after less than one month (approx. 17 days).

Previous studies on wildlife warning reflectors indicated also that the colour of reflectors might affect their effectiveness (Riginos et al. 2018). Many different colours of reflectors are available, with red and white or amber being the most popular (Benten et al. 2018a). In our research, the red reflectors were used. While people perceive red as a warning signal, most mammals are unable to detect that colour (Benten et al. 2018a). It might be argued that warning reflectors in an alternative colour could have been more effective on the railway lines. Nevertheless, lack of effectiveness of wildlife warning reflectors presented in our studies is in line with previous studies that examined red (Zacks 1986; Waring et al. 1991; Riginos et al. 2018), blue and multi-coloured wildlife warning reflectors (Brieger et al. 2017; Kämmerle et al. 2017; Benten et al. 2018b). Additionally, D'Angelo et al. (2006) tested four colours of reflectors (red, white, blue, amber) and revealed that the colour of reflector had no influence on the effectiveness of wildlife warning reflectors.

In our study, we did not find any differences between reaction to an oncoming train during day and night for red fox and brown hare, while roe deer escaped from an oncoming train more often during the day (when light from reflectors is far less likely to be visible due to ambient light). Ungulate prey can use increased vigilance to reduce their risk of predation, but various factors (i.e. large predators, human disturbances) will modify this response (Proudman et al. 2020). During daytime, the vigilance of animals might be higher (Lima and Bednekoff 1999), also as a response to disturbance from humans (Proudman et al. 2020). Indeed, our study area is located close to the borders of a large city and is heavily penetrated by human and (also free-ranging) dogs.

It may have been best to evaluate the effectiveness of a method preventing animal-vehicle collisions with a Before-After-Control-Impact (BACI) research design. Yet, in this case, we were not able to apply this as wildlife warning reflectors were already mounted along railway lines before we could test them. Therefore, we decided to deactivate them (i.e. cover) to provide control samples for the test period (Schafer et al. 1985; Barlow 1997; Riginos et al. 2015; Riginos et al. 2018). Unfortunately, due to unforeseen circumstances (part of the equipment was stolen and impossible to restore), this part was abandoned after two months (as opposed to the intended half a year). This resulted in a smaller sample size for the control period, which might have biased the results. The other factor that needs to be acknowledged is that seasonality was not accounted for in our research, i.e. testing and control periods were during different months, i.e. control period was conducted at the beginning of the year (February-March), while the test period of research (active reflectors) was registered during autumn and beginning of winter (August–January), during seasonal migration of animals caused by the rut/mating season (Krauze-Gryz et al. 2017). Again, low samples in a control period might also be connected with the seasonal changes in animal behaviour. Nevertheless, we believe that, even with those shortcomings, our results are important as they clearly showed lack of any influence of reflectors on animal behaviour.

Conclusions

Our study did not show reflectors being able to modify animal behaviour to an oncoming train. Roe deer more often escaped as a response to an oncoming train at days than at nights (contrary to what was expected, i.e. reflectors working at night) and the flight behaviour (i.e. time of escape) did not change between periods when the devices were active or inactive. Based on our results, we conclude that (red, as used in our study) wildlife warning reflectors were not an effective tool for mitigating wildlife–vehicle collisions on railways.

Acknowledgements

We are very grateful to Henrik Andrén who helped us with statistical analysis.

The manuscript was partly financed by Warsaw University of Life Sciences (WULS) with funds from the Own Scholarship Fund (Własny Fundusz Stypendialny SGGW w Warszawie).

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Nature Conservation 47: 317–333 (2022)
doi: 10.3897/natureconservation.47.70704
https://natureconservation.pensoft.net

RESEARCH ARTICLE

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Preliminary results on the bird protection effectiveness of animal deflectors on railway overhead lines based on electrical current evaluation

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Academic editor: Sara Santos | Received 15 August 2021 | Accepted 11 January 2022 | Published 25 March 2022

http://zoobank.org/3F40FDCB-1BA8-44A1-B562-90DAC22190A8

Citation: Kornhuber S, Pampel H-P, Görlich J, Leiblein-Wild M, Jöckle C (2022) Preliminary results on the bird protection effectiveness of animal deflectors on railway overhead lines based on electrical current evaluation. In: Santos S, Grilo C, Shilling F, Bhardwaj M, Papp CR (Eds) Linear Infrastructure Networks with Ecological Solutions. Nature Conservation 47: 317–333. https://doi.org/10.3897/natureconservation.47.70704

Abstract

In contrast to other transportation systems, railway systems feature special characteristics, which may cause specific hazards to birds. Among other things, there is the risk of electrocutions resulting from short circuits. To protect the birds and minimize these short circuit events, the DB Netz AG has installed so-called animal deflectors on the insulators of the overhead lines. Since this effort, the number of short-circuit events in the respective sections has decreased, according to DB Netz AG. The principal mechanism of action of the animal deflectors is based on mechanical defense, combined with electrostatic discharge on contact. Although the number of short circuit events has been reduced by using animal deflectors, the detailed function of the animal deflector in different environmental conditions has not been investigated up to now. This research project aims to determine whether, and to what extent, the use of animal deflectors in retrofitting overhead lines may contribute to bird protection and which currents can be measured at retrofitted insulators under different environmental conditions. Hence the current should be measured when using animal deflectors on railway overhead lines for different isolator states and body resistances (5 kΩ, 3 kΩ, 1kΩ, 0.5 kΩ). The results show an influence of measured current depending on the insulator state. Our preliminary results indicate that the use of an animal deflector (KTA) to the tested polymeric insulator and pollution severity can be recommended, since, based on the investigations, no danger to small birds and small animals can be identified. However, the use of the animal deflector (KTA) for the tested porcelain insulator and pollution severity should not be recommended as they showed high animal hazards during pollution and fog conditions. However, these results cannot be transferred to other different insulator types and pollution severities. Investigating the electrical current to the type of insulator used and the expected pollution severity is recommended.

Keywords
Animal deflector, overhead railway line, polymeric insulator, porcelain insulator, stationary current, transient impulse current

Introduction

Compared to other transport infrastructures, electric railways have unique features that can cause specific hazards for birds. Overhead line systems of electric railways provide birds with a variety of resting places. In particular, simultaneous contact with system components of different electrical potentials can risk damaging currents flowing, or even trigger a short circuit.. In order to reduce the number of circuits caused by birds and small mammals, the company DB Netz AG is increasingly using a so-called animal deflector (German: Kleintierabweiser – KTA, shown in Fig. 1) mounted on the insulating part of the high-voltage insulators.

The animal deflector (KTA) does not protect larger birds and does not meet the requirements of the Federal Nature Conservation Act (§ 41 BNatSchG, according to which only constructive measures are to be provided for new installations). Thus, it only can be used for retrofitting existing overhead lines. The animal deflector provides a mechanical defense in combination with a repelling effect caused by discharging static electricity. DB Netz AG estimates KTA as a suitable tool to protect birds and small animals efficiently, as the number of short-circuit events of retrofitted sections seems to decrease. Some nature conservation organizations, however, criticize the functionality of animal detectors and suspect an additional hazard to birds and small mammals, instead.

However, up to now, the detailed function of the animal deflector under different environmental conditions has not been investigated. To close this gap of knowledge and to enable data-based evidence on the question of the suitability of animal detectors for bird protection, a research project of the German Centre for Rail Traffic Research (DZSF) was conducted. In this research project, the following questions were addressed:

- Which levels of electrical currents occur when a small bird touches the KTA?
- How does pollution of the insulator and environmental influences impact the electrical current?
- Do the currents exceed the stimulus threshold of small birds?
- Are small birds endangered by the occurring currents?
- Are short circuits to be expected if the KTA is touched by a small bird?
- Which recommendations and further possibilities can be derived from these results?

However, no reproducible and repeatable measurement results gauging electrical current through the small animal or small bird during contact with the animal

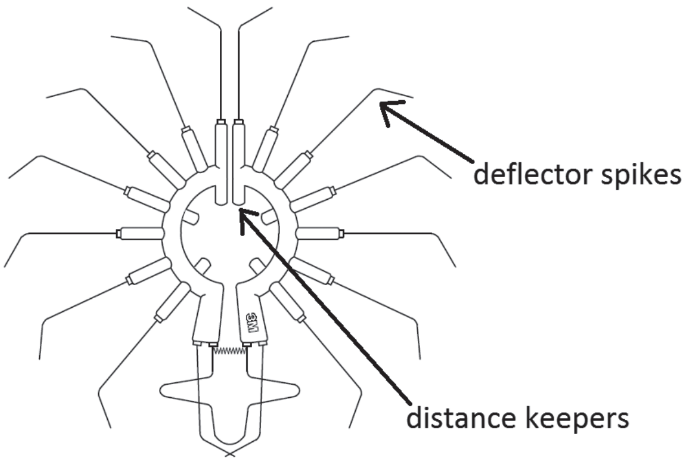

Figure 1. Setup of an animal deflector.

deflector (KTA) at different polluted and wetted insulators are available. So, the aim of the presented experiments and results is to determine practice-relevant electrical parameters that can affect birds when they touch an animal deflector (KTA) mounted on an insulator. Furthermore, a measurement setup and process, and an electric model schematic, which allows a calculation-based investigation, have been developed.

Investigation methods

To control the scope of the experiment and the variety of parameters, conditions close to "real conditions" are defined for the respective influences and simulated as far as possible by means of introduced reproducible experimental methods. For this reason, international common-sense standards and documents (e.g. IEC and CIGRE) and the investigation procedure based on a consensus of an interdisciplinary project advisory group (e.g. ornithology experts, railway experts, bird-life conservation NGOs) were used.

The following parameters are defined as relevant to practice, i.e., influencing the magnitude of the electrical effects in practice (reality):

- the type of insulator with associated KTA (hereinafter referred to as test specimen), the condition of the surface of the test specimen,
- environmental influences acting on the test specimen,
- the arrangement of the test body in the system,
- the size of the small bird's body resistance, and
- the position of the small bird before approaching the KTA.

The electrical resistance of birds can vary due to their physical characteristics (size, density, and type of feathers, total proportion of water contained in the body). The

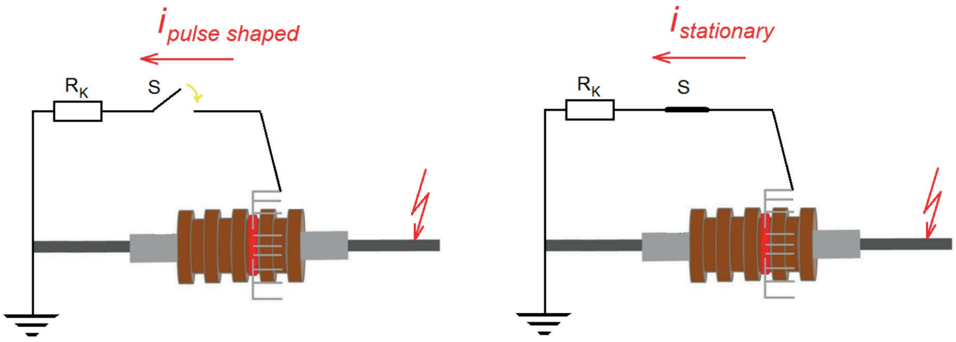

Figure 2. Measured electrical current at the moment of contact (left) and during the steady-state condition (right), S: Switch; RK: Animal Resistor.

small birds and animals are simulated by technical resistors. The measurements are carried out with four different equivalent resistors (5, 3, 1, and 0.5 kΩ).

The electrical quantities recorded during the experiments are the alternating voltage across the insulator and the transient behavior of the current flowing through the equivalent resistor from the moment of contact with the KTA. The current at the time of contact is pulse-shaped (Fig. 2 – left) and changes to a stationary behavior after longer contact with the KTA (Fig. 2 – right). The case of a bird sitting on earth potential is simulated, as from the electrical point of view, this is the more critical combination. The simulation of the contact is realized experimentally with a switch (Fig. 2).

The dimensions, the material, and the design of the insulator can have a strong influence on the amount of charge available on the electrodes of the KTA and thus on the pulsed current flowing at the time of contact with the KTA. Furthermore, the electrical current flowing through the bird when the KTA is then permanently touched also depends on the material and the dimensions of the insulator. A special dependency exists regarding the behavior with pollution and/or moistened insulating material surfaces. For example, the surfaces of polymeric insulators might be water-repellent (hydrophobic). This property can be transferred to the layers of dirt adhering to the insulating material. Due to this hydrophobic transfer, there is no or not such a strong reduction of the insulating capacity compared to the porcelain insulator. When a polluted porcelain insulator is moistened, on the other hand, a closed conductive layer can be formed, which can lead to a lower insulating capacity with increased flow through the bird and to an increased risk of a flashover. For the investigations done within this research, one typical polymeric insulator type (Fig. 3) and one typical porcelain insulator type (Fig. 4) from DB Netz AG were used.

Measurement setup and process

In Fig. 5, the test circuit is shown. The test voltage is applied from the main supply by using a regulation transformer and a high voltage transformer. The voltage of 16 kV at 50 Hz is applied. In the project report (Görlich et al. 2021), an investigation on the influence of the frequency difference between 16.7 Hz and 50 Hz was conducted and concluded:

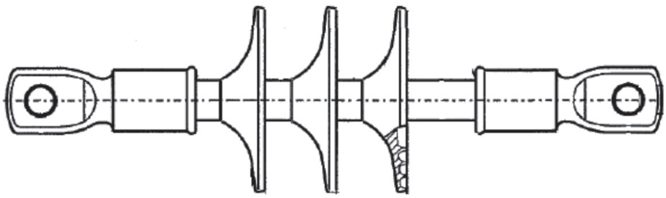

Figure 3. Polymeric Insulator under investigation.

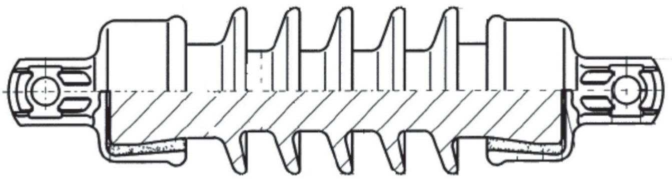

Figure 4. Porcelain insulator under investigation.

- for the impulse discharge behavior no influence of the frequency is observed because the accumulated charge, which is independent of the supplying frequency, is responsible for the behavior.
- for the pollution flashover characteristics, the resistive behavior is mandatory. This is frequency-independent.
- for the behavior which is mainly dominated by the displacement current (clean insulator, polluted and dry insulate), the frequency has a direct influence. However, the currents are both very small (tens of μA) compared to the reference values and limits.

The animal deflector is mounted in accordance with the procedure, and two independent metal spikes are connected to each other for reflection in the worst case in a real application, which is leading to an increased electrical charge. By using a switch, the spikes of the animal deflector are conducted with a combination of resistors which provide the body resistance of the birds and also include the measurement shunt for measuring the current, which is recorded by using a transient analyzer.

In Fig. 6, the test setup at dry tests and rain tests is shown, which was set up quite close to the real setup at a railway. With this additional setup, a comparison to the fog chamber optimized setup for evaluating the influence of stray capacitances was provided.

In Fig. 7, the setup in the fog chamber is shown.

During the investigations the following conditions were applied to the polymeric insulator:

- cleaned insulator in dry, rainy, and icy conditions
- light-polluted insulator in dry, rainy, and wetted by fog conditions
- heavy-polluted insulator in dry, rainy, and wetted by fog conditions

During the investigations following conditions were applied to the porcelain insulator:

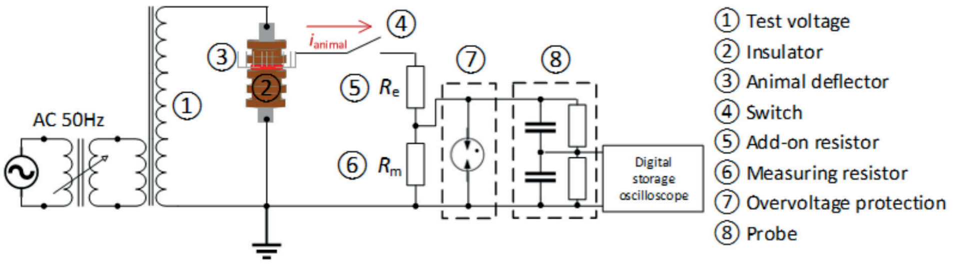

Figure 5. Setup of the Test Circuit.

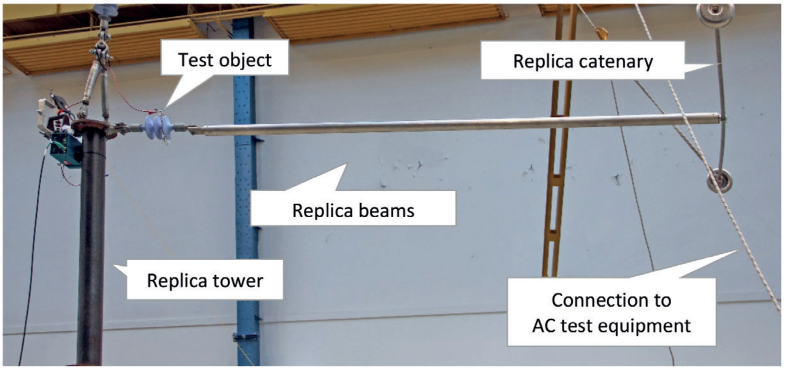

Figure 6. Test setup for dry test and rain test at TU Dresden.

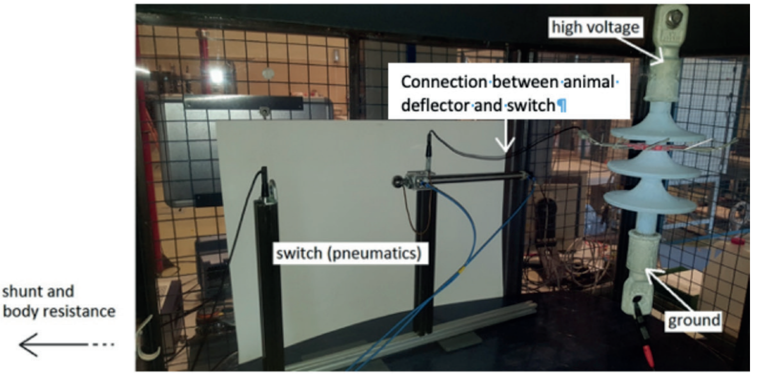

Figure 7. Test setup in the fog chamber.

- cleaned insulator in dry
- light-polluted insulator in wetted by fog conditions
- heavy-polluted insulator in wetted by fog conditions

The polluted conditions were applied by using the recommendations of the CIGRE Technical Brochure 555 (2013) proposing a procedure for the contamination of

Table 1. Overview of the used artificial pollution suspension for light and heavy pollution.

Light pollution	Heavy pollution
1000 g Water	1000 g Water
20 g Highly dispersible silica	25 g Highly dispersible silica
0,2 g NaCl	2,5 g NaCl
Conductivity of suspension: 450 µS/cm (at 20 °C)	Conductivity of suspension: 4,1 mS/cm (at 20 °C)

insulators for laboratory tests, which refers to the preparation of suitable contamination layers according to IEC 60507 (2013), Chapter 6. In accordance with IEC 60507 (2013), chapter 6.3, a suspension with light contamination and a suspension with strong contamination (Table 1) are prepared for the investigations. The conductivity of the contamination is adjusted via the salt (NaCl) content. The required quantities were determined by preliminary tests.

A corresponding number of test specimens is taken from the quantity of cleaned, prepared insulators. The contamination suspension is applied to these using the immersion method in accordance with IEC 60507 (2013). For this purpose, the insulators with KTA are immersed in the respective contamination suspension and immediately pulled out again. (Fig. 8).

The impurity layer is then dried and stored for 24 h under the atmospheric conditions prevailing in the test room (air temperature 23 °C to 24 °C, humidity 45% to 50% r.h.).

At the test specimen standard rain according to IEC 60060-1 (2011), section 4.4. with the following parameters were applied:

- mean rainfall vertical 1.5±0.5 mm/min horizontal 1.6±0.5 mm/min
- The specific electrical resistance of the rainwater 100±5 Ohm
- The temperature of rainwater 16 °C
- Pre-stress time in stress-free condition 15 min

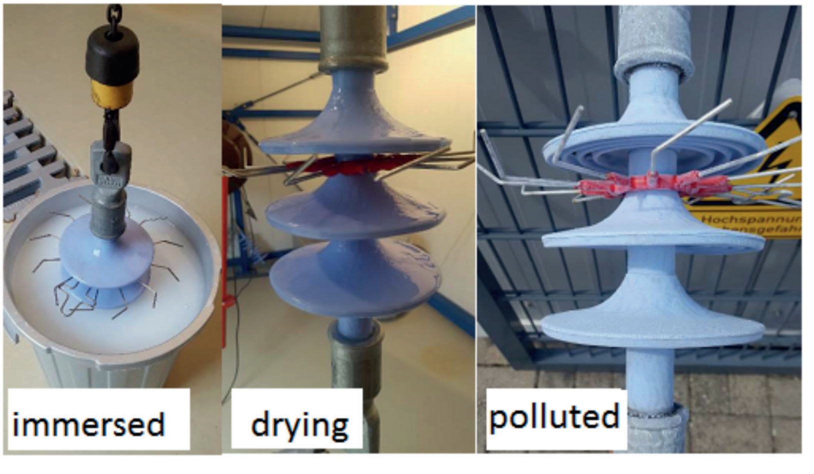

Figure 8. Applying the contamination layer - example, polymeric insulator

In addition to the specifications in IEC 60060-1 (2011), uniform sprinkling and wetting are set on the insulator by visual inspection. The measurement is carried out after the pre-stress time with continuous rain. The test setup is shown in Fig. 9.

The pollution layer is moistened with a modified clean fog specified in CIGRE Technical Brochure 481 (2011). For this purpose, the artificially polluted insulator is fogged with a non-conductive fog at room temperature in a fog chamber (Fig. 10) with the following parameters:

- Generation of the fog: 2 Defensors type 505, Defensor AG Pfäffikon
- Volume of fog chamber: 4.5 m^3
- Precipitation rate: 0.03 ml/(cm^2 - h)

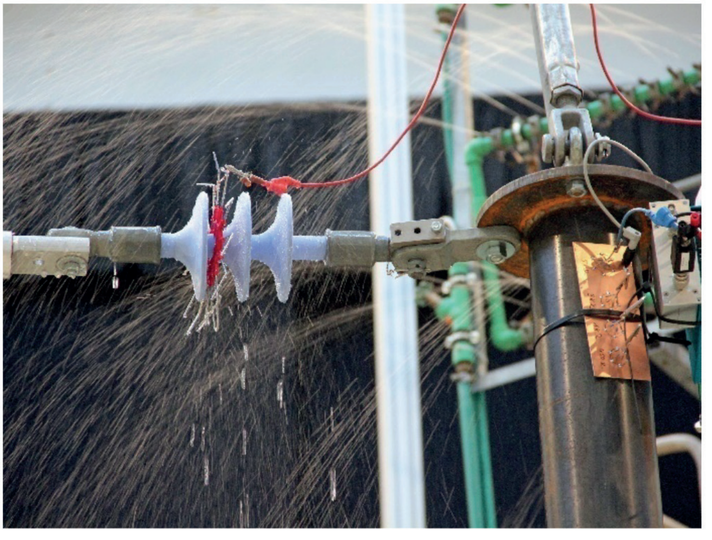

Figure 9. Investigation of the insulator during the rain test.

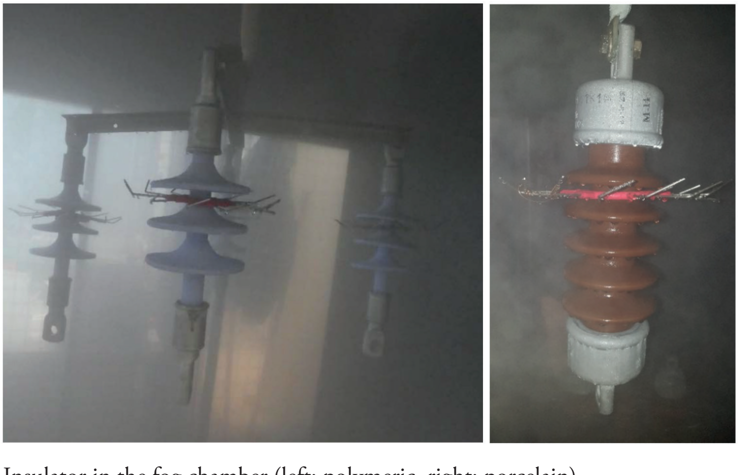

Figure 10. Insulator in the fog chamber (left: polymeric, right: porcelain).

Figure 11. Iced insulator.

- Fog conductivity: 2 μS/cm
- Time of fogging without voltage stress condition 2 h

The generated fog leads to slow moisture penetration of the pollution layer without washing off. This simulates the dewing or fogging of pollution layers in reality.

The approach described by the Institute of Electrical and Electronics Engineers (IEEE) Task Force on Insulator Icing Test Methods in Farzaneh et al. (2003) is used to simulate a practical ice formation. This publication presents the state of knowledge developed by the IEEE Task Force together with the CIGRE Ice/Snow Tasks Force. According to Bär (2016), a glaze with a transparent and clear appearance and cylindrical ice is proposed for investigations with bird protection fittings. This icing is classified as the most critical variant and occurs at low wind speeds. The results of the icing procedure are shown in Fig. 11.

Measurements and data analysis

The current measurement is done as described using a resistor as a shunt and recorded by a transient recorder.

In Fig. 12 the transient current behavior at the moment of contact of the small bird with the animal deflector is shown. What is remarkable is the very fast discharge of the charge carriers, which are stored at the metal electrodes of the animal deflector. The rise time of the measured values is approx. 2 ns. The value of the peak current shows up to 10 s of amperes. The whole impulse with its damped behavior lasts up to 30 ns.

In contradiction to the very fast transient behavior at the moment of the contact, the steady-state current follows in line with the theory of the source frequency of 50 Hz and is shown in Fig. 13. The polymeric insulator with the animal deflector at clean surface and under dry conditions shows a clear capacitive behavior with a peak current of approx. 20 μA.

For the evaluation of the measurement results the following values were derived from the measurement data:

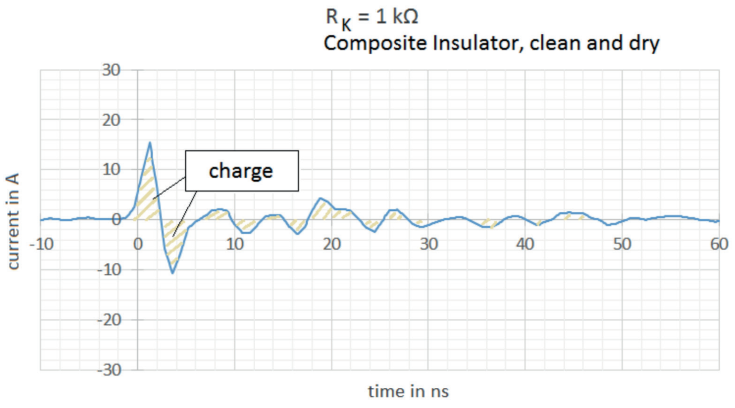

Figure 12. Transient current behavior at the moment of contact with a polymeric insulator.

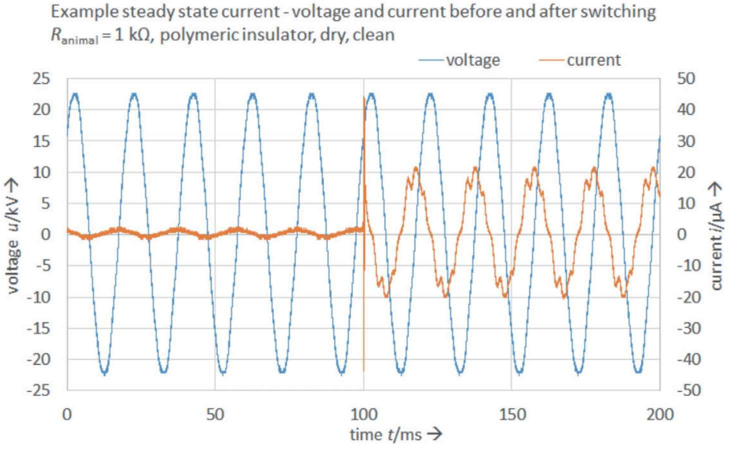

Figure 13. Steady-state current behavior for a polymeric insulator..

- the transient current in the moment of the contact of the animal deflector, the carried charge, and the energy with the equations are used:

$$Q = \int |\, i(t) \,| \cdot dt$$

$$E = R \cdot \int i(t)^2 \cdot dt$$

- the steady-state conditions, the root mean square value of the current is used

Evaluation criteria

Based on the theoretical considerations and the measured values, three basic scenarios have to be distinguished with regard to the exposure of birds and small animals to electric currents flowing through the KTA:

1. transient current by transport of the charge from the animal deflector at the time of contact with the animal deflector by the small bird or small animal (time range few 10 ns) – see Fig. 14
2. stationary current when the bird or small animal continuously touches the animal deflector (time range ms) - see Fig. 15
3. electric arc as a result of flashover and flow between high-voltage contact and earth (so-called earth fault) on the bird or small animal (time range ms) - see Fig. 16

The third scenario with the current or direct thermal effects of the arc on a bird or small animal leads to direct damage to the living creature in addition to the electrical effects, especially due to the thermal effects. The occurrence of this scenario shall be prevented. Consideration of limit and guide values for this scenario is not expedient.

For the assessment of the measured values, the following values are defined for the respective scenarios presented in this project:

Reference stimulus threshold

The "reference value stimulus threshold" describes a current value above which the animal can feel a biological effect. Current values that fall below this value are not noticeable due to biological effect mechanisms.

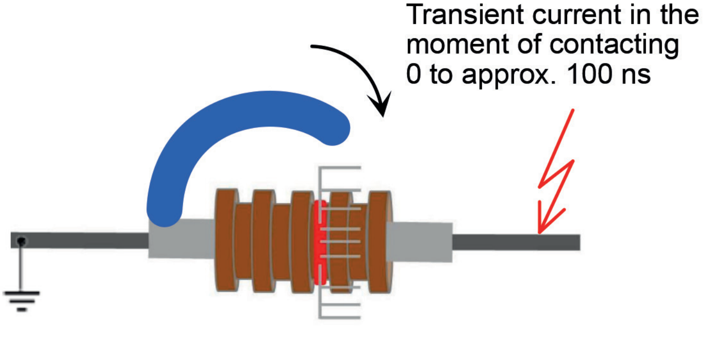

Figure 14. transient current when the switch is closed (bird or small animal is indicated with a bow).

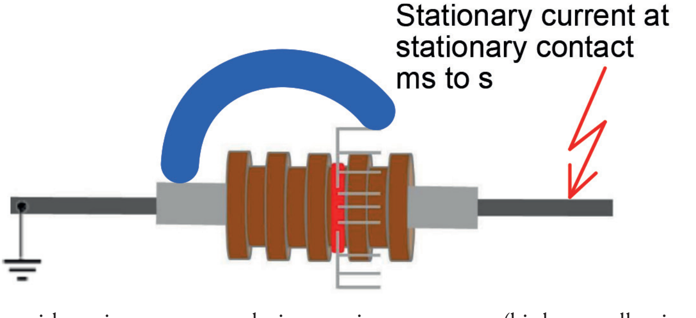

Figure 15. Flow with stationary current during continuous contact (bird or small animal is indicated with an arc).

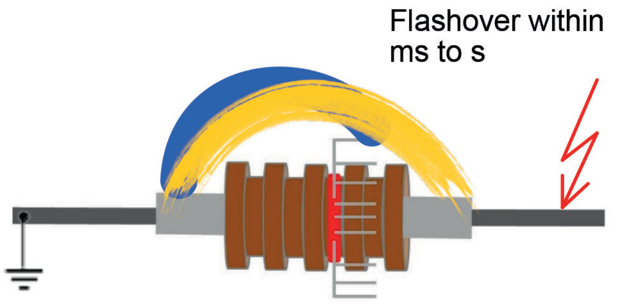

Figure 16. Flashover at the KTA (bird or small animal is indicated with an arc).

Hazard threshold

If the "threshold value danger" is exceeded, it can be assumed that the bird will be directly or indirectly harmed by the electrocutions.

In the following, the determination of limit and reference values for current will therefore concentrate on scenarios 1 (transient current) and 2 (stationary current).

The values are gained by using a detailed literature study and intensive discussions in the interdisciplinary project advisory group and summarized in Table 2. A short overview of the based literature is mentioned in (Osypka (1963), DIN EN 60335-2-76 (VDE 0700-76) (2015), "weidezaun.info" VOSS GmbH & Co. KG (2019), DZSF (2019), Meyer and Jeromin (2016), Jeromin et al. (2013), Operational Manual hotShock 300 (2017), VDE-AR-N 4210-11 (2011), Pearce et al. (1982), Leitgeb (2000)). The detailed analysis is described in the research report Görlich et. Al. (2021).

Results

Based on the measurement results and its derived values, the evaluation was done by comparing with the reference values according to Table 2. The evaluation results are presented in Table 3.

In detailed for each insulator following summarized results can be found:

Table 2. Concluded reference stimulus threshold and hazard threshold.

	Transient current pulse stress	Stationary current stress
Time interval of the stress	few 10 ns	ms to s
Hazard threshold	1 Joule	2 mA
	Osypka (1963), DIN EN 60335-2-76 (VDE 0700-76) (2015), "weidezaun.info" VOSS GmbH & Co. KG (2019), DZSF (2019), Meyer and Jeromin (2016), Jeromin et al. (2013), Operational Manual hotShock 300 (2017)	VDE-AR-N 4210-11 (2011)
Reference stimulus threshold	Not available	500 μA
		Pearce et al. (1982), Leitgeb (2000)

Table 3. Overview of measured values compared with thresholds of Table 2.

Insulator Typ	Insulator Condition	Ambient	Reference Stimulus Threshold	Hazard Threshold	
			Stationary current stress Time interval of the stress ms to s	Stationary current stress Time interval of the stress ms to s	Transient current puls stress Time interval of the stress few 10 ns
POLYMERIC INSULATOR	Cleaned	Dry	Not exceeded	Not exceeded	Not exceeded
		Rain	Not exceeded	Not exceeded	Not exceeded
		Ice	Not exceeded	Not exceeded	Not exceeded
POLYMERIC INSULATOR	light polluted	Dry	Not exceeded	Not exceeded	Not exceeded
		Rain	Not exceeded	Not exceeded	Not exceeded
		Fog	Not exceeded	Not exceeded	Not exceeded
POLYMERIC INSULATOR	heavy polluted	Dry	Not exceeded	Not exceeded	Not exceeded
		Rain	Not exceeded	Not exceeded	Not exceeded
		Fog	Not exceeded	Not exceeded	Not exceeded
PORCELAIN INSULATOR	Cleaned	Dry	Not exceeded	Not exceeded	Not exceeded
	light polluted	Fog	**Exceeded**	**exceeded**	Not exceeded
	heavy polluted	Fog	**Exceeded**	**exceeded**	**Not available** Due to flashover no measurement was possible

Polymeric insulator

For the polymeric insulator investigated for the risk at the moment of contact it can be concluded that for all environmental conditions the energies measured at the body resistance are below the hazard limit value of 1 J. The current pulse of the investigated polymeric insulators (or comparable types) is below the hazard limit value.

For the polymeric insulator examined for the risk at stationary contact it can be concluded that for all insulator situations that the currents measured at the body resistance are below the hazard limit of 2 mA. This can be attributed to the hydrophobic properties of polymeric insulators. When the polymeric surface is wetted, no closed pollution layer is formed, but instead, individual droplets are formed, which greatly reduces the current. This effect also occurs with polluted polymeric insulator surfaces since the layer of dirt also takes on a water-repellent effect due to the hydrophobic transfer.

For the evaluation of the stimulus results in the moment of contact, it was not possible to determine a reference value for the stimulus threshold for pulsed flow. For this reason, no statement can be made about the triggering of the receptors on the basis of the measured values. Thus, it cannot be conclusively clarified whether small birds react when touching the animal deflector.

For the polymeric insulator investigated for the stimulus result at stationary contact it can be concluded for all insulator states that the currents measured at the body resistance are below the defined reference value of the stimulus threshold of 500 μA.

Porcelain insulator

For the examined porcelain insulator for the risk at the moment of contact it can be concluded that for the insulator states cleaned and light-polluted (in case of moisture penetration with mist) that the energies measured at the body resistance are below the limit value of hazard of 1 J. An evaluation of the heavily polluted, wetted fog porcelain insulator is not possible due to the spontaneous flashover.

For the examined porcelain insulator for the risk at stationary contact it can be concluded that for the insulator states cleaned and dry that the currents measured at the body resistance are below the limit value of the risk of 2 mA. For the examined porcelain insulator, it can be determined for the insulator states light-polluted wetted with fog that the currents determined at the body resistance are above the limit value hazard of 2 mA. In the case of a heavy-polluted porcelain insulator, spontaneous flashover occurs with a current-starved arc, whereby a bird would be exposed to thermal damage in addition to electrical damage.

For the evaluation of the stimulus results at the moment of contact, no reference values for the irritation threshold could be determined. For this reason, no statement can be made about the triggering of the receptors based on the measured values.

For the evaluation of the stimulus results for stationary contact for the examined porcelain insulator, it can be determined for the insulator states cleaned dry that the currents determined by measurement on the body resistance are below the defined reference value of the stimulus threshold of 500 μA. It can be assumed that no stimulus is triggered due to the electrical flow. In the case of the examined light pollution wetted by fog, the reference value of the stimulus threshold but also the danger threshold is exceeded. In the case of a heavily polluted porcelain insulator, spontaneous flashover with a high-current arc occurs, whereby a bird would be exposed to thermal damage in addition to electrical damage.

Discussion

Compared to other transport infrastructures, electric railways have unique features that can cause specific hazards for birds. Overhead line systems of electric railways provide birds with a variety of resting places. In particular, the simultaneous contact with system components of different electrical potentials possesses a risk of damaging currents flowing or even triggering a short circuit for birds. The company DB Netz AG is increasingly using an animal deflector (German: Kleintierabweiser – KTA) mounted on the insulating part of the high-voltage insulators. The animal deflector does not provide protection for larger birds and does not meet the requirements of the Federal Nature Conservation Act (§ 41 BNatSchG, according to which only constructive measures are to be provided for new installations). They may, therefore, only be used for retrofitting existing plants. This investigation was done because no measurement results of the electrical current at animal deflectors in different conditions are available. With these results a measurement-based evaluation of the effectiveness of the animal deflector is supported.

Basically, a distinction must be made between three scenarios:

- The bird touches the animal deflector, and the electrostatic discharge causes a transient impulse current through the small bird or animal (The time range of the discharge process is up to about 100 ns).

- The bird touches the KTA for a longer period (time range ms to s): A stationary electrical flow through the living being occurs.
- The contact with the bird causes a flashover with a corresponding thermal effect.

To assess the electrical flow through birds and small animals, hazard thresholds (damage) and reference values for the stimulus threshold for stationary electrical flow were determined based on literature research, physiological principles, and analogy relationships. A reference value for the stimulus threshold for transient impulse current could not be determined.

Regarding the examined polymeric insulator, the following conclusions can be made:

- No exceedance of hazard thresholds is detected;
- It is not possible to conclusively assess whether the stimulus threshold is triggered by transient impulse current (no reference value for the stimulus threshold could be determined);
- For these reasons, the use of investigated animal deflector (KTA) to the examined polymeric insulator type (or insulators of comparable design) can be recommended, since, based on the investigations, no danger to small birds and small animals can be identified.

For the examined porcelain insulator following conclusions can be done:

- No exceedance of hazard threshold value can be detected in clean and dry conditions;
- An exceedance of hazard threshold value can be detected when light-polluted and wetted by fog layer;
- The formation of a flashover can be observed in the case of heavy pollution and wetted by fog layer;
- Therefore, no recommendation is given for the application of the use of the investigated animal deflector (KTA) for the investigated porcelain insulator type (or insulators of comparable design).

However, besides the extensive investigations undertaken, the following areas can be listed as possible investigation areas:

- Other types of insulators (e.g. glass type cap and pin insulators, different lengths) and animal deflectors were not investigated. Therefore, it need to be added, that the behavior of the deflector and the effects to the small animals and birds depend on the insulator design and its material. For this reason, investigations needs to be done regarding different insulator designs or materials as well as pollution types.

- Besides the examined electrical mode of operation, the animal deflector may have a mechanical and optical mode of operation, whereby the investigations into the behavior of small birds and animals towards the animal deflector are not part of this research work. Further investigations to evaluate the optical repelling effect are necessary.

- For a better evaluation of the measured values, especially with respect to a reference value of the stimulus threshold, further physiological examinations are necessary.

Our preliminary results indicate that the use of an animal deflector (KTA) to the tested polymeric insulator and pollution severity can be recommended because, based on the investigations, no danger to small birds and small animals can be identified. However, the use of the animal deflector (KTA) for the tested porcelain insulator and pollution severity should not be recommended as they showed high animal hazards during pollution and fog conditions. However, these results cannot be transferred to other different insulator types and pollution severities. Investigate the electrical current to the used type of insulator and the expected severity of pollution is recommended..

Acknowledgements

We thank the "BMVI Network of Experts" of the Federal Ministry of Transport and Digital Infrastructure of Germany (BMVI) for funding through the Federal Railway Authority, Germany (project number 2018-U-10-1217). The authors also thank the interdisciplinary project advisory group for their discussions and valuable contributions in the project meetings.

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