Green roads and highways to protect biodiversity: Monitoring the impacts of the N4 national highway (TRAC N4), South Africa, on wildlife

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ABSTRACT

Transport infrastructure, in this instance, roads and highways, is a critical element of sustainable human economic development and society by driving development and serving as the main mode of transport. In South Africa, road corridors are especially important in improving access from rural areas into areas of economic zones, which promotes development, job creation, and accessibility needs. In addition, road transport provides an enabling environment for freight movement and contributes ~74% of total land freight income in the sector in South Africa. However, when roads are not built following the bounds of sustainability, they may have negative impacts on both humans and the environment. Poorly planned transport infrastructure can have severe impacts on ecological connectivity and species survival. Roads can create barriers to wildlife movement, limiting terrestrial wildlife's ability to find essential ecological resources such as water, food, and mates.

Road fragmented landscapes may accelerate incidents of wildlife-vehicle collisions. Whilst these incidents almost always result in wildlife mortality, they can also impact the overall health and functionality of ecosystems. Furthermore, they could risk human safety by causing injuries to road users. These impacts are particularly relevant in South Africa, which is home to iconic wildlife, with a wide array of habitats that harbour over 20,000 different species of flora and fauna, whilst still transitioning to a green economy. The present study expands on previous research by emphasising the urgent need for adopting road development projects that optimise social and economic benefits while safeguarding biodiversity and ecosystems through the inclusion of ecological connectivity.

Firstly, the global use of camera trapping techniques as a research tool for monitoring crossing-structure use by wildlife in road fragmented landscapes was evaluated. Whilst the global

trend in road ecology studies that deployed camera traps to evaluate crossing structure use has showed a geographical bias, it was clear that camera trap use to monitor wildlife crossing structures is still an emerging area of research. In addition, although the evaluation showed that the camera trap approach was successful in monitoring animals' use of crossing structures, the study design, sampling, and surveying techniques deployed by each study varied considerably and were not standardised. This highlighted the need and significance of studies to maintain consistency in the protocol of monitoring crossing structure so that studies will be comparable in terms of use patterns.

Secondly, green transport infrastructure has become an important element of sustainable development frameworks. Maintaining ecological connectivity between road-fragmented natural landscapes plays a significant role in conserving wildlife populations. The present study has comprehensively assessed the relevance of South Africa's national policies on sustainable road transport development in maximising the ecological functionality of road networks through promoting the inclusion of ecological connectivity. This thesis further proposed a synthesised analytical framework for promoting transport infrastructure sustainability that presents a user-centric integrated model and establishes road project planning and design that optimise social and economic benefits while minimising negative ecological impacts through strategic collaborations.

Thirdly, this study has explored wildlife roadkill patterns and animal movement on a national highway that bisects landscapes of grasslands, freshwater ecosystems and wetlands, which are suitable homes for a variety of species. This doctoral study further researched the usefulness of road specialised structures (bridges, culverts, viaducts and tunnels) in helping animals to move across the TRAC N4 Toll Route, so we can reduce roadkill incidents and improve landscape ecological functionality. This will assist in promoting the consideration and inclusion of ecological connectivity and biodiversity needs in road transport development sustainability frameworks in South Africa.

PREFACE

The data described in this thesis were collected along the TRAC N4 toll route, Republic of South Africa, from November 2022 to December 2024. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs, Dr Manqoba M. Zungu and Mrs Wendy J. Collinson-Jonker.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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Thabo I. Hlatshwayo

March 2025

I certify that the above statement is correct, and as the candidate's main supervisor, I have approved this thesis for submission.

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Prof Colleen T. Downs

Supervisor

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DECLARATION 1 - PLAGIARISM

I, Thabo I. Hlatshwayo, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

PUBLICATION 1- Journal of Ecology and Evolution (Provisionally accepted)

A systematic review of global road ecology camera trap studies that monitored animals' use of wildlife crossing structures in road fragmented landscapes

Thabo I Hlatshwayo, Manqoba M Zungu, Wendy J Collinson-Jonker, Colleen T. Downs

Author contributions:

TIH, MMZ, and WJC conceived the paper with CTD. TIH collected and analysed data, and wrote the paper. MMZ, WJC and CTD contributed valuable comments to the manuscript.

PUBLICATION 2- Journal of Environmental Management (Published)

Mainstreaming ecological connectivity and wildlife needs in green road transport infrastructure planning in South Africa

Thabo I Hlatshwayo, Manqoba M Zungu, Wendy J Collinson-Jonker, Colleen T. Downs

Author contributions:

TIH, MMZ, and WJC conceived the paper with CTD. TIH collected and analysed data, and wrote the paper. MMZ, WJC and CTD contributed valuable comments to the manuscript.

PUBLICATION 3- Formatted for Journal of Biological Conservation (not submitted)

Protecting the unprotected: Monitoring the ecological impacts of a major South African highway on terrestrial vertebrate movement and conservation

Thabo I Hlatshwayo, Cameron T, Cormac, Manqoba M Zungu, Wendy J Collinson-Jonker, Colleen T. Downs

Author contributions:

TIH, CTC, MMZ, and WJC conceived the paper with CTD. TIH and CTC collected and analysed data, and wrote the paper. MMZ, WCJ and CTD contributed valuable comments to the manuscript.

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Evaluating the spatial and temporal patterns of wildlife use of existing road drainage underpass structures along a major South African highway

Thabo I Hlatshwayo, Cameron T, Cormac, Manqoba M Zungu, Wendy J Collinson-Jonker, Colleen T. Downs

Author contributions:

TIH, CTC, MMZ, and WJC conceived the paper with CTD. TIH and CTC collected and analysed data, and wrote the paper. MMZ, WCJ and CTD contributed valuable comments to the manuscript

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Thabo I. Hlatshwayo

March 2025

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Noting that my first significant conservation career has been at the Endangered Wildlife Trust (EWT), I am grateful for the fantastic opportunities and the logistical support provided by the EWT throughout my PhD journey. This great institution has significantly shaped my conservation career and made me belong to a community that comprises individuals who are dedicated to promoting inclusive biodiversity conservation mandates. Special thanks go to the following people who guided and helped me grow as the Wildlife and Transport Project Field Officer at EWT: Lourens Leeuwner, for being an amazing line manager; Dr Lizanne Roxburgh and Erin Adams, for always being there when I needed advice and assistance on data analysis and GIS mapping tools.

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CHAPTER 1

General introduction

1.1 Conservation of terrestrial biodiversity

Terrestrial ecosystems have highly rich and diverse biodiversity (Beraldi-Campesi, 2013; Simmonds et al., 2021; Rao et al., 2023) and are important for supporting human livelihoods and economic development (Reddy et al., 2018; Kong et al., 2022). These ecosystems are home to a wide variety of species that are dependent upon land surface habitats such as forests, savannas, deserts, riverine and wetlands for any critical part of their life cycles (Mucina & Rutherford, 2006; Rao et al., 2023). Since the well-being of people is largely reliant on the planet having a rich biodiversity (Reddy et al., 2018), it is important that the precious nature of what lives on land surfaces be sustainably conserved from degradation (Pollock et al., 2020; Simmonds et al., 2021). Despite terrestrial landscapes being the only available space for human and terrestrial wildlife (Beraldi-Campesi, 2013), human anthropogenic activities continue to degrade and destroy natural landscapes at unsustainable rates globally (Thomas et al., 2017; Kuncoro et al., 2024). Moreover, rates of fragmentation of terrestrial ecosystems present severe challenges for biodiversity and humanity (IPBES, 2019; Simmonds et al., 2021).

As the demand for land for human infrastructural development, including transport infrastructure, increases, more terrestrial ecosystems are encroached (Kong et al., 2022; Kuncoro et al., 2024), leading to people losing connection with nature. Global assessments show that human anthropogenic activities have altered approximately three-quarters of the earth's land surface within the last millennium (Shukla et al., 2019). Henceforth, unsustainable human actions have driven over 680 vertebrate species to extinction since the 16th century and caused a ~20% decline in the average abundance of native species (UN Report, 2019), severely reducing the integrity of global terrestrial habitat. Although the adoption of coordinated actions to reverse the threat is lacking, the risks of how unsustainable land conversion for human development will affect global biodiversity and humanity need to be better understood in planning for a sustainable future (Paemelaere et al., 2023; Kuncoro et al., 2024).

1.2 Anthropogenic threats

Human activities through burning fossil fuels, pollution and deforestation continue to impact the natural environment negatively (Tinker et al., 1996; Elmqvist et al., 2013; Moullec et al., 2021), and these have triggered numerous environmental issues such as climate change, poor air and water quality, colonisation by alien invasive species, degradation, and fragmentation of habitats (Morris, 2010; Winkler et al., 2021; Son et al., 2024). Since the Industrial Revolution in the late 19th century, the human population has drastically increased with no sign of slowing down (Lucas, 2018; Guyot et al., 2021). This means that there will be an increase in demand for natural resources (Alberti et al., 2007; Huang et al., 2010), accelerating the colonisation of the natural landscape. By nature, natural landscapes are habitats for diverse wildlife species, including all vertebrates, invertebrates and plants. Across the globe, the transformation of natural landscapes for urbanisation, industrialisation and agricultural production has accelerated the loss of terrestrial biodiversity (Bradshaw, 2012; Concepción et al., 2015; Hassell et al., 2021; Fornal-Pieniak et al., 2024). Due to these anthropogenic developments, increased natural landscapes and their ecosystems are increasingly encroached and fragmented, which disturbs ecosystem structure and functioning (Concepción et al., 2015; Winkler et al., 2024). This reduces terrestrial ecosystems and their biodiversity (Pereira et al., 2010; Ramesh & Downs, 2015; Winkler et al., 2024).

1.3 Infrastructure development

Infrastructure consists of physical structures that are planned to facilitate sustainable development through critical investments that play a vital role in fulfilling energy needs (coal, hydropower, powerlines and oil), transport corridors (roads, railways), water (pipelines, canals) and telecommunications (internet cables) (Woetzel et al., 2016). Development in infrastructure is considered a fundamental need to boost continental, regional, national and local economies through promoting inclusive and sustainable industrialisation (Collinson et al., 2019; Juffe-Bignoli et al., 2021; Nyumba et al., 2021; Son et al., 2024). To this end, the global human population is estimated to be ~7.8 billion, and is anticipated to rise to 9.7 billion by 2050 (UN World Population Prospects, 2019c); hence, this tremendous growth will undoubtedly increase the global need for infrastructure investments (Gundes, 2022).

Human reliance on infrastructure such as power, water, transport and digital communication for survival is accelerating the demand for more infrastructure investments. Across the globe, average spending on infrastructure development between 2016 and 2040 is projected to be ~3.2 trillion per year (Global Infrastructure Hub and Oxford Economics, 2017). According to the UN Economic Commission for Africa (2019b), over 25 million km of new paved roads are globally projected by 2050 for connecting people with areas of economic zones such as production facilities and industries. In addition, over 50,000 large dams and reservoirs are planned for construction to improve access to potable water, with 90% of these projects designated for the least developed and developing continents (UN Economic Commission for Africa, 2019b).

Although development corridors such as roads, railways and powerlines are considered fundamental for boosting continental, national, and local economies through promoting inclusive and sustainable industrialisation (Collinson et al., 2019; Juffe-Bignoli et al., 2021; Nyumba et al., 2021; Kuncoro et al., 2024), their contribution to deteriorating suitable habitats must not be overlooked. A notable example includes the 33 development corridors of over 53,000 km length in Africa, potentially crossing 400 protected areas (Laurance et al., 2015). As much as these development corridors will promote the economic development strategy, it is worth noting that they will be major drivers of habitat and biodiversity loss (Collinson et al., 2019; Juffe-Bignoli et al., 2021; Kuncoro et al., 2024). These would accelerate the encroachment of natural landscapes and further reduce biodiversity composition and production. Focusing future developments towards habitat mosaics that comprise both natural and human-managed landscapes with wildlife connectivity is key in addressing the consequences of land structural transformation (Paemelaere et al., 2023; Zhang et al., 2024). This is particularly needed in developing regions such as sub-Saharan Africa, where many people rely on natural resources to sustain livelihoods (Thuiller et al., 2006; Downs et al., 2021).

1.4 Status of transport infrastructure development in Africa

Transportation and infrastructure play an abundant role towards achieving the objectives of the sustainable development goals through trade and economic development (Meijer et al., 2018; Menhas et al., 2019; Sons et al., 2024). Transportation corridors are linear infrastructure, such as roads and railways. They facilitate the link between geographical space and human activities (Shi et al., 2018), making them a catalyst for investments and economic transformation (Onjala, 2018; Kuncoro et al., 2024). Transport infrastructure development is globally anticipated to increase as more countries continue to harness the benefits of transportation corridors (Onjala, 2018; United Nations, 2019a). In Africa, the implementation of the African Continental Free Trade Area (AfCFTA) by the African Union has caused massive needs for transport infrastructure development. As a result, the African Union (AU), through the Agenda 2063 continental framework, has worked out plans for developing cross-border corridors throughout the continent (Ndoye, 2022; Balbaa et al., 2023). Since transport corridors play a pivotal role in integrating and strengthening trade in this region, the Programme for Infrastructure Development in Africa (PIDA) has projected plans for establishing modernised roads and railway corridors across Africa.

i) Road corridor infrastructure

Road corridors, which this study focuses on, remain the main transport infrastructure across Africa (Kah & Bate, 2020; Balbaa et al., 2023). In this region, the bulk of movement of people to access basic amenities of life, such as economic zones, healthcare, education, and employment opportunities, is facilitated through road corridors (Menhas et al., 2019; Balbaa et al., 2023). Most people in rural areas completely depend on road corridors for connectivity (Kah & Bate, 2020; Kuncoro et al., 2024). To meet the framework of the PIDA, the African Union has set up programmes for developing cross-border road corridors (United Nations, 2019b; Balbaa et al., 2023). A typical example includes the development of the Trans-African highway network (Table 1.1), which consists of 10 transport corridors of 57,300 km planned to connect African countries to seaports (Figure 1.1).

Figure 1.1: Map showing the proposed Trans-African Highway Network in Africa. (Source: Accessibility and Infrastructure in Border Cities, 2019).

Table 1.1: Description of the proposed Trans-African Highway Network Project in Africa.

#	Highway	Route number	Length (km)
1	Cairo – Dakar	TAH 1	8,640
2	Algiers – Lagos	TAH 2	4,500
3	Tripoli - Windhoek - Cape Town	TAH 3	9,610
4	Cairo - Gaborone - Cape Town	TAH 4	8,860
5	Dakar - N'Djamena	TAH 5	4,500
6	N'Djamena - Djibouti	TAH 6	4,220
7	Dakar – Lagos	TAH 7	4,010
8	Lagos – Mombasa	TAH 8	6,260
9	Beira – Lobito	TAH 9	3 520
10	Djibouti - Libreville - Bata	TAH 10	9 979

ii) Railway corridors

Africa is known as the largest producer of large volumes of minerals, steel, agricultural crops and other commodities that are natural markets for railways (Weng et al., 2013). However, the presence of landlocked countries makes it difficult to establish multimodal transportation of freights, particularly the 15 African landlocked countries (Yang & Chang, 2019). To maintain their nation’s competitive advantage, these countries must invest in developing transport infrastructure that connects landlocked countries to the coast (Bonfatti & Poelhekke, 2017; Balbaa et al., 2023). To address this need, the Programme for Infrastructure Development in Africa has set up plans for upgrading 17,200 km of existing railways and establish approximately 12,000 km of new railway lines across the continent (African Union, 2021). Through support from the Chinese government, Kenya has constructed a Standard Gauge Railway (SGR) that connects the port of Mombasa with the capital city of Nairobi to support the country’s Vision 2030 development agenda (Nyumba et al., 2021; Lape et al., 2023). As much as these transport corridor developments benefit trade and economic transformation, policy provisions promoting integrated sustainability in these infrastructure's planning, design and construction are critically needed (Gonçalves et al., 2022; Ament et al., 2023). These policies should comprise standards for planning infrastructure that connects the habitat mosaic of natural and human-modified areas to help reduce their ecological impacts (Van Teeffelen et al., 2012; Collinson et al., 2019; Paemelaere et al., 2023).

1.5 National roads in South Africa

Typically, ~750,000 km of roads bisect the landscape of South Africa (SANRAL, 2014; Ross & Townshend, 2019), with about 21% of these being paved whilst the remaining are unpaved (Ross & Townshend, 2019). All officially proclaimed roads in South Africa are managed by various authorities. District roads are managed and maintained by provincial or local road authorities, whilst the majority of regional roads and all National Roads are managed by the South African National Roads Agency Limited (SANRAL) since the 1970s (SANRAL, 2014; Borole, 2022). National roads connect major cities and form the highest category in the numbering system of routes in South Africa (Falkner, 2012). To date, the country has 15 National Roads (Table 1.2).

Table 2.2: The 15 national road networks of South Africa (modified from Falkner, 2012).

Road name	Length (km)	Their southern and northern terminus
N 1	1940	Cape Town–Worcester–Beaufort West–Colesberg–Bloemfontein–Kroonstad–Johannesburg–Roodepoort–Pretoria–Polokwane–Musina–Beit Bridge–(Beitbridge, Zimbabwe)
N 2	2255	Cape Town–Somerset West–George–Port Elizabeth–King William's Town–East London–Mthatha–Kokstad–Port Shepstone–Durban–KwaDukuza–Empangeni–eMkhondo–Ermelo
N 3	578	Durban–Pietermaritzburg–Harrismith–Johannesburg
N 4	718	(Lobatse, Botswana)–Skilpadshek–Zeerust–Rustenburg–Pretoria–eMalahleni–Nelspruit–Komatipoort– (Maputo, Mozambique)
N 5	235	Winburg–Bethlehem–Harrismith
N 6	538	East London–Queenstown–Aliwal North–Bloemfontein
N 7	666	Cape Town–Clanwilliam–Springbok–Vioolsdrif– (Keetmanshoop, Namibia)
N 8	583	Groblershoop–Kimberley–Bloemfontein–Ladybrand–Maseru Bridge–(Maseru, Lesotho)
N 9	517	George–Graaf-Reinet–Middelburg (EC)–Colesberg
N 10	1000	Port Elizabeth–Cradock–Middelburg (EC)–De Aar–Prieska–Upington–Nakop–(Keetmanshoop, Namibia)
N 11	773	Ladysmith–Newcastle–Volksrust–Ermelo–Middelburg (MP) –Mokopane–Groblersbrug– (Palapye, Botswana)
N 12	1342	George–Oudtshoorn–Beaufort West–Kimberley–Klerksdorp–Potchefstroom–Johannesburg–eMalahleni
N 14	1186	Springbok–Upington–Vryburg–Krugersdorp–Pretoria
N 17	330	Johannesburg–Springs–Ermelo–Oshoek– (Mbabane, Eswatini)
N 18	317	Warrenton–Vryburg–Mahikeng–Ramatlabama– (Lobatse, Botswana)

A toll financing system was introduced in the 1980s following the amendment of the National Roads Act of 1971 to improve road infrastructure for the benefit of the economic well-being of South Africa (Borole, 2022). Hence, SANRAL contracted three toll operators to design, construct, expand, rehabilitate, finance, and operate several toll routes in South Africa. This included the following concessionaires (modified from Linden et al. (2022)) that the Endangered Wildlife Trust (EWT; non-governmental, non-profit South African conservation organisation) partners with to gather wildlife roadkill data:

i). N3 Toll Concessions (N3TC) – manages the 415 km segment of the N3 toll route that links the port of Durban with the economic hub of Johannesburg.

ii). Bakwena N1N4 Toll Concessions – Operated by Pt Operational Services (Pty) Ltd, is responsible for the 385 km of the N1N4 toll route covering the N1 from Pretoria to Bela Bela in Limpopo and the N4 beginning in Pretoria through Rustenburg until the border of Botswana.

iii). Trans African Concessions (TRAC) – manages the N4 Toll roads (discussed in the study area section)

1.6 Road ecology

With over 64 million kilometres of roads traversing the globe, large portions of natural landscapes remain severely disconnected into smaller fragments (Collinson et al., 2019; Perumal et al., 2021; Sons et al., 2024), restricting the free movement of terrestrial wildlife. This causes several animals to avoid crossing roads, whilst those who attempt to cross often risk colliding with vehicles, which may lead to an injury or wildlife roadkill (Forman & Alexander, 1998; Fahrig & Rytwinski, 2009; Collinson et al., 2015; Hlatshwayo et al., 2023). Since roads are built almost everywhere on the planet, it is imperative to explore the effects of roads on natural landscapes and biodiversity. Road ecology is a field of science that integrates two disciplines: civil engineering (road infrastructure and traffic) and ecology, which studies the physical environment and the organisms that live in it. Road ecology is known as a branch of ecological science that focuses on the quantification and mitigation of road impacts on wildlife (Van der Ree et al., 2015), while according to Balkenhol & Waits (2009) "the goal for this discipline is to gather sufficient data to enable scientists to advise road engineers and planners on how to design transportation infrastructures that are socio-economically and ecologically sustainable to enhance road safety for both humans and wildlife".

As much as the discipline of road ecology has been ongoing for many years, some clear geographic biases still exist. Hence, recent reviews indicate that most road ecological research originates in developed regions, mainly North America and Europe (Pinto et al., 2020; Silva et al., 2021). This geographical bias highlights the need for more road ecology research in low-income countries where massive road development is proliferating (Lala et al., 2021; Villalobos-Hoffman et al., 2022). Whilst the focus of road ecology studies in low-income countries is still mainly on data collection and quantifying hotspots, developed regions like Western Europe, North America and Canada have already advanced into establishing mitigation measures (González-Gallina et al., 2018; Laidlaw et al., 2021; Villalobos-Hoffman et al., 2022). Hence, the introduction of wildlife crossings in locations where wildlife frequently crosses the road is a key conservation tool to conserve biodiversity in road-fragmented landscapes (Puig al., 2012; Stewart et al., 2020; Laidlaw et al., 2021; Tuttu et al., 2023).

1.7 Major road ecological threats to terrestrial species

In a world where transport infrastructure is rapidly expanding, understanding the interactions of people and wildlife with road infrastructure as an ecological threat is increasingly becoming relevant (Dhiab & Selmi, 2021; Nyumba et al., 2021). Roads have numerous impacts on biodiversity and the environment, and these can be articulated as follows:

I) Physical disturbance,

II) Habitat fragmentation,

III) Chemical pollution,

IV) Sediment effect of roads,

V) Increasing the extent of anthropogenic activities in previously inaccessible landscapes,

VI) Increased wildlife mortality.

1.7.1 Physical disturbance

In normal circumstances, when road corridors are constructed or expanded, the landscape needs to be cleared so that the existing land cover can be transformed into a well-constructed road. In particular, road construction and expansion may result in deforestation processes (Llagostera et al., 2022), which may accelerate land degradation by making the soil vulnerable to landslides and sediments (Olander et al., 1998; Forman et al., 2003; Alamgir et al., 2019; da Silva et al., 2023; Zhang et al., 2024). Moreover, when roads are built for human development, such as houses, commercial areas and agriculture, the land becomes degraded and susceptible to uncontrolled colonisation and establishment of alien invasive species due to land disturbances that reduce the land's resistance to non-native species (Gassó et al., 2009; Follak et al., 2018; Son et al., 2024).

1.7.2 Habitat fragmentation

For wildlife, road networks can present a whole new world which requires animals to suddenly grapple with the appearance of roads that dissect their wild habitats (Shannon et al., 2014; Buxton et al., 2020; Tuttu et al., 2023; Battisti, 2024) and the vehicular traffic that comes with it. The presence of poorly designed roads on terrestrial ecosystems creates the partition of habitats into smaller isolated units (Van Bohemen, 1998; Newell et al., 2022; Winkler et al., 2024). This results in landscape fragmentation through the creation of barriers to animals that require migration (Olander et al., 1998; Fahrig & Rytwinski, 2009; Gonçalves et al., 2022;

Tuttu et al., 2023; Zhang et al., 2024). Some animals may avoid crossing roads, which cut animals off from parts of their ecosystems or from meeting other members of their populations (Collinson et al., 2015; Buxton et al., 2020; Zungu et al., 2020; Tuttu et al., 2023). Fragmentation occurs because subpopulations, feeding and breeding habitats have been isolated, which reduces habitat ecological values (Forman & Alexander, 1998; Jacobson et al., 2016; Newell et al., 2022; Winkler et al., 2024).

1.7.3 Chemical pollution

Roads are a source of light, noise, and chemical pollution (Altringham & Kerth, 2016; Boroiu et al., 2018; Magdin et al., 2024). Road corridors that have high traffic volumes increase the release of greenhouse gases (carbon dioxide) and heavy metals (zinc, cadmium, and nickel), all of which may have a serious accumulation of chemicals near roads (Forman & Alexander, 1998; Forman et al., 2003; Kupka et al., 2021). The combustion of gasoline containing tetraethyl lead and the wearing of tyres containing lead oxide may result in lead contamination of roadsides (Loganathan et al., 2013). During rainstorms, runoff pollutants may alter soil chemistry, get absorbed by plants and further degrade stream ecosystems (Kupka et al., 2021; Magdin et al., 2024).

1.7.4 Sediment effect of roads

Roads may contain numerous sediments and solids such as small particulate organic matter (microplastics, sewage, soil and gravel); these suspended particles may have negative biological and physical effects on adjacent water systems (Forman, 1998; Dodd & Whiles, 2020; González-Bernardo et al., 2023). High levels of suspended sediments in streams interfere with the primary productivity of water systems by shading algae and macrophytes (Rowlands, 2019; Dodd & Whiles, 2020). This normally results in poor habitat quality and low reproduction rates for aquatic animals.

1.7.5 Increasing the extent of anthropogenic activities in previously inaccessible landscapes

The presence of road corridors may increase access to previously inaccessible natural landscapes (Vanthomme et al., 2013; Laurance et al., 2014; Collinson et al., 2019), which may trigger illegal activities. Numerous studies have shown that roads increase the extent of anthropogenic activities in remote areas by providing access to wildlife, which may initiate illegal hunting and feed the illegal wildlife trade (Clements et al., 2014; Pattiselanno & Krockenberger, 2021).

1.7.6 Increased wildlife mortality

Poorly designed road corridors traversing natural landscapes have influenced the movement ecology and behaviour of animals. Whilst some species avoid crossing roads, those that attempt to cross risk becoming roadkill (Fahrig and Rytwinski, 2009; Shilling et al., 2021; Hlatshwayo et al., 2023). On the other hand, road verges may form a potential habitat that fosters diverse vegetation (or micro-habitats) that attracts grazing animals (Oxley et al., 1974; Milton et al., 2015; Hlatshwayo, 2021), often causing them to wander onto the road, directly accelerating the risk of becoming roadkill (Figure 1.2).

Figure 1.2: Noticeable ecological impact of roads referred to as roadkill (showing A – Grey crowned crane (*Balearica regulorum*), B – Southern African python (*Python natalensis*) and C – serval (*Leptailurus serval*). (Photographs© T Hlatshwayo).

1.8 Animal behavioural responses to road and traffic

Road-fragmented landscapes introduce wildlife populations into a new community, requiring them to develop new strategies to adapt to modified habitats (Evans et al., 2019; Tuttu et al., 2023). Understanding the different behavioural responses of animals to unpredictable road traffic can provide critical information that could help develop mitigation measures suitable for reducing the threats of road corridors to wildlife (Buxton et al., 2020). Hence, different taxa in Africa demonstrate different responses to these events, as discussed below and illustrated in Table 1.3.

i) Road avoidance

The presence of roads that crisscross natural landscapes increases habitat fragmentation. For animals, this introduces severe challenges to their movement patterns and behaviour (Paterson et al., 2019; Ament et al., 2023; Battisti, 2024). As a result, some individuals tend to adopt an avoidance behaviour by avoiding crossing roads. As this happens, it directly lowers animal space use patterns, reproduction and survival rates due to limited resources (Jaeger et al., 2005; Loraamm et al., 2021). Individuals that avoid crossing roads are unfortunately cut off from parts of their ecosystems as they are unable to access important resources (food, mates and breeding sites) on the other side (Collinson et al., 2015; Buxton et al., 2020; Newell et al., 2022).

ii) Changed activity patterns

When road corridors fragment natural ecosystems, several major constraints to animal movement are triggered. Thus, forcing individual species to develop adaptation strategies to respond to the fragmentation effects of roads (Evans et al., 2019; Ament et al., 2023; Tuttu et al., 2023; Battisti, 2024). These include modifying their behaviour, social ecology, and diet through increased nocturnality (Bateman & Fleming, 2012). Buxton et al. (2020) reported that in the United States of America (USA), white-tailed deer (*Odocoileus virginianus*) have shown a behavioural shift of reducing their diurnal activity as a risk-avoidance strategy to road-induced negative impacts. Although African elephants (*Loxodonta africana*) are frequently detected using road corridors in many national parks in Africa, they were reported to adjust their activity patterns on roads to avoid vehicular traffic in Zimbabwe (Gaynor et al., 2018). This shows that the expanding human footprint on the natural environment forces animals to seek refuge by altering their movement to the periods when humans are less active.

Table 1.3: Four wildlife behavioural responses to roads and traffic, outlining the impacts (positive and/or negative), with some species examples (modified from Forman & Alexander, 1998 in EWT-TRAC Report 2021).

#	Wildlife Behavioural Response	Impact	South African Species Examples
1	Non-responders	These animals fail to detect or make avoidance behaviour toward oncoming vehicles. They continue to try to cross the road, and the likelihood of a successful crossing decreases with increasing traffic. These species are vulnerable to population reductions and fragmentation effects.	Amphibians Invertebrates Livestock Snakes 
2	Pausers	These animals can detect the danger posed by the oncoming traffic but respond by stopping (or continuing scavenging). The longer they pause, the higher the risk of them being hit by the oncoming vehicle. High traffic volume presents a complete barrier to these species.	Amphibians Chameleon Owls Tortoise Snakes 
3	Speeders	These species flee from danger but may flee directly into an oncoming vehicle. Shy species may be at risk from a barrier effect and population fragmentation.	Antelope Guineafowl Rabbits/Hare Rodents 
4	Avoiders	These are careful species, often crossing roads only when there are low traffic volumes. They experience the lowest road mortality rates but may suffer from population fragmentation depending on how often traffic volumes get low.	Carnivores Domestic dogs African Elephant 

1.9 Wildlife crossing, a solution to reducing road-related ecological impacts

Global road ecological research has shown that wildlife crossings in the form of under-crossings and over-crossings improve landscape connectivity whilst decreasing roadkill incidents (Clevenger & Huijser, 2011; van der Ree et al., 2015; Brehme et al., 2023; Tuttu et al., 2023). Wildlife crossings are structures built either over or under a road to connect patches of road-fragmented landscape for facilitating movements (Ament et al., 2014; Kociolek et al., 2015; Stewart et al., 2020; Ament et al., 2023; Donaldson et al., 2023) and provide important benefits to both human and wildlife populations. Although Colletti et al. (2009) report that the first wildlife crossing was built in France and other European countries at the beginning of the 1950s, since then, they have developed into an established concept of road ecology globally. Furthermore, Kociolek et al. (2015) assert that wildlife crossings have reduced roadkill incidents involving deer-sized or larger animals by an average of 87% in the USA.

Coupled with roadside fencing, wildlife crossings form an effective tool for reducing incidents of wildlife-vehicle collisions (Van der Ree et al., 2015; Spanowicz et al., 2020; Brehme et al., 2023). Fencing alone causes smaller and more isolated populations, which ultimately reduces the probability of survival for animals (Huijser & Gunson, 2019; Brehme et al., 2023). Henceforth, this limits the ability of animals to find mates, food and other essential resources for survival, reducing reproductive success (Huijser et al., 2008). This means that instead of blocking the road entirely with the fencing system, road engineers are encouraged to use roadside fencing to funnel animals towards the closest crossing structures, as illustrated in Figure 1.3. There are several designs globally of fencing; however, it is suggested that positioning the fence-ends at an angle of 45° to the road creates the possibility of wildlife navigating the end (Figure 1.3). The curvature at the end is designed to motivate animals to move back towards the crossing structure.

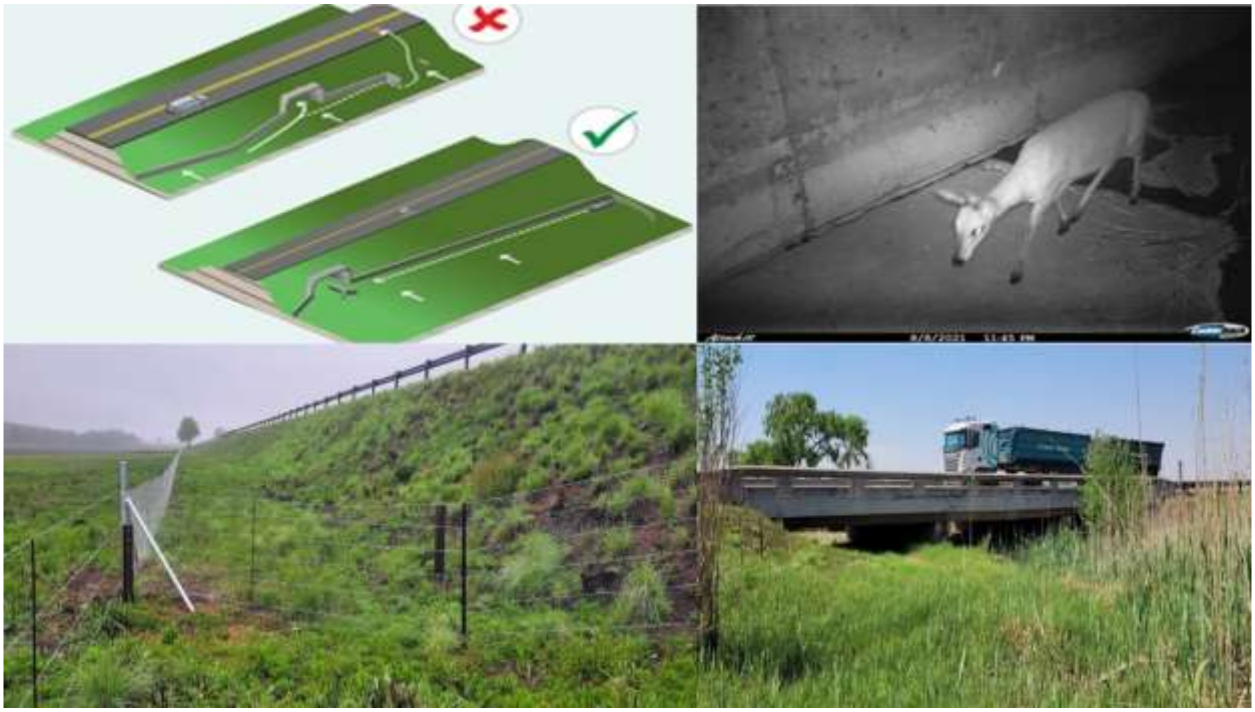

Figure 1.3: An example of wildlife undercrossing structure design (modified from Clevenger & Huijser (2011), credits: Marcel Huijser/WTI).

1.10 Benefits of wildlife crossing structures

The adoption and inclusion of wildlife crossing structures in the structural plan and design of transport infrastructure comes with a variety of benefits, and these may be summarised as shown below (modified from Ament et al., 2019a; Brehme et al., 2023):

i) facilitate the movement of organisms, genetic material, and ecological processes, and provide important benefits to both human and wildlife populations;

ii) allow species to move across the landscape to reach food, water, and mates;

iii) facilitate seasonal migrations, once-in-a-lifetime dispersal events to seek new territories, and multi-generational range shifts in response to climate trends;

iv) provide ecosystem services by: regulating air and water quality, regulating water flow, maintaining soil structure and quality, erosion control, pollination of crops and other plants, and climate regulation;

v) promotes coexistence between infrastructure and biodiversity, and citizens or human (road users) through reduced conflict

1.11 Types and designs of wildlife crossings

When designing wildlife crossings, several design characteristics need to be considered; this includes species needs, physical attributes of landscapes as well as tailoring them to local contexts (Kintsch et al., 2015; Stewart et al., 2020; Donaldson et al., 2023). Although Kitsch and Cramer (2011) discuss seven classes of wildlife crossings, generally, there are two forms of wildlife crossings: undercrossings, such as box or pipe culverts and spans under bridges, and overcrossings in the form of extensive bridges and canopy bridges (Figure 1.4).

Figure 1.4: Examples of wildlife crossing (A, B – under-crossing (credits: P Cramer and EWT-TRAC) and C, D – over-crossing (green bridge: J Richert Blue Valley Ranch and canopy bridge: WWF-Peru).

1.12 Camera trapping as a data collection tool for road ecology

Globally, there has been widespread recognition of the use of camera traps to monitor terrestrial wildlife in the wildlife conservation discipline (Wilson et al., 2018; Burton et al., 2024). Camera trapping is a data collection tool that relies on mounted cameras that are remotely triggered to automatically capture images or video clips of wildlife species that pass in front of them (Boitani, 2016; Orban et al., 2024). Camera trapping is a non-invasive method widely recommended for monitoring terrestrial biodiversity, which is critical in identifying areas that require conservation strategies (Mann et al., 2015; Bitani et al., 2023; Burton et al., 2024). Although the use of camera traps for wildlife research has shown a drastic increase over the past two decades, only a few camera trap studies have been conducted in Africa (12.3 %, Agha et al., 2018), despite this continent being known for harbouring numerous biodiversity hotspots.

In road ecology, there has been a growing interest in exploring the behavioural patterns that different species adopt to overcome the presence of road networks in their natural habitats, as well as animal activity in the vicinity of the road. The use of camera trapping in road ecology provides the opportunity to monitor animal behaviour and physiology on a variety of scales (e.g., temporal, spatial or biological organisation) (Cook et al., 2004; Orban et al., 2024), and these can range from individual to community interactions. Camera trapping could provide a wealth of data in the field that can allow the linking of behaviour and physiology of free-ranging animals in human-modified landscapes, as illustrated in Figure 1.5. These data may include location information from telemetry, motion patterns from accelerometers, estimates of proximity to other animals, still images and video, and physiological data (e.g., metabolic rate) from a range of sensors (Moll et al., 2007; Cordier et al., 2022; Mugerwa et al., 2024). Camera traps will provide a reliable approach to monitoring animal behaviour and utilising modified road underpass structures (Moll et al., 2007; Cordier et al., 2022; Orban et al., 2024). This means that instead of adopting roadside fencing, which produces a negative impact by preventing ecological connectivity, our study will use roadside fencing to funnel wildlife towards the closest crossing structures, resulting in safe crossings for animals.

Figure 1.5: Example of camera trap data captured on the N4 National Road showing animals using underpass structures: A- common duiker (*Sylvicapra grimmia*), B- serval (*Leptailurus serval*), C- rock monitor lizard (*Varanus albigularis*), boomslang (*Dispholidus typus*) and common warthog(*Phacochoerus africanus*). (Credits: EWT-TRAC).

1.13 Role of policies and legislation in mainstreaming ecological connectivity

The consideration of biodiversity needs and the protection of threatened habitats in transportation infrastructure planning and design remains a major challenge in numerous low-income countries (Zuniga-Teran et al., 2020; Ament et al., 2023), particularly in Africa, where there is a high focus on a linear infrastructure development agenda for socio-economic development. Although the United Nation's Sustainable Development Goals promote establishing Green Infrastructure and making space for nature within built landscapes, there is still a lack of biodiversity considerations in the planning and development of transport infrastructure investments (Georgiadis et al., 2020).

Several processes, such as strategic environmental impact assessments (biodiversity-inclusive), large-scale zoning to avoid the most vulnerable areas for biodiversity, and the adoption of ecological connectivity through overpasses, and underpasses to preserve species movements are critical in achieving green transport corridors (Zainol et al., 2021; Papp et al., 2022; Ament et al 2023), they remain unlegislated and recognised in transportation planning in many African countries. To effectively plan, construct, operate and maintain sustainable Transportation Linear Infrastructure, national and regional policies, strategies, guidelines, and standards promoting the adoption and implementation of green-transport corridors should be developed (Georgiadis et al., 2020; Ament et al., 2023). These policies and standards should be integrated and comprise actionable management elements to identify and conserve wildlife corridors through mainstreaming ecological connectivity. Furthermore, the policy framework on sustainable transport infrastructure should promote continuous community engagement and strategic partnerships to ensure inclusivity and multi-functionality in their implementation (Zuniga-Teran et al., 2020)

1.14 Study area

The main study area in this study was the section of the N4 toll route falling between the Solomon Mahlangu off-ramp in Pretoria and the Lebombo border post, located between South Africa and Mozambique (Figure 1.6). The toll route is made up of a 570 km segment that is managed by Trans African Concessions (Pty) Ltd. (TRAC) and forms part of the most important trade routes in the region (Gelderblom, 2021). It passes through some of the largest industrialised areas of South Africa (mining and smelting). In addition, it passes through landscapes that are human-modified in the form of residential and commercial areas as well as agriculture (livestock, domestic animals).

Some sections of the highway traverse natural landscapes that are of priority for wildlife, hence this makes it important that the rich biodiversity that inhabits its surroundings become protected from the potential risks of road while improving driver safety.

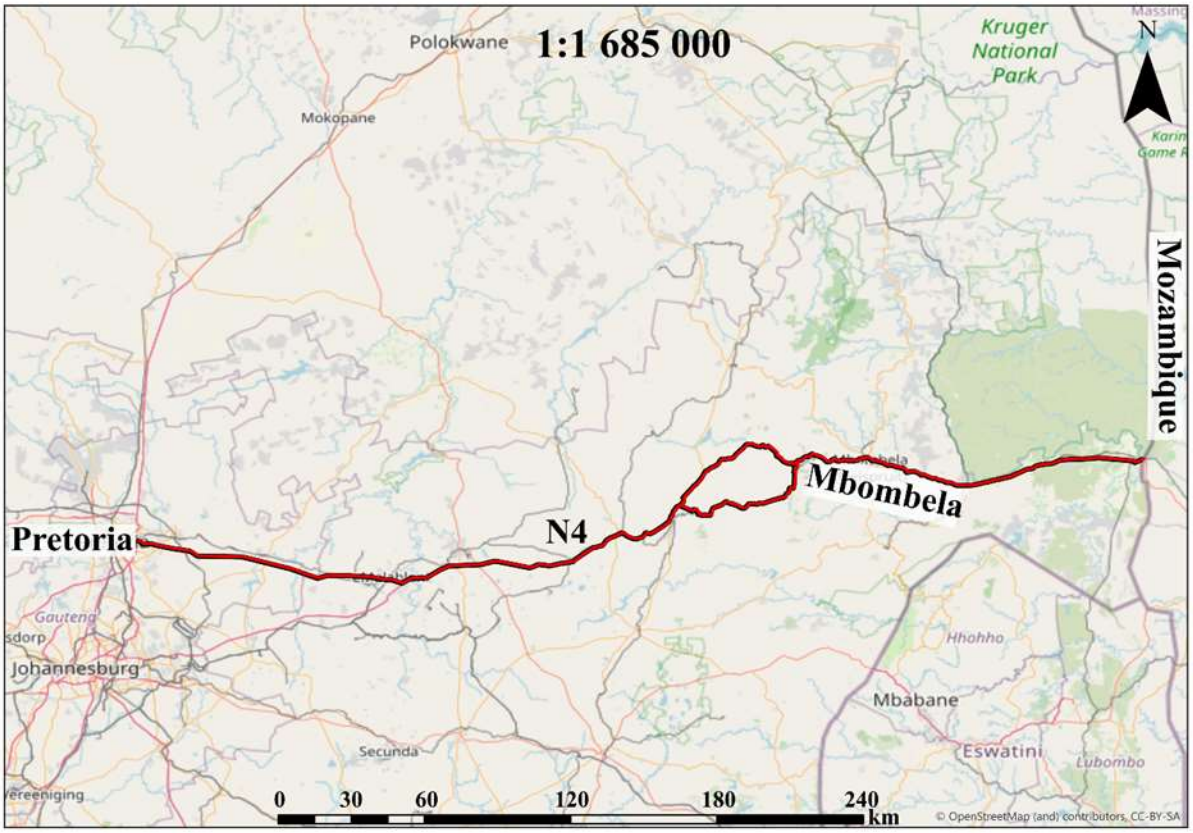

Figure 1.6: Map showing the South African section of the TRAC N4 Toll Route.

1.15 Problem statement

Transport linear infrastructure (roads, railways, and transmission lines) considerably alters natural ecosystems (Laurance et al., 2009; Papp et al., 2022), negatively impacting biodiversity. When transport infrastructure is poorly planned, it may have severe impacts on ecological connectivity and species survival. Roads, in particular, can create barriers to wildlife movement, limiting the ability of terrestrial wildlife to find water, food, and mates (Collinson et al., 2019; Su et al., 2023;

Fairbank et al., 2023; Battisti, 2024). Furthermore, road-fragmented landscapes accelerate incidents of wildlife-vehicle collisions (Collinson et al., 2015; Su et al., 2023; Zhang et al., 2024); whilst these incidents almost always result in wildlife mortality, they also impact populations of threatened and endangered species, and they may also cause road safety concerns for road users (people). These impacts are particularly relevant in South Africa, which has diverse and robust wildlife populations and is still transitioning to a green economy.

Projects designated to promote the adoption and inclusion of ecological connectivity and permeability for wildlife to reduce transport infrastructure-related impacts have increased globally (Ament et al., 2019b; Paemelaere et al., 2023); however, there is still limited research exploring these dynamics in Africa. Although Environmental Impact Assessments (EIAs) are significant in protecting threatened species and habitats from major impacts during development (Swangjang, 2018; Enríquez-de-Salamanca, 2024), their evaluation processes fail to address the lack of ecological connectivity in transport infrastructure planning. For this reason, road infrastructure-related impacts on biodiversity and landscape are usually overlooked because of various reasons. These include agencies lacking capacity and resources during the EIA processes (Jaeger, 2015; Paemelaere et al., 2023) and poor sustainability policies that advocate for the inclusion of ecological connectivity in transport corridor development. The lack of wildlife crossing and landscape connectivity research in the Sub-Saharan region limits the gathering of databases on wildlife ecology and behaviour adjacent to roads. Yet, without these data, it becomes impossible to develop statewide connectivity action plans and effective roadkill-reduction measures (Ament et al., 2019a). If there is adequate information on where mitigation interventions are needed, it becomes easier to develop construction elements that need to be applied during the road design phase for maintaining ecological connectivity (McGuire et al., 2021). Therefore, the present study expands on previous research by emphasising the urgent need to adopt road development projects that optimise social and economic benefits while safeguarding biodiversity and ecosystems by including ecological connectivity. The present study observed an urgent need to assess the relevance of national South African policies on road transport development in promoting the ecological functionality of road networks. Furthermore, this study has explored wildlife roadkill patterns and animal movement on a national highway that bisects landscapes of grasslands, freshwater ecosystems and wetlands, which are suitable homes for a variety of species. This doctoral study further researched the usefulness of road specialised structures (bridges, culverts, viaducts and tunnels) in helping animals move across the TRAC N4 Toll Route, reducing roadkill incidents and improving landscape ecological functionality. This will assist in enhancing road safety for wildlife and all other road users.

1.16 Aim and objectives

The overall aim of the study was to explore the negative impacts of road transport infrastructure on wildlife persistence and behaviour in South Africa, with special interest in the TRAC N4 toll route. Specifically, the objectives were:

- To systematically review and assess global camera trap peer-reviewed research that monitored the use of crossing structures by wildlife to navigate landscapes fragmented by roads.
- To collate and comprehensively review the relevance and effectiveness of key South African policies on road transport infrastructure development in mainstreaming ecological connectivity and wildlife needs.

- To monitor the spatial and temporal patterns of terrestrial vertebrate roadkill along the N4 highway in South Africa
- To explore crossing structures used by wildlife on the N4 Toll Route (TRAC N4), Gauteng Province, South Africa.

1.17 Structure of the thesis

The main body of this thesis was organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) serves as the introductory chapter, which provides the literature review of the concepts covered in this study. The next four chapters (Chapter 2, 3, 4 and 5) are empirical chapters, with each one covering a specific objective. Each chapter is formatted according to the journal to which it is intended to be (or has been) submitted. Because of this thesis format, a certain degree of repetition was unavoidable, especially in the methods section. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis. These chapters were arranged following this outline:

Chapter 1: An introduction providing the background information;

Chapter 2: A systematic review of global road ecology camera trap studies that monitored animals' use of wildlife crossings in road-fragmented landscapes;

Chapter 3: Mainstreaming ecological connectivity and wildlife needs in green road transport infrastructure planning in South Africa;

Chapter 4: Protecting the unprotected: Monitoring the patterns of terrestrial vertebrate roadkill along a major South African National Highway;

Chapter 5: Evaluating the spatial and temporal patterns of wildlife use of existing road drainage underpass structures along a major South African highway;

Chapter 6: The concluding chapter that discusses, synthesises and summarises the findings and recommendations of the overall study.

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CHAPTER 2

A systematic review of global road ecology camera trap studies that monitored animals' use of wildlife crossing structures in road fragmented landscapes

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Running header: Road ecology camera trap studies monitoring crossing structure use

2.1. Abstract

Much research has emphasised the importance of incorporating wildlife crossing structures in the design of transport linear infrastructure to facilitate landscape connectivity. While evaluating crossing structure effectiveness is important, low-cost monitoring techniques such as camera traps are widely used for monitoring wildlife crossing structures. However, the efficacy of these camera traps has not been reviewed, and many studies that evaluate crossing structure use through camera trapping are sometimes misguided and lack a proper camera trap study design. Our study reviewed and assessed camera trap use as well as protocols in peer-reviewed research that monitored crossing structures used by wildlife in road-fragmented landscapes to establish camera trap survey methods that will improve the effective estimation of crossing structure functionality. We found 84 peer-reviewed publications from 2001 to 2024 that used camera trapping to monitor wildlife use of crossing structures. The included peer-reviewed studies varied considerably in terms of global geographical distribution and represented publications from 25 countries and six continents. The geographical trend has indicated that most studies were conducted in the global north region (63.1%), with most studies published in North America. The camera trap protocol applied varied considerably between studies, especially regarding camera trap placement and monitoring study design. This showed that camera trap usage for monitoring crossing structure use is still an emerging area of research. We recommend that further research develop standardised camera trap guidelines for monitoring crossing structure use by wildlife, as this will improve the quality of studies estimating the efficacy of crossing structures in reducing road-related biodiversity threats. Furthermore, camera trap studies exploring wildlife use of crossing structures should consider modifying and monitoring existing crossing structures not purposely built for wildlife (culverts,

bridges, and tunnels) as this could potentially provide a less costly method of restoring landscape connectivity, especially for the global south countries.

Keywords: Barrier effect, Camera trapping, Landscape connectivity; wildlife-crossings; wildlife-vehicle collisions; sustainable transport planning

2.2. Introduction

The expansion and development of transport linear infrastructure is rapidly expanding and continues to accelerate the loss and decline of wildlife species through landscape fragmentation (Grilo et al. 2015; Brunen et al. 2020). Furthermore, with limited information on the importance of promoting ecological connectivity through crossing structures, it is critically imperative that trends are reliably monitored and quantified to make planning and design decisions that promote wildlife needs and ecological connectivity (Hlatshwayo et al. 2024). However, many countries in the global south still struggle to advocate for the recognition and inclusion of wildlife crossing structures in transportation planning and design (Hlatshwayo et al. 2024). Consequently, the lack of road ecology research and robust monitoring of transport-related biodiversity impacts remains a significant obstacle that hampers the adoption and mainstreaming of ecological connectivity in transportation planning. To overcome this, more robust monitoring of existing road drainage culvert structures in the sub-Saharan region is needed in a timely manner, as these structures could potentially help compensate for wildlife loss due to transport corridors. As such, this will provide a cost-friendly approach to reducing incidents of wildlife roadkill by connecting fragmented landscapes.

Considering the high cost of launching wildlife crossing structures in transportation planning, which requires costly investment (Seiler et al. 2016), several studies have reported that existing road structures that are not purposely built for wildlife, such as existing culverts, viaducts, and bridges, have the potential to connect road-fragmented landscapes and provide safe crossing corridors for wildlife when modified to accommodate wildlife needs (van der Grift and van der Ree 2015; Craveriro et al. 2019; Bhardwaj et al. 2020). Whilst the recognition of existing road drainage culvert structures in providing effective wildlife movement corridors that facilitate connectivity in road-fragmented landscapes is promoted (Ng et al. 2004; Murphy-Mariscal et al. 2015; Zhang et al. 2019), their benefits in promoting wildlife movements remain poorly quantified and harnessed in the sub-Saharan region. Considering that the fragmentation of natural habitats by transport corridors continues to influence the abundance and movement activity of wildlife, research investigating the effectiveness of wildlife crossing structures and existing road crossing structures in linking fragmented habitats is urgently needed (Bhardwaj et al. 2020; Warnock-Juteau et al. 2022), particularly in Africa.

Using camera traps as a monitoring tool in ecological research has introduced a significant shift in wildlife monitoring and conservation. Camera traps have proven to be a less costly, effective, non-invasive method of studying aspects of animal ecology that were previously difficult to sample in the conservation community (Harrison and Kelly 2022). Camera traps are widely used to study animal movement and behavioural patterns, and their application in ecological research has undeniably improved the understanding of the ecology of wildlife and their conservation planning (Galvis et al. 2014; Rovero and Kays 2021). Globally, camera trapping has become a preferred tool for sampling animal populations on terrestrial land. Deploying camera trapping in road ecology as a tool for gathering data on crossing structure use has significantly improved the understanding of the ecology of wildlife and how these structures can be modified to provide safe wildlife passages in road-fragmented landscapes (Lehnen et al. 2024; Yamashita et al. 2024).

The adoption of camera trapping in road ecology research has provided an opportunity for monitoring road-crossing structures on various scales (e.g., temporal, spatial, or biological organisation) (Cook et al. 2004; Young et al. 2023; Dodd et al. 2024). Considering that natural ecosystems supporting rare and iconic species are extensively degraded because of unsustainable transport linear infrastructure development (Laurence et al. 2015; Ng et al. 2020; Downs et al. 2021; Young et al. 2023), there is a need to improve the understanding of how ecological connectivity can be incorporated in transportation planning to safeguard vulnerable habitats and species. Therefore, innovative approaches for mainstreaming biodiversity and planning for green transportation for a sustainable future are required (Hlatshwayo et al. 2024), particularly in regions earmarked for infrastructure developments.

Whilst this process is a significant undertaking and requires financial investments (Bastille-Rousseau et al. 2018; Tucker et al. 2018), the lack of effective monitoring and animal movement data in landscapes that are intersected by transportation corridors remains a major challenge for many countries in the global south. Although robust monitoring of existing road crossing structures using camera trapping has demonstrated the usefulness of these structures in sustaining ecological connectivity in fragmented ecosystems, the impacts these structures have on reducing transport-related biodiversity threats remain poorly recognised in many developing regions. Furthermore, many camera trap studies that explore the use of crossing structures by wildlife tend to lack a proper study design, particularly the camera trap protocol. The disparities in camera trap protocol make it difficult for the study design to be repeated in other studies monitoring crossing structure use in other parts of the world.

Using a literature review of published peer-reviewed studies, we reviewed camera trap use for monitoring animal crossing structure use as a monitoring tool for effectively examining the use of crossing structures in restoring landscape connectivity. We evaluated the protocol used by these studies by assessing the survey design of setting up the camera trap to improve some of the existing disparities that weaken the reliability of camera trapping in monitoring wildlife crossings. We addressed three questions: 1) What is the recognition rate and geographical trends of camera trap publications that monitored animal use of structures that were not purposefully designed for wildlife use? 2) How are camera trapping survey methods used to monitor wildlife crossing structures? Furthermore, our study highlighted essential study design parameters that will improve camera trap study design that road authorities can adopt to reduce road-related biodiversity impacts, particularly in developing regions where a lack of research on wildlife crossings still exists.

2.3. Methods

2.3.1. Data collection

We conducted a systematic literature search and review of peer-reviewed journal articles in September 2023 and January 2025 using comprehensive databases of scientific publications: Google Scholar® (https://scholar.google.co.za/) and Semantic Scholar® databases through the programme Publish or Perish (Harzing 2022). The review comprised only peer-reviewed literature spanning the years 2001 to 2024 that used camera trapping as a tool to evaluate the use of crossing structures (underpasses and overpasses) by wildlife for mitigating wildlife-vehicle collisions (WVCs) and facilitating safe movement passages for wildlife in fragmented landscapes. Our review process did not include grey literature items, as conclusions may not be scientifically sound because rigorous peer-review processes are lacking. The search string used the following words to identify each publication: camera traps, wildlife crossings, cameras underneath underpasses, cameras under culverts, under-crossings, eco-bridges, overcrossings, canopy bridges, crossing corridors, roadkill mitigation measures, landscape fragmentation, and ecological connectivity. We used a Microsoft Excel© spreadsheet to collate the data from each publication and descriptive statistics to analyse the data. We conducted geospatial analyses to map the studies' locations using global information systems (GIS) software to visualise the global distribution.

2.3.2. Criteria for inclusion and exclusion

Only published peer-reviewed articles that deployed camera traps to monitor animal use of crossing structures (wildlife or non-wildlife designated crossings) were considered for this review. The total number of retrieved research articles was 31,600 publications, most of which were removed after screening. Only 1,250 articles qualified for further processing, and many articles (n = 1131) were excluded from this review because they did not meet the inclusion criteria (Figure 2.1). Studies were excluded if they 1) did not monitor wildlife crossings, 2) were non-peer-reviewed (grey literature) or inaccessible publications/non-English studies, 3) did not present any camera trap protocol and quantitative dataset even though they used camera traps, 4) did not gather data through the use of camera trapping, and 5) duplicates as summarised in Figure 2.1.

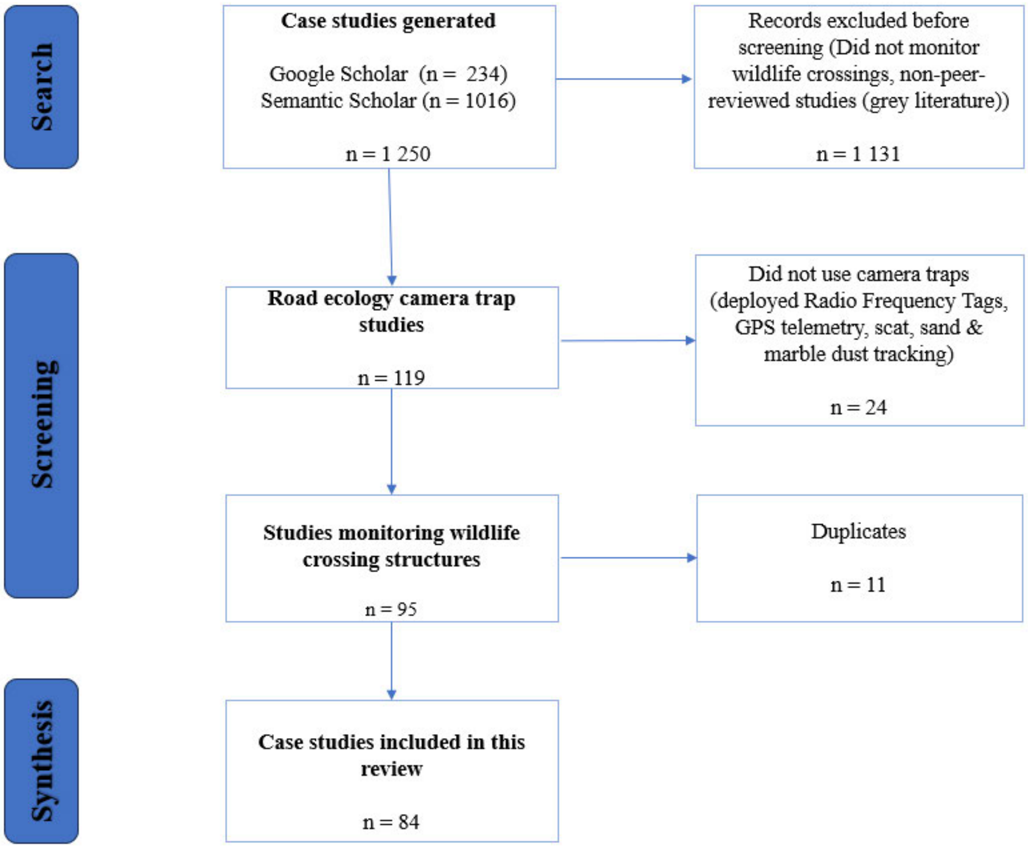

Figure 2.1: Screening processes of road ecology camera trapping and wildlife crossing structure studies (modified from Drake et al. 2022).

Our search criteria yielded 119 peer-reviewed articles that qualified for further examination, and the titles, abstracts, and keywords of these articles were scanned. However, 24 of these articles were eliminated because although they monitored crossing structures, they did not use camera traps but relied on radio frequency tags, global positioning system (GPS) satellite transmitters, and track beds. An additional 11 articles were further omitted from analyses as they were duplicates. Consequently, 84 peer-reviewed studies (Supplementary Information Table S2.1) that monitored wildlife using crossing structures with camera traps were used for the qualitative synthesis. The search, screening, and inclusion of peer-reviewed studies are summarised in the schematic flow chart (Figure 2.1).

2.3.3. Analyses of camera trap practice, design and use in road ecology

For each of the 84 identified studies, we reviewed the studies and recorded information on habitat and land use types, species, and classification of taxa of focus monitored (Supplementary Information Table S2.1). In addition, we evaluated the camera trap design protocol used by collating information on the following parameters: i) type of structure surveyed, ii) size dimensions (width, height and length), and iii) number of camera trap devices deployed at each structure, height and angle they were mounted at. We further assessed the monitoring study design by gathering information on monitoring timing, frequency and period, as well as the strengths and weaknesses of each study design (Supplementary Information Table S2.1). Our choice of electing to review peer-reviewed publications resulted in knowledge generated by grey literature (dissertations, conference papers and technical reports) being omitted because they did not undergo a rigorous review process. Nonetheless, the overall results found in the reviewed publications still indicate the global trends of the status of camera trap studies that monitored wildlife crossings using camera trapping techniques.

2.4. Results

2.4.1. Trends in camera trap studies that monitored animal use of wildlife crossing structures

In total, 84 peer-reviewed studies that monitored crossing structure use by wildlife using camera traps in road-fragmented landscapes were evaluated in this study (Supplementary Information Table S2.1, Table S2.2). These studies originated from 25 countries across six continents (Table

2.1, Figure 2.2). The published peer-reviewed studies varied globally, with the majority of studies conducted in North America (47.6%, n = 40); of these, the United States of America (USA) accounted for the highest publications (n = 24), followed by Canada (n = 11), Costa Rica (n = 3) and Mexico (n = 2). Although many of the peer-reviewed studies originated from the global north countries (61.9%, n = 52), the global south region was represented by 38.1% of studies (n = 32). Most of the global south studies were published in Asia (n = 14, Table 2.1 and Supplementary Information Table S2.1). Only two peer-reviewed studies (2.4%) were published in Africa (Kenya and South Africa, Table 2.1, Supplementary Information Table S2.1) despite the continent's rich biodiversity and increasing development plans for transport infrastructure (Laurance et al. 2015; Nchofoung et al. 2022).

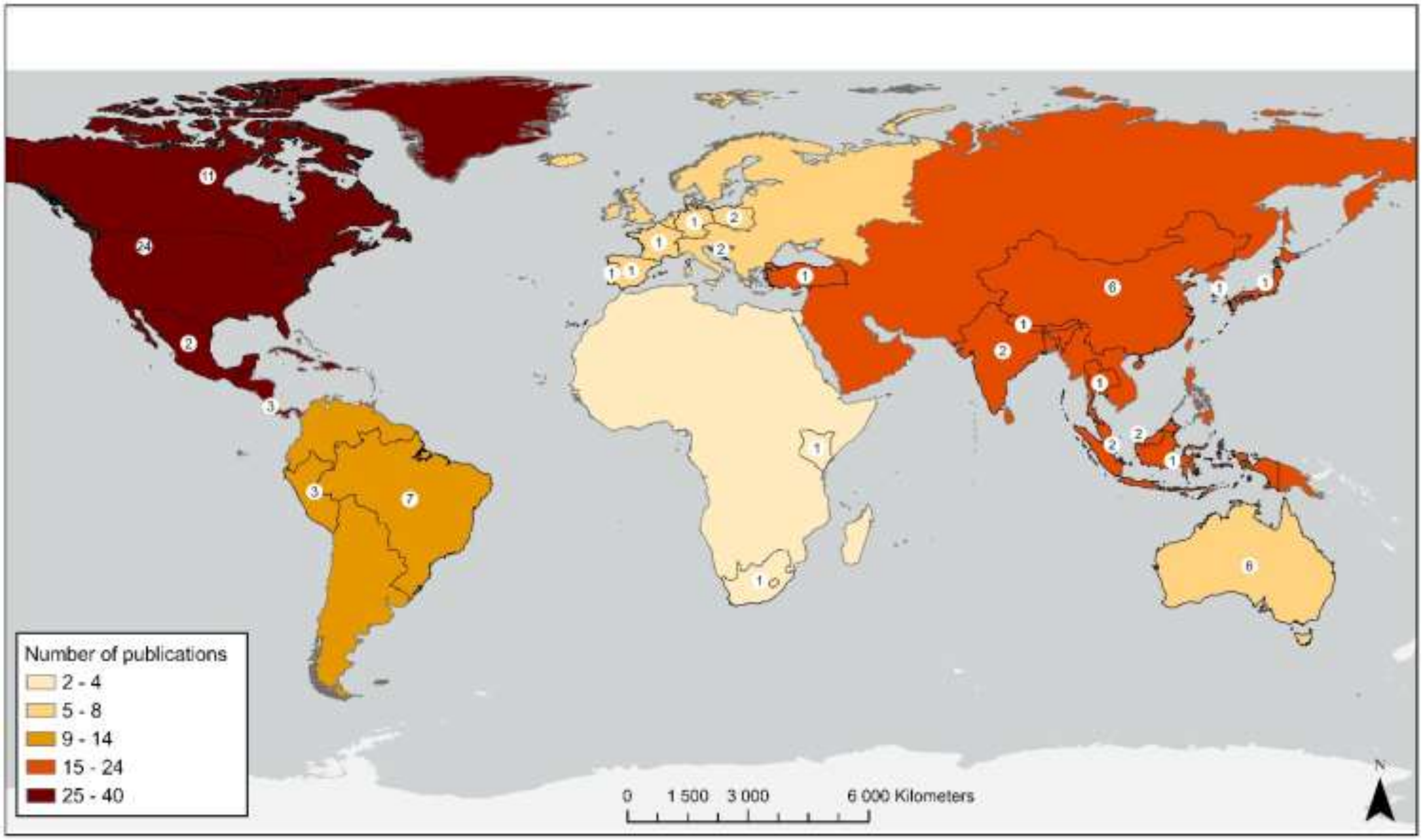

Figure 2.2: Geographical locations of the 84 peer-reviewed publications from 2001 – 2024 that monitored animal use of wildlife crossing structures.

Table 2.1: Summary of the included camera trap peer-reviewed studies that monitored animal use of wildlife crossing structures versus non-wildlife crossings (* indicate studies that surveyed both wildlife overpasses and underpasses).

Continent	Level of development	Country	Structures constructed for wildlife			Structures not specifically designed for wildlife	Comb. of both wildlife and non-wildlife structures	# of studies
			Canopy bridge	Wildlife underpass	Wildlife overpass	Existing drainage underpass		
Africa	Global South	Kenya	-	-	1	-	-	1
		South Africa	-	-	-	1	-	1
								2
Asia	Global North	Japan	-	-	-	-	1	1
		Korea	-	1	-	-	-	1
		Singapore	1		-	-	1	2
	Global South	China	-	3		3	-	6
		India	-	2		-	-	2
		Indonesia	1	-	-	-	-	1
		Malaysia	1	-	-	1	-	2
		Nepal	-	1	-	-	-	1
		Thailand	-	-	-	1	-	1
		Turkey	-	1	-	-	-	1
								18
Australia	Global North	Australia	3	1	-	2	-	6
								6
Europe	Global North	Croatia	-	1*	1	-		2
		France	-	1	-	-	-	1
		Germany	-	-	1	-	-	1
		Poland	-	1	1	-	-	2
		Portugal	-	-	-	1	-	1
		Spain	-	-	-	-	1	1
								8
North America	Global North	United State of America (Arizona, California, Maryland, Montana, Nevada, Texas, Vermont, Virginia,	-	9	1 1*	8	5	24

		Washington, Wyoming)						
		Canada	-	6	2*	3	-	11
	Global South	Costa Rica	2	1	-	-		3
		Mexico	-	-	-	1	1	2
								40
South America	Global South	Brazil	4	1	-	2	-	7
		Peru	3	-	-	-	-	3
								10
Overall			***15***	***28***	***5 + (4*)***	***23***	***9***	***84***

The findings of our review indicated that there were more published studies of wildlife designed crossing structures (n = 52 studies; 61.9 %) over those that monitored animal use of structures that were not purposefully designed for wildlife use (n = 24 studies; 28.6 %) (Table 2.1). These include existing road drainage culverts, standard bridges, and viaducts. Moreover, Several studies (10.7%; n = 9) did not monitor a specific crossing structure type but focused on monitoring a combination of wildlife-designed structures and existing structures that were not specifically designed for wildlife. For wildlife-designed crossing structures, wildlife underpass crossings such as eco-ducts and eco-bridges were predominantly studied than wildlife overpass crossings.

Our systematic review showed a temporal trend with the first published study that investigated the use of camera traps to monitor wildlife-crossing structures in 2001 in Canada (n = 1), with no further studies until 2008 (Figure 2.3, Supplementary Information Tables S2.1). Thereafter, the temporal trend of peer-reviewed studies in this research area has steadily increased. Of the 84 identified peer-reviewed publications, only 20.2% (n = 17) were published between 2001 and 2015, whilst 79.8% (n = 67) were published in recent years (2016–2024). The publication trend indicated a rapid increase in the studies exploring camera trapping tools in monitoring crossing structures by wildlife in transport-fragmented landscapes (Figure 2.3).

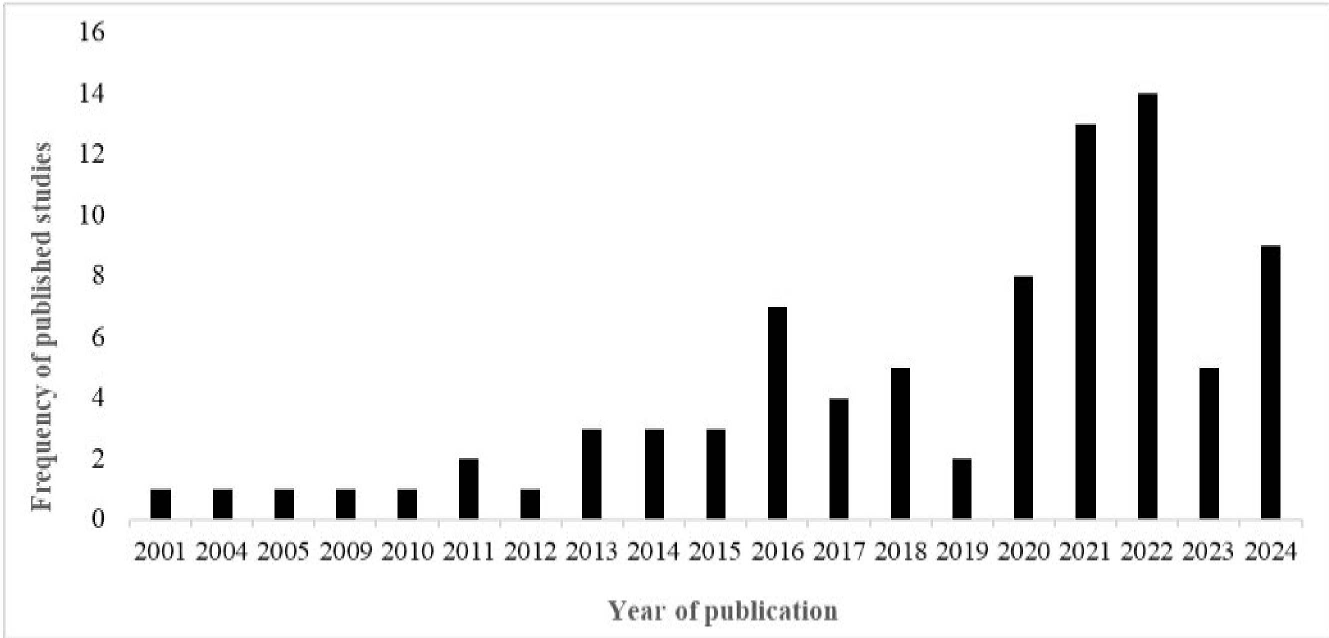

Figure 2.3: Annual trends in peer-reviewed publications (n = total of 84 reviewed articles) that assessed the effectiveness of wildlife crossing structures in promoting connectivity of road-fragmented landscapes through camera trapping between 2001 and 2024.

2.4.2. Habitat and land use type, as well as species of focus

Most of the reviewed camera trap studies were conducted in landscapes with forest cover (63.1%, n = 53), and with agriculture being the common land use within these forest remnants. The remaining camera trap studies were conducted in conservation areas such as nature reserves, national parks and rangelands (9.5%, n = 8), grassland ecosystems (7.1%, n = 6), deserts (4.8%, n = 4), mountainous ecosystems (2.4%, n = 2) and lakes (2.4%, n = 2). Six of the peer-reviewed studies (7.1%) surveyed road corridors that bisected terrains that had heterogeneous land cover and land use, and three (3.6%) studies did not specify the characteristics of the vegetation cover that was surveyed (Figure 2.4, Supplementary Information Table S2.1).

From the reviewed publications, most studies focused on surveying communities of animals (multi-taxa, mammals, and herpetofauna) rather than monitoring a single or a few multiple species (Figure 2.4, Supplementary Information Table S2.1). Notably, 23 studies (27.4%) focused on monitoring multi-taxa, and those that focused on animal groups mainly favoured terrestrial mammals (n = 27, 32.1%), followed by arboreal species (n = 11, 13.1%) and herpetofauna (n = 4, 4.8%) (Figure 2.4, Supplementary Information Table S2.1). The remaining 19 studies (22.6%) were conducted on either a single species or a few multiple species (Supplementary Information Table S2.1).

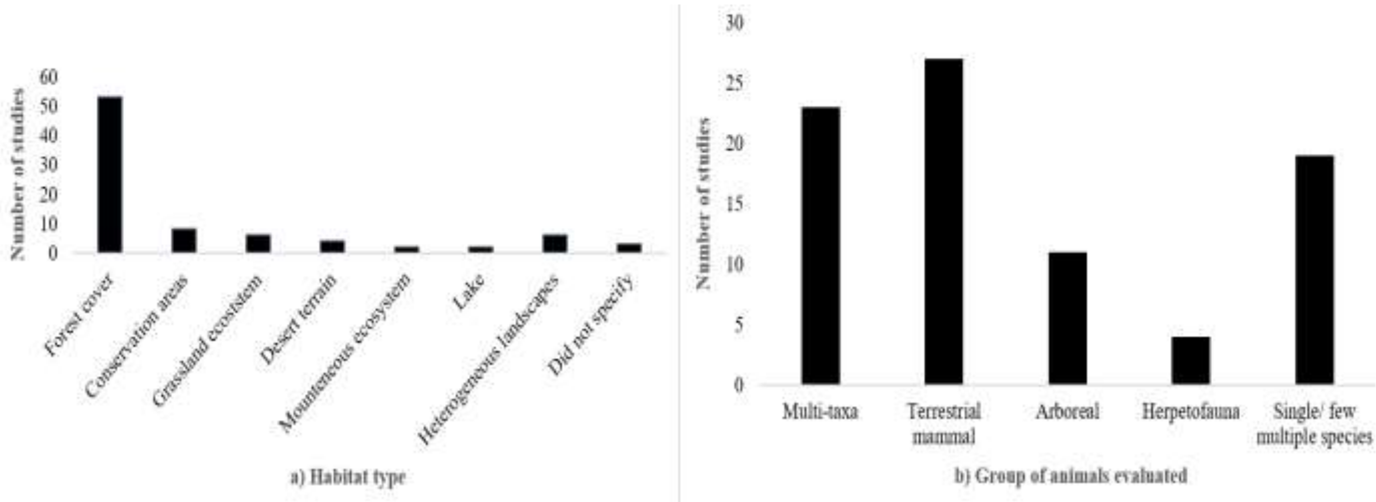

Figure 2.4: Summary of 84 studies evaluating crossing structure uses by wildlife, including a) the surveyed habitat type and b) groupings of species monitored. Several studies reported on multiple species and, as such, were counted in multiple categories.

2.4.3. Protocol for monitoring wildlife crossing structure

Although the objectives and target species/animal group for the evaluated wildlife crossing structure were clearly described and identified in all the studies, the camera trap design and methods applied by each study to assess crossing structures use varied considerably. Whilst timing, frequency and duration of the monitoring applied by each study differed, most of the peer-reviewed publications monitored the structures for an extended duration (longer monitoring period) (67.9%). This included 23 studies (27.4%) that had a survey period ranging between ≥12 months and < 1.6 years, six studies (7.1%) that surveyed for a period between ≥1.6 years and <2 years, as well as 28 studies (33.3%) that had surveys extending for over 2 years. Almost a third of the published studies (31.0%, n = 26) surveyed the crossing structure for a short monitoring period and of this, 13 studies surveyed for less than 6 months, whilst the remaining 13 surveyed for less than 12 months (Figure 2.4d, Supplementary Information Table S2.1). Only one study did not specify the period it monitored the crossing structure (1.2%).

i) Structural design parameters

Crossing structure height and width are important determinants of the acceptance and use of the structure by animals. In the present study, the majority of the conducted studies (67.9%) did not report on the dimensions of the structures they monitored. As such, these studies could not provide information regarding the relationship between the openness ratio index of the structure and the rate of use of the crossing structures by the species or animal group they targeted. Moreover, only approximately one-third of the peer-reviewed publications (32.1%, n = 27) included size dimensions (height, width and length) of the crossing structures they monitored (Supplementary Information Table S2.1).

While monitoring to investigate if targeted animal species are using the monitored crossing structures is regarded as a crucial step in determining the success of the crossing structure (van der Grift and van der Ree 2015), the reviewed studies showed that several factors contribute to determining the effectiveness of the crossing structure. Of the 84 reviewed publications, 38.1% of the studies (n = 32) have reported on the significance of roadside funnel fencing in promoting the use of crossing structures by animals, whilst 61.9% (n = 52) did not report on fencing (no fencing/ fencing information not specified). For studies that provided information on fencing, the roadside funnel fencing had varying heights and lengths. The fencing height ranged between 0.51 and 2.5m, with most studies recommending installing fencing heights of ≥2 m. Although some of the studies have monitored crossing structures that had short lengths (<200 m), many of the studies recommend the installation of roadside funnel fencing extending for longer lengths, depending on the landscape.

ii) Camera trap sampling and monitoring

Whilst a wide variety of monitoring techniques can be used to monitor the efficacy of crossing structures, most reviewed studies showed that camera traps are a suitable monitoring tool for evaluating crossing structure use and animal movement. Most of the peer-reviewed studies (75.0%, n = 63) provided information regarding the number of camera traps deployed to monitor an individual structure (Figure 2.5b, Supplementary Information Table S2.1). Of these, 14.3% (n = 12) used only one camera trap, 32.1% (n = 27) used two or three cameras, and 28.6% (n = 24) used multiple cameras (≥ 4) to monitor an individual structure depending on its openness ratio index. About a quarter (25.0%) of the studies did not specify the number of camera traps deployed to survey each crossing structure (Figure 2.5b, Supplementary Information Table S2.1). The use of multiple camera devices when monitoring crossing structures allowed the identification of complete/confirmed crossing and incomplete/unconfirmed crossing (Mitchell et al. 2022).

Most of the reviewed road ecology camera trap studies set the camera traps to record data in 'photo mode' (75.0%, n = 63). Few studies (13.1%, n = 11) set the camera to record data in 'video mode', and 9.2% of studies (n = 8) had the cameras recording data in both 'photo and video mode' to examine the behaviour of animals using crossing structures in fragmented landscapes. Only two studies (2.4%) did not provide information regarding the calibration of the camera traps (Figure 2.5a, Supplementary Information Table S2.1). Notably, many publications (n = 58, 69.0%) did not indicate the height at which camera traps were placed. Studies that monitored under-and-overpass crossing structures placed camera traps at varying heights; height categories 1) 0.25 – 0.5 m comprised 16.7% (n = 14), 2) 0.6 – 1 m comprised 8.3% (n = 7), 3) 1.1 – 1.5 m comprised 1.2% (n = 1) of the studies and no study placed camera trap devices at a height ranging between 0 – 0.24 m (Figure 2.5c, Supplementary Information Table S2.1).

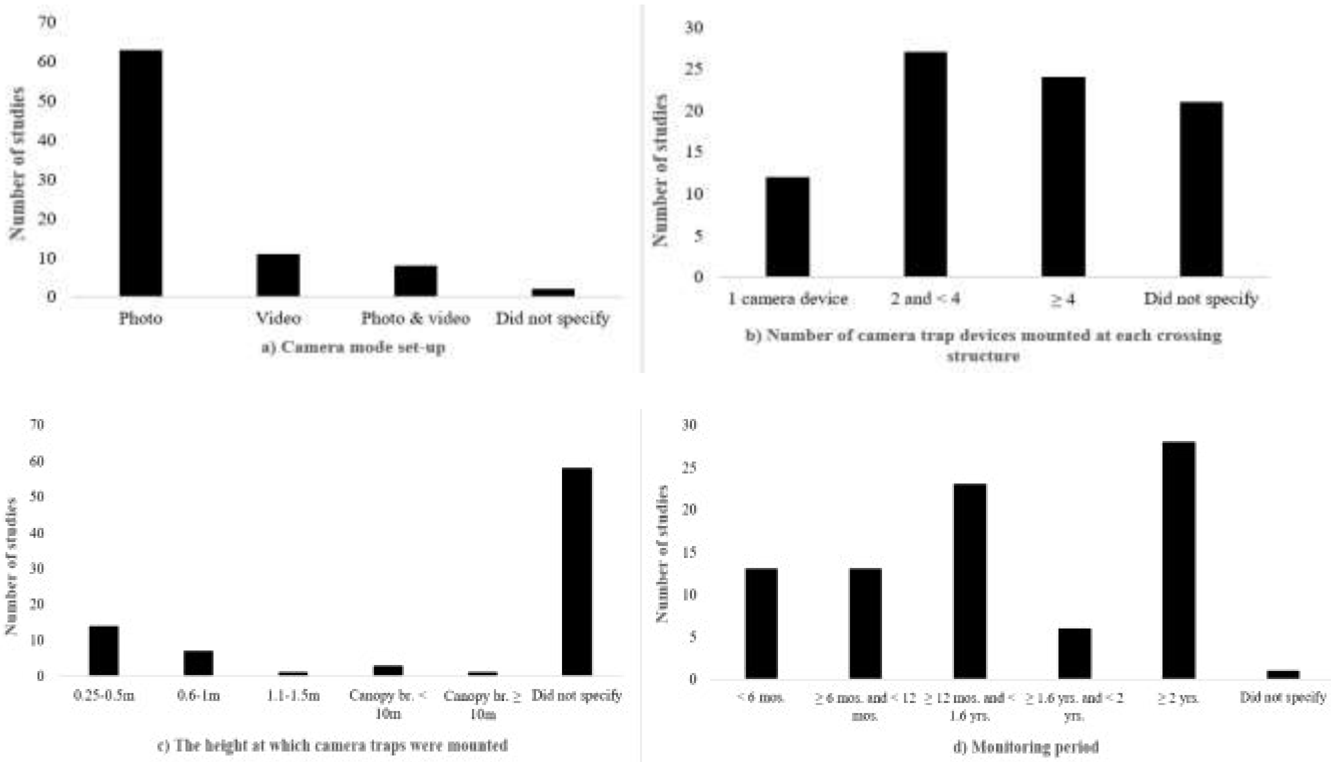

Figure 2.5: Summary of 84 studies evaluating crossing structure use by wildlife, including a) the camera trap mode set-up, b) the number of camera trap devices deployed at each crossing structure, c) the height at which the camera traps were mounted (canopy br. – canopy bridge), and d) the period of monitoring (mos. – months and yrs. – years).

While most of the studies have found camera traps suitable for estimating crossing structure use by animals, some studies (3.6%, n = 3) found camera traps to have poor detection rates for small- to medium-sized vertebrate species compared with other monitoring techniques (e.g., permanent video surveillance recording). Moreover, 25,6 % of the studies further emphasised the need for using a combination of monitoring techniques to evaluate animal use and movement across crossing structures (e.g., remotely triggered cameras, passive integrated transponder (PIT), and track beds). In addition, approximately 30.0 % of the reviewed publications indicated that the population density in the adjacent habitat needed to be evaluated in addition to surveying crossing structure use by wildlife to allow comparison between the animals within the habitat versus those recorded using the crossing structure.

iii) Canopy bridges

Notably, the design of canopy bridge overpasses depends on the type of road and the landscape characteristics. The results on canopy bridges showed that the design and canopy installation methods deployed by the reviewed studies varied considerably (Supplementary Information Table S2.1). The reviewed studies monitored three different canopy bridge designs: a stepladder bridge, a pipeline bridge (bamboo), and a single-rope bridge. The canopy design protocol indicated that the diameters (wideness) of the canopy structures varied, with the diameter for the stepladder bridge ranging from 30 – 40 cm, the pipeline bridge had a diameter of ~15 cm, and the single-rope bridge had a diameter of ~3 cm. The height of the canopy structure ranged between 2.73 and 26.8 m, whilst the length was generally determined by the width of the road, with a maximum length of 85 m. Although the preference of arboreal species varied considerably, the studies showed that rope ladders and pole bridges were the most suitable canopy designs.

2.5. Discussion

2.5.1. Trends in camera trap studies

Globally, the number of camera trap studies monitoring crossing structure use by wildlife has increased considerably, particularly in the past two decades, improving our understanding of how to mitigate the impacts of transport infrastructure on biodiversity. Although existing drainage underpasses and culverts not specifically designed for wildlife usage may still be effective in addressing landscape connectivity, their value is still under recognised. As such, our findings on the use of camera traps to monitor animal use of crossing structures demonstrated that only a small fraction (28,6 %) of studies focused on structures that were not purposefully designed for wildlife usage.

Despite increasing camera trap studies monitoring crossing structure use by wildlife, our review showed that a geographical bias exists regarding camera trap publications in road ecology (i.e., research) and adoption (i.e., implementation) of ecological connectivity globally. The global north countries have received significant road ecology camera trap focus (63.1%, n = 53), with many of these studies conducted in North America (47.6%, n = 40). This could be explained by the fact that the discipline of transportation ecology has been long established in North America and Europe, with the earliest studies dating back from the past two decades (see Forman and Alexander 1998; Forman et al. 2000). The least studies (36.9%, n = 31) were published in global south countries, but approximately half of the studies were from Asia, with a considerable number of studies that focused on monitoring existing drainage culverts. This research demonstrated that gathering baseline information on the presence, activity and abundance of wildlife or certain target species on existing transport infrastructure that are not purposely made for wildlife has the potential to shape future mitigation planning (Bhardwaj et al. 2020; Warnock-Juteau et al. 2022), particularly in the global south countries.

Only two peer-reviewed studies were published in Africa despite the continent having increased linear infrastructure development projects (Nchofoung et al. 2022) and being rich in biodiversity (Güneralp et al. 2017; Cordier et al. 2022). The shortage of studies exploring wildlife crossing-structure use by wildlife in the majority of low-income regions, particularly Africa, may be explained by several factors. These include the lack of political support, limited funding for supporting road ecology research, financing the adoption and implementation of designated wildlife crossings, and the lack of a clear and integrated policy framework on sustainable transport infrastructure (Hlatshwayo et al. 2024; Cormac et al. 2025). Recently, Kenya has built the elephant underpass bridge (Green et al. 2018) and the standard gauge railway corridor in Tsavo National Parks (Okita-Ouma et al. 2021). While these projects indicate efforts for balancing transport, linear infrastructure development, and biodiversity conservation, they are also pioneering in Africa's sustainable development agenda.

2.5.2. Species of focus

Distinct types of wildlife crossing structures have been developed to restore and maintain landscape connectivity for specific species or solely for entire terrestrial and arboreal communities in different landscapes. All the reviewed publications had surveyed crossing structures in landscapes fragmented by roads, making them critical in improving knowledge of animal behaviour and population dynamics in human-altered environments (Bhardwaj et al. 2020; Goldingay et al. 2022). Our review found road ecology camera trap studies that assessed the use of wildlife crossing structures by communities of animals (i.e., vertebrates, mammals, herpetofauna, and arboreal species) to be common as opposed to those that focused their surveys on a single or a targeted few species. There was a strong use of camera traps for mammalian studies (32.1%, n = 27), followed by multi-taxon studies (27.4%, n = 23) and studies that targeted specific or a few species (22.6%, n = 19). We suggest this is because a wide variety of species have adapted to use road-crossing structures for daily dispersal or seasonal migrations, which confirms their significance in connecting landscapes and facilitating safe animal movements (Murphy-Mariscal et al. 2015; Saxena and Habib 2022). Moreover, camera traps are not specific to what animals they capture. So even when studies are designed with a specific species in mind, many other animals are often captured on the cameras that researchers can report on. Only 13.1% of studies (n = 11) focused on arboreal animals, while fewer, 4.8% (n = 4), of studies were conducted on herpetofauna. This lack of research focus on herpetofauna is likely because camera traps have poor detectability for this group of vertebrates (Boyle et al. 2001).

2.5.3. Protocol for monitoring wildlife crossing structure

Monitoring wildlife-crossing structures through camera trapping involves selecting the best study design and camera placement method for the target species, the structural type monitored and the research questions (Moore et al. 2021; Brennan et al. 2022). This includes setting the camera device appropriately and mounting it to the correct height as guided by the study objectives (Jackson et al. 2005). The reviewed studies' camera trap study design and methods lacked standardisation. The lack of standardised camera trap protocol for monitoring wildlife crossing structures (e.g., number of camera devices per structure, mounting height of cameras above ground level, positioning of camera traps, failure to account for openness ratio index, period and frequency of monitoring) could have ecological and practical implications for the study design. This could potentially result in unsuccessful monitoring efforts, bias in the interpretation of the results, and further impact the ability of the study to quantify the effectiveness of crossing structures (Moore et al. 2021). Hence, site-specific camera trap placement guidelines for monitoring wildlife crossings must be developed for each wildlife crossing structural design and its associated habitat type and fauna. This should consider the structural design, the openness ratio index of the structure, the road and landscape characteristics, the animal taxon/ targeted species of interest, as well as the study objectives (van der Drift and van der Ree 2015; Dodd et al. 2024).

While camera traps have become the most preferred method of monitoring crossing structure use because of their cost-effectiveness and ability to record excellent images and videos, some reviewed studies presented several demerits of using camera traps. Some studies reported that camera trapping had low detection rates, particularly for small- to medium-sized vertebrate species such as herpetofauna (Boyle et al. 2001). In addition, Young et al. (2023) have argued that camera traps failed to detect about 43% of small mammal crossings and 17% of medium-sized mammal crossings. This could result from the images obtained having low photographic quality (blurry photographs) because of the animals' size, behaviour, and how well they trigger the camera trap. As such, this can hinder accurate identification of the targeted species of interest (Dorning and Harris 2019). For example, while roads most frequently impact smaller vertebrates such as reptiles and amphibians, there is insufficient information regarding how crossing structures could sustain their dispersal and seasonal migration movements (van der Ree et al. 2007). The height and angle at which the camera is mounted relative to the animal's movement path can impact detection, and study designs that mount camera traps at lower heights (0.3-0.5 m) could improve the detection of small- to medium-sized animals. Many of the reviewed studies did not report their camera trap photographic delay settings. However, Pomezanski and Bennett (2018) have indicated that using a time-lapse interval of 30-s may be suitable for monitoring small- to medium-sized vertebrate species. This outlines the importance of increasing our knowledge of using camera traps effectively to improve our understanding of monitoring animal-use of crossing structures.

Study designs that deploy camera traps outside the crossing structure, with the camera facing towards the entrance/exit of the structure, have proven to be effective (Barrueto et al. 2014). As the camera trap is placed some distance (~5 m) from the structure, it allows the recording of animals as they enter or exit the investigated structure. Camera trap placement for smaller culverts (e.g., mounting camera traps at the entrance and exit of each) and for small bridges (e.g., setting the camera inside each and facing towards the entry or exit) could improve detection probability (Wang et al. 2018). Deploying multiple camera trap devices per structure helps increase the area of view covered. Moreover, complementing camera traps with another monitoring approach, such as track-bed, animal-sign survey, and passive integrated transponders (PIT), could improve data quality (van der Gift and van der Ree 2015; Dodd et al. 2024). Although studies on canopy bridges reported that the stepladder and wooden pole canopy design are most suitable (Linden et al. 2020; Garcia et al. 2022), installing the structure at low heights may increase human-wildlife interactions. As such, canopy bridges should be installed at reasonable heights (guided by transport engineers), depending on the road and landscape characteristics, which could help improve their effectiveness. While the camera batteries can last for extended periods, frequent maintenance fieldwork for downloading data, changing batteries and improved data storage could help prevent data loss and the switching out of the camera devices (Dodd et al. 2024).

2.5.4. Improving the effectiveness of monitoring of crossing structure use using camera trapping

Although camera trapping is increasingly used for determining animal presence, behaviour and temporal activity patterns (Cordier et al. 2023), including monitoring crossing structure use, several factors may affect its effectiveness. The timing, frequency, and period (duration) of monitoring largely influence the effectiveness of estimating crossing structure use by wildlife (van der Grift et al. 2013; Rytwinski et al. 2015; van der Grift and van der Ree 2015). Understanding the life cycle of the target species will help predict the proper timing of monitoring, particularly for seasonal species (e.g., migratory species). This means that seasonal monitoring efforts are most suited in this case, so camera traps may be deployed during the breeding season when individuals are most active. Notably, the majority of the reviewed studies did not specify the monitoring frequency they employed, so this variable was excluded from the analysis. However, van der Ree et al. (2007) found that the monitoring frequency varied amongst studies depending on the study design. Whilst the monitoring frequency could range from monitoring daily to once per month or even a few months a year, estimating crossing structure use for only a few weeks or months cannot provide robust information for comprehensively assessing the use rate of the structure. Camera trap study design where camera traps are deployed and set to collect data on crossing structure use 24 h per day, and for more extended monitoring periods are recommended (van der Grift et al. 2013; Chakraborty et al. 2021; Lehnen et al. 2024). This will allow the capturing of species that exhibit movement preferences. Some species are only active during certain times of year or times of day, or avoid moving at certain times of year or times of day. Therefore, discontinuous monitoring will miss important animal data using the crossing structure (Pomezanski and Bennett 2018). The reviewed studies' monitoring periods varied from 5 days to 5 years. Deploying camera traps for extended periods, especially multiple years, will provide robust information regarding the activity, use patterns and behaviour of animals at the crossing structure under changing environmental conditions.

When conducting studies assessing the efficacy of crossing structures used by wildlife, the monitoring should not be limited to recording passing animals at the crossing structures. In addition to monitoring the frequency of crossing structure uses, baseline information entailing variables at control sites should be quantified (van der Grift and van der Ree 2015; Andis et al. 2017; Goldingay et al. 2022). This includes gathering wildlife mortality data before the installation of the crossing structure or, in the case of monitoring existing crossing structures (non-wildlife crossing structures), prior records of road mortality data will generate an evidence-based evaluation of before-after-control-impact (Soanes et al. 2024). Deploying camera traps in the surrounding habitat to estimate the area's animal abundance and species diversity will provide important baseline information regarding the target species that could potentially use the crossing structure being evaluated. This is because the population density of an ecosystem largely influences the rate of crossing the structure (van der Grift and van der Ree, 2015).

2.6. Conclusions

Our study reviewed global peer-reviewed publications that have monitored animal use of road-crossing structures using camera traps. Through reviewing these studies, it was clear that camera trap use to monitor wildlife crossing structures is still an emerging area of research. Although our evaluation showed that the camera trap approach was successful in monitoring animals' use of crossing structures under or over roads, the study design, sampling, and surveying techniques deployed by each study varied considerably and were not standardised. This highlights the need and significance of studies to maintain consistency in the protocol of monitoring crossing structure so that studies will be comparable in terms of use patterns. While the majority of countries within the global south region appeared to be lagging, poor reporting on biodiversity loss in the transport sector, limited finance for green transport planning, lack of funding for road ecology research, poor multi-sectoral cooperation and poor political buy-in remain the major setbacks (Hlatshwayo et al. 2024). While adopting and implementing wildlife-designated crossing structures for connecting fragmented landscapes is critical for harmonising transportation planning and biodiversity conservation, proper guidelines for improving the quality of monitoring crossing structure use and effectiveness using camera traps are needed.

Several studies have recommended modifying existing crossing structures accordingly to reduce the fragmentation effects of roads (Gagnon et al. 2015; Murphy-Mariscal et al. 2015; Warnock-Juteau et al. 2022). Whilst this potentially makes road drainage underpass structures usable to wildlife, it introduces a cost-effective measure for restoring landscape connectivity for wildlife (Bhardwaj et al. 2020). Moreover, this could be a starting point for global south countries to achieve sustainable green transportation planning. Therefore, we recommend that in addition to monitoring wildlife mortality data, further studies should explore the effectiveness of existing drainage culverts using camera trapping, especially in regions where building wildlife crossings is still a challenge. Moreover, further studies that seek to refine camera trap monitoring protocols for improving the use of camera traps in evaluating crossing structure effectiveness are needed.

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2.9. Supplementary Information

Supplementary information Table S2.1: Summary list of references of camera trap studies reviewed in the present study from 2001 to 2024.

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Supplementary information Table S2.2: Camera trap studies that have monitored wildlife crossings indicating the continent and country of publication, the country's economic status (New World Bank country classifications by income level: 2022-2024), studied taxon/order or species, year of publication, as well as the reference) published from 2001 to 2024.

Continent	Country	Economic status	Taxa/group	Year	Reference
North America	Canada	Global North	Cougar	2001	Gloyne & Clevenger, 2001
			Elk & white-tailed deer	2022	Nojoumi et al., 2022
			Amphibian	2011	Pognucco et al., 2011
			Reptile	2015	Baxter-Gilbert et al., 2015
			Herpetofauna	2021	Boyle et al., 2021; Read et al., 2021
			Mammal	2014	Barrueto et al., 2014
				2022	Warnock-Juteau et al., 2022
			Multi-taxa	2016	Martinig & Bélanger-Smith 2016
				2018	Pomezanski & Bennett, 2018
	Arizona (USA)	Global North	Elk & white-tailed deer	2015	Gagnon et al., 2015
			Mammal	2021	Chen et al., 2021
			Multi-taxon	2024	Hamilton et al., 2024 a
				2024	Hamilton et al., 2024 b
	California (USA)	Global North	Mammal	2004	Ng et al., 2004
				2018	Longcore et al., 2018
				2022	Jensen et al., 2022
			Multi-taxa	2015	Murphy-Mariscal et al., 2015
	Maryland (USA)	Global North	Multi-taxa	2012	Sparks & Gates, 2012
				2017	Sparks & Gates, 2017
	Vermont (USA)	Global North	Multi-taxa	2013	Bellis et al., 2013
	Montana (USA)	Global North	Mammal	2016	Huijser et al., 2016
				2017	Andis et al., 2017
	Nevada (USA)	Global North	Ungulate	2016	Simpson et al., 2016
	Virginia (USA)	Global North	Deer & bear	2016	Donaldson et al., 2016
	Washington (USA)	Global North	Deer	2010	McCollister & Van Manen, 2010
			Mammal	2020	Millward et al., 2020
	Texas (USA)	Global North	Felid	2021	Schmidt et al., 2021
			Multi-taxa	2023	Sheikh et al., 2023

				2024	Lehnen et al., 2024
			bobcat (*Lynx rufus*)	2024	Yamashita et al., 2024
			Mammal	2024	Roy et al., 2024
	Wyoming (USA)	Global North	Pronghorn and Mule deer	2016	Sawyer et al., 2016
	Mexico	Global South	Mammal	2018	González-Gallina et al., 2018
				2021	Manteca-Rodríguez et al., 2021
	Costa Rica	Global South	Multi-taxa	2022	Villalobos-Hoffman et al., 2022
			Arboreal	2021	Laidlaw et al., 2021
				2022	Flatt et al., 2022
Asia	China	Global South	Multi-taxa	2016	Wang et al., 2016
				2023	Lu et al., 2023
			Mammal	2018	Wang et al., 2018
				2024	Maierdiyali et al., 2024
				2024	Ding et al., 2024
	Thailand	Global South	Multi-taxa	2020	Charaspet et al., 2020; Sukmasuang et al., 2020
	Nepal	Global South	Multi-taxa	2020	Poudel et al., 2020
	India	Global South	Predator-prey	2022	Saxena & Habib, 2022
			Mammal	2022	Saxena & Habib, 2022
			Multi taxa	2021	Chakraborty et al., 2021
	Korea	Global North	Mammal	2007	Choi & Park, 2007
			Wildlife	2021	Seo et al., 2021
	Malaysia,	Global South	Arboreal	2022	Yap et al., 2022
			Mammal	2019	Ghazali et al., 2019
				2021	Zainol et al., 2021
	Japan	Global south	Mammal	2022	Asari et al., 2022
	Singapore	Global North	Arboreal	2022	Ow et al., 2022
			Mammal	2024	Tay et al., 2024
	Indonesia	Global South	Javan palm civets and Javan slow lorises	2021	Nekaris et al., 2021
	Turkey	Global South	Wild Boar (Sus scrofa Linnaeus)	2023	Tuttu et al 2023
Europe	Croatia	Global North	Wolves	2016	Šver et al., 2016
			Multi-taxa	2014	Guzˇvica et al., 2014
	France	Global North	Mammal	2017	Jumeau et al., 2017
	Germany	Global North	Wolves, red deer, roe deer, wild boar	2021	Plaschke et al., 2021

	Poland	Global North	Mammal	2019	Iwiński et al., 2019
				2020	Mysłajek et al., 2020
	Portugal	Global North	Mammal	2011	Mateus et al., 2011
	Spain	Global North	Vertebrate	2009	Mata et al., 2009
South America	Brazil	Global South	Water opossum	2020	Priest et al., 2020
			Marmosets and tamarins	2024	Lopez-Ramirez et al., 2024
			Golden lion tamarins	2022	Secco et al., 2022
			Arboreal	2013	Teixeira et al., 2013
				2022	Garcia et al., 2022
			Mammal	2020	Abra et al., 2020
			Multi taxa	2021	Alves et al., 2021
	Peru	Global South	Arboreal	2017	Gregory et al., 2017
				2019	Balbuena et al., 2019
				2022	Gregory et al., 2022
Australia	Australia	Global North	Squirrel glider	2013	Soanes et al., 2013
			Arboreal	2015	Soanes et al., 2015
				2022	Mitchell et al., 2022
			Multi-taxa	2022	Goldingay et al., 2022
				2023	Charles et al., 2023
				2023	Young et al., 2023
Africa	Kenya	Global South	African elephants	2018	Green et al., 2018
	South Africa	Global South	Mammal	2014	Pearcy, 2014

CHAPTER 3

Mainstreaming ecological connectivity and wildlife needs in green road transport infrastructure planning in South Africa

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Running header: Wildlife use of existing road-underpass culverts for crossing road-fragmented landscapes

3.1. Abstract

Launching green transport infrastructure is important for sustainable development frameworks and fosters sustainable land-use practices. Policy provisions promoting integrated sustainability in road infrastructure planning are critical and should incorporate biodiversity needs. We synthesised key existing South African policies for road infrastructure to assess their implementation and effectiveness in mainstreaming ecological connectivity in their framework of green transport planning. We have developed an analytical framework for advancing the sustainability of transport infrastructure and used it to review the policies. Furthermore, we used the Driving Forces-Pressures-State-Impacts-Responses (DPSIR) framework to examine and provide information on the drivers and pressures of transport expansion and poor mainstreaming of ecological connectivity in transportation planning in South Africa. Our results showed that the reviewed policies articulated sustainability elements for enhancing social and economic justice in the transportation sector. They had standards for developing road infrastructure that is climate change-resilient with reduced emissions but had no provisions for mainstreaming ecological connectivity for restoring key ecosystems and threatened species. The policies lacked clear sustainability standards and integration. The DPSIR analysis identified a lack of policy interventions promoting ecological connectivity among the pressures that accelerate transport-related biodiversity impacts. Furthermore, it provided planning responses for improving sustainable land-use planning for road development projects. We propose the integration and inclusion of biodiversity needs in transportation policy frameworks for promoting green transport infrastructure in South Africa. A comprehensive national ecological connectivity conservation strategy must be developed for linear infrastructure fragmented landscapes to promote integrated land use planning and ecological connectivity for wildlife.

3.2. Introduction

Transport infrastructure, in this instance, roads, is a critical element of sustainable human economic development and society (Ruiz and Guevara, 2020; Paul, 2023). Road transport provides an enabling environment for freight movement and contributes ~74% of total land freight income in the sector in South Africa (White Paper on National Transport Policy, 2021). Although roads play a vital role in the economy and mobility of South Africa, when they are not built following the bounds of sustainability, they may have negative impacts on both humans and the environment (Watkins, 2012; Eliasson and Proost, 2015; McLeod and Curtis, 2022; Tiang Chin Fung et al., 2023).

The ecological impacts of transport corridors tend to be deleterious, including climate change effects mainly because of deteriorating air quality, global warming, and noise pollution from rapidly growing vehicle volumes and congestion (de Paula and Marins, 2018; Lu and Chen, 2023). Furthermore, transport corridors may adversely impact biodiversity and ecosystems by isolating wildlife populations and reducing habitats and connectivity for terrestrial vertebrates (Shi et al., 2018; Santoro et al., 2023; Young et al., 2023). The State of the World's Migratory Species Report (2024) indicated that the conservation status of migratory terrestrial species is deteriorating, and road corridors form part of the physical infrastructure that drives the loss of terrestrial species and ecosystems through fragmentation. Transport corridors are also associated with increasing wildlife-vehicle collisions, which are globally reported to cause wildlife roadkill (Clevenger et al., 2003; Collinson et al., 2015; Ament et al., 2023; Hlatshwayo et al., 2023), alter animal activity and distribution patterns, and may exacerbate the invasion and spread of exotic species (Fahrig and Rytwinski 2009; Georgiadis et al., 2020; Son et al., 2024). To effectively improve the sustainable development of transport infrastructure, environmental conservation planning forms a key theme of the road policy framework (Sahraoui et al., 2021; Gonçalves et al., 2022; Ament et al., 2023).

To improve the sustainability of transport planning and development in South Africa, several national frameworks, policies, legislation, and standards delineating the commitment to sustainable practices have been developed. There is a consensus that these standards and policies must integrate biodiversity considerations into their sustainable development frameworks and implementation. To achieve this, more dialogue involving multisectoral players such as the scientific community, engineers and planners, as well as political decision-makers are needed (Van Der Ree et al., 2011; Watkin, 2012; Hejnowicz and Thorn, 2022; Torres et al., 2023; Dodd et al., 2024). The White Paper on National Transport Policy (2021) and the South African Government's Green Transport Strategy (2018) commit to launching green transport infrastructure through minimising negative environmental side effects. This includes measures for reducing the causes and effects of global warming, forecasting and reducing emissions, traffic congestion, and improving poor road safety (Lalendle et al., 2021; Ayadi et al., 2022).

Whilst South Africa's national policies on sustainable road transport commit to adopting holistic practices, they do not incorporate standards for mainstreaming ecological connectivity. Their framework of establishing green transport infrastructure in biodiversity-rich ecosystems does not integrate biodiversity considerations sustainably. Despite environmental impact assessment legislating a legal requirement for quantifying the negative ecological impacts of proposed development projects, many environmental impact assessments fail to undertake ecological connectivity assessments strategically for transport development projects (Laurance, 2022).

Hence, when governance, policies, and planning of transport infrastructure do not incorporate a clear regulatory framework for the inclusion and consideration of ecological connectivity, conservation mandates will continue to restrict the construction of wildlife crossing structures (green bridges/eco-bridges) (Brodie et al., 2016; Keeley et al., 2019). Launching sustainable transport policies and frameworks that promote connectivity at all scales of governance, planning, and implementation is critically needed to establish a roadmap to green transport infrastructure (Brodie et al., 2016; Georgiadis et al., 2020; Chagas et al., 2023). The South African Biodiversity Act of 2004 clearly mandates that every province develop a biodiversity plan considering connectivity areas (Keeley et al., 2019). While this aligns well with the mandate of the 2030 Agenda for Sustainable Development, South Africa still has a vacuum for developing integrated policy frameworks for sustainable transport infrastructure.

South Africa is an upper-middle income country, and with its newly emerging economy, regional development of linear infrastructure is expanding, requiring more land for transport corridor construction, and other development projects that will be fulfilled by changing the function and designation of natural cover. Understanding landscape fragmentation because of the unsustainable development of transport infrastructure is significant for developing effective policies that support conservation and restoration efforts that would result in the establishment of green infrastructure. Our study evaluated the imperativeness of South Africa's policies in promoting mainstreaming ecological connectivity in the transitioning process to greener transport infrastructure. We further synthesised strategies for promoting a new era of more environmentally-friendly and sustainable road infrastructure by following the analytical framework for promoting sustainable transport infrastructure. Our study employed the DPSIR framework to analyse the driving forces, pressures, states, impacts, and responses and the dynamics of transport-induced habitat fragmentation. We believe this shall form a critical road map for addressing ecological connectivity backlogs and further provides a structured approach to evaluate environmental quality and inform policymaking in the transport sector in South Africa. By analysing driving forces, pressures, states, impacts, and responses (DPSIR), we provide stepping stones for addressing the challenges posed by the unsustainable development of transport corridors in the natural environment in South Africa. Lastly, we make policy recommendations for mainstreaming ecological connectivity to conserve biodiversity in national policy frameworks to improve sustainable development mandates in South Africa.

3.3. Methods

3.3.1 Conceptualisation of the analytical framework

Developing holistic approaches for mainstreaming biodiversity conservation in the transportation sector through mitigating wildlife roadkill incidents, the spread of alien invasive species, and mainstreaming ecological connectivity forms a critical sustainability challenge in transportation planning and design. In this study, an analytical policy framework was developed by critically conceptualising comprehensive sustainability standards, as shown in Fig. 3.1, for mainstreaming sustainable transport infrastructure development. This framework was developed by referring to global biodiversity and infrastructure handbooks and action plans that include ecological connectivity, and it was used in this study to appraise the imperativeness and effectiveness of existing national road transport policies on sustainable road development in South Africa.

Using the model of the three traditional pillars of sustainable development (Milani et al., 2021), Global Strategy for Ecologically Sustainable Transport and other Linear Infrastructure (Georgiadis et al., 2020), The Handbook to Mitigate the Impacts of Roads and Railways on Asian Elephants (Dodd et al., 2024), and the United Nations 2030 Agenda for Sustainable Development Goals, an analytical policy framework was developed by establishing four sustainability standards for appraising transport sustainability elements (Fig. 3.1). These standards were developed to distinguish between several metrics aligning with the long-term goals of sustainable transportation development in the transportation sector. These metrics promote the integration of climate change, landscape vulnerability, cooperation between stakeholders and practitioners, and biodiversity considerations into the policy agenda;

this will improve consistency in policy mechanisms and compliance with the implemented policy (Georgiadis et al., 2020; Ament et al., 2023). Lastly, the transport sustainability standards are planned to establish further a clear vision and broader objectives for transport legislation to integrate and respond to the increasing risk of neglecting ecological sustainability investments (Gonçalves et al., 2022; Ament et al., 2023; Torres et al., 2023). Accordingly, the proposed analytical framework argues that developing a road policy for South Africa should consider four sustainability standards, and these include the following:

i) Social justice

Around the world, numerous communities derive their livelihoods and well-being from natural resources through ecosystem services and tourism. Transport infrastructure, in particular, provides many socio-economic benefits to local communities by improving access to social facilities and employment (Quium, 2019; Georgiadis et al., 2020). However, they may drive community resettlement, economic displacement, and social and cultural changes because of the arrival of new migrants and settlers, which may disrupt people's livelihoods if not addressed holistically (Ament et al., 2023). Hence, the policy agenda for sustainable transport infrastructure development should be integrated with spatial and land-use planning. This will help in halting and reversing nature loss by establishing eco-friendly communities (eco-towns) that are resilient and connected with nature (Roman, 2022). This could further be planned to promote local markets with small-scale industry by localising production and allowing ease of movement and mobility for all people, no matter their circumstances (e.g., cyclists, pedestrians, people in wheelchairs). This will help launch transport infrastructure development that is adequate for inclusive growth participation, particularly for low-income regions (Dodd et al., 2024; Ament et al., 2023).

ii) Economic justice

This relates to the role of transport infrastructure projects in promoting economic prosperity, trade, poverty alleviation, and supporting the biodiversity economy and investment through sustainable means. Whilst the demand for the provision of transport infrastructure is increasing, particularly in countries with emerging economies, financing these development projects through public revenues such as taxes and government borrowing is becoming more unsustainable (Woetzel et al., 2016; Chu and Muneeza, 2019). Policies promoting the strategic partnerships and participation of international financial institutions, global, regional and local development banks, bilateral institutions and private sector institutions in financing and managing the development of green transport corridors should be launched and regulated.

iii) Environmental sustainability

The rapid expansion of transport infrastructure development, particularly in the Global South, emphasises the urgent need for risk monitoring and evaluation as a pivotal approach for influencing informed decision-making and developing viable policies for implementing green transport infrastructure (Walters, 1986; Ament et al., 2019; Patterson et al., 2023). The protection of the environment and its natural assets through supporting transport infrastructure development that is resilient to climate change, mainstream biodiversity and ecosystems by conserving ecological connectivity needs to be incorporated at the beginning of the planning phase of transport projects (Georgiadis et al., 2020; Ament et al., 2023; Dodd et al., 2024). Conducting an integrated environmental impact assessment that considers impacts on threatened and non-threatened species and ecosystem functions, including ecological connectivity for transport infrastructure projects, is critical in redefining economic models and policies that support environmental sustainability (Laurence, 2022; Patterson et al., 2022). This will efficiently and effectively avoid, minimise, mitigate, restore, and compensate (or offset) for ecological impacts by following the mitigation hierarchy and will further allow a holistic transitioning to a green economy (Ament et al., 2023).

iv) Institutional sustainability

Regulatory policies promoting the collaboration of crucial players and institutions are important in shaping the sustainability mandates for the transportation sector. This should support cross-disciplinary corporations and include stakeholders with different skill sets, such as the research community (i.e., scientists), local stakeholders, government and private sectors, road agencies (i.e., engineers and planners), as well as policymakers (i.e., politicians), as this will improve integrated governance (Georgiadis et al., 2020; Ament et al., 2023). It will enhance the level of recognition of all sustainability challenges in transportation planning and ensure that the right policies and planning decisions are established. This will promote co-production, build capacity in road planning and design, and catalyse practical implementation of integrated solutions at the local, regional, and national levels (Ament et al., 2019).

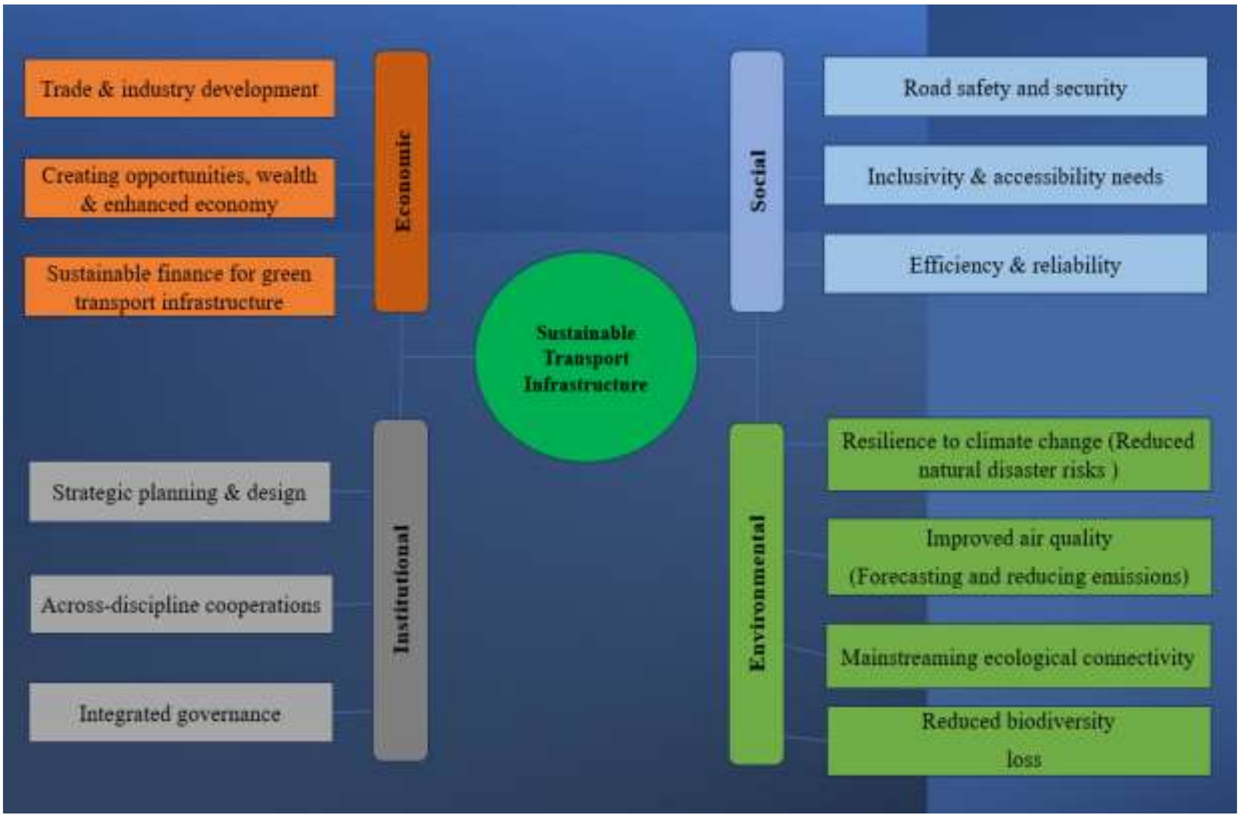

Figure 3.1: Analytical framework for mainstreaming sustainable transport infrastructure development.

3.3.2. Collating relevant policies for sustainable road transport infrastructure development

We conducted a search of proposed and implemented South African road infrastructure development policy documents, as well as infrastructure development strategy and action plans between 20 January 2024 and 20 February 2024. We carried out a comprehensive literature search and indexing to retrieve relevant policy documents from Google search, websites of the Department of Road and Transport (https://www.transport.gov.za/) and the Department of Forestry, Fisheries and Environment (https://www.dffe.gov.za/). The search string- "sustainability, green transport infrastructure and sustainable development" were used to search relevant policy documents for this study. The search results were refined to include national development policy instruments, biodiversity strategies, strategic plans, and development programs that seek to promote sustainable development and environmental protection. The relevant policy instruments were grouped together for further evaluation.

3.3.3 Evaluation of policy effectiveness following the analytical framework evaluation criterion

To appraise the effectiveness of the collated sustainable transport policies in mainstreaming ecological connectivity, our study deployed a qualitative approach to data analyses. In the first phase, we carried out a skimming of all the identified policy instruments, strategic plans, and programs to select relevant materials. Then, in the second phase, we conducted a detailed qualitative analysis of the relevant collated policies on each policy document to assess their "effectiveness" in promoting ecological connectivity in their strategies for implementing green transport corridors. We used the synthesised analytical framework for mainstreaming sustainable transport infrastructure development (Fig. 3.1) to perform in-depth content analyses of the identified national policy documents, biodiversity strategies, and action plans by critically evaluating the full texts. We have qualitatively evaluated the policy's commitment to economic, social, environmental, and institutional contributions in promoting the development of smart, economically viable green transport infrastructure in South Africa. Finally, the data collected through the policy review process were analysed and interpreted.

3.3.4. Drivers-Pressure-State-Impact-Response framework

This study deployed the Drivers-Pressure-State-Impact-Response (DPSIR) framework to demonstrate the chain of causal links that lead to poor consideration and mainstreaming of ecological connectivity in transportation planning in South Africa. Furthermore, we highlighted several interventions required to reverse and halt the perpetual impacts of transport-induced ecosystem and biodiversity threats in South Africa. Through this framework, we have structured and organised indicators from an interdisciplinary perspective (human anthropogenic activities, their ecological impacts, and integrated interventions/responses) to influence effective decision-making regarding the sustainable implementation of green transport corridors in South Africa. In this study, we have summarised and classified the DPSIR factors relating to poor integration of ecological connectivity and biodiversity considerations in green transportation planning policies in South Africa by establishing the link between driving force and pressure. Moreover, we examined the indicators of pressures that lead to changes in the state by analysing the link between State and Impact. For instance, a chain of causal links beginning with 'driving forces' (human population, transport infrastructure demand and expansion) through 'pressures' (increased encroachment of natural landscapes) to 'state' (landscape fragmentation) and 'impacts' (degraded ecosystems and biodiversity loss) requiring integrated responses (mainstreaming ecological connectivity in the scope of environmental impact assessment). As explained in Kyere-Boateng and Marek (2021), the DPSIR framework is essential in connecting causes (drivers) exerting some effects on the environment (pressure), altering its condition (state) by impacting the functioning of the ecosystem (impacts) and we may generate effective integrated environmental management interventions (responses).

3.4. Results

3.4.1. General overview of the reviewed policy documents

In the past decade, South Africa has embarked on several transport sustainability strategies for supporting green infrastructure planning; however, the country still lags behind the Global North in addressing transport-induced biodiversity and ecosystem impacts. In this review study, we could not find any stand-alone government strategy regulating the consideration of and mainstreaming ecological connectivity. The policy review found four relevant policy and strategy documents (from 2014 – 2021) regulating sustainable road transport development and environmental protection and operation, and all of these documents were assessed (Table 3.1).

The comprehensive assessment of sustainable elements of the four collated South African policies on road transport and sustainable development (Table 3.1, Supplementary information Table S3.1) indicated that the policies cover most of the sustainable elements. We found that the four key South African sustainable development and transportation policies were closely related to following the three traditional pillars of sustainable development: social, economic, and environmental. The reviewed policy documents have identified strategies, guidelines, and practices that constitute the South African concept of sustainable development; however, they do not explicitly address all aspects of sustainability of transportation infrastructure. For instance, although all the reviewed transport policy documents had articulated commitments and standards for developing road infrastructure that is climate change-resilient with reduced emissions, their sustainability development strategies did not provision for mainstreaming ecological connectivity for restoring land cover, fragmentation of sensitive ecosystems and securing migration of wildlife populations.

Table 3.1: A general summary of the policy documents included in the meta-evaluation and their objectives as expanded in the Supplementary Information Table S1 (DOT: Department of Transport; GTS: Green Transport Strategy).

Policy name	Year	Policy objective
Roads Infrastructure Policy for South Africa: Policy Framework	2014	1. To provide policy directions for the planning and development of road infrastructure. 2. To ensure that that road corridors are delivered and maintained in an integrated manner.
The Draft Roads Policy for South Africa	2017	1. To provide an over-arching policy that covers all aspects of the roads sector, and which is adopted and applied to all three spheres of government, 2. To prescribe national principles, requirements, guidelines, frameworks and national norms and standards, which must be applied 3. To reduce the effect of the transportation system on the environment; 4. To minimise risk, which also includes preventative actions to reduce the potential impact of extreme events and their effects on the facilities, and the effects of facility damage on the public.
South African Government's Green Transport Strategy (GTS)	2018	1. To enable the transport sector to contribute its fair share to the national effort to combat climate change in a balanced fashion, taking into account the DOT and the sector's primary mandate of promoting socio-economic development. 2. To promote sustainable development. 3. To facilitate the sector's just transition to a climate resilient and low-carbon economy and society. 4. To this end, it is expected that the GTS will serve as a blueprint that will guide and steer the sector in that direction.
White Paper on National Transport Policy	2021	1. To provide policy strategies for government to establish safe, reliable, effective, efficient, and fully integrated transport operations and infrastructure for passengers and freight in a socially, economically, and environmentally sustainable manner.

3.4.2. The policy's commitment to sustainable development

The results of our study demonstrated that all the assessed national policy documents have clearly articulated their commitment and sustainability elements for enhancing social justice in the transportation sector (Table 3.2, Supplementary Information Table S3.1). They also promote social sustainability and entail specific goals of improving road safety and security, accessibility and inclusiveness, and efficiency and reliability to meet the social justice provisions in the transport sector. The policy review indicated clear targets for ensuring economic sustainability in the transportation sector through measures that enhance trade and industry development, opportunities for economic growth, as well as securing sustainable finance for developing transport infrastructure have been clearly incorporated into the policy documents, as illustrated in Table 3.2 and Supplementary Information Table S3.1.

The results of the policy review showed that the environmental parameters evaluating the sustainability of transport policies were biased and not directed towards addressing all the transportation-induced ecological threats equally. All of the reviewed policies in this study have committed to establishing road transport infrastructure that is resilient to climate change, promoting the development of climate adaptation strategies and reducing transport-induced emissions (improved air quality) (Table 3.3, Supplementary Information Table S3.1). However, the policies still fail in terms of developing strategies for mainstreaming ecological connectivity and reducing biodiversity loss from road transport, despite road corridors being among the major drivers of habitat fragmentation and biodiversity loss through wildlife roadkill incidents. The Green Transport Strategy for South Africa (2018) and Draft Roads Policy for South Africa (2017) recommend the consideration and establishment of ecologically functioning transport corridors in road infrastructure planning by ensuring connectivity. However, their connectivity model is only focused on promoting functional roads that connect rural communities with cities and synergistic connections to areas of economic opportunities, with no consideration for integrating ecological connectivity in transportation planning and design.

The results of our present study also indicated that although the three traditional pillars of sustainability do not have provisions for institutional sustainability, the reviewed policy documents have identified several guidelines and mandates that promote institutional involvement in championing sustainable development planning of road infrastructure (Table 3.3, Supplementary Information Table S3.1). Furthermore, our findings showed that the policies have incorporated several mandates for improving strategic planning and design, integrated impact assessment, across-discipline cooperations, and integrated governance in road infrastructure development.

Table 3.2: Summary of policy contributions and targets to social justice and economic sustainability in the transport sector. sector (included in the policy = ✓ and not included in the policy = ⊗).

Policy	Social sustainability			Economic sustainability		
	Road safety & security	**Accessibility & inclusivity**	**Efficiency & reliability**	**Trade & industry development**	**Opportunities for economic growth**	**Financing sustainable transport infrastructure**
White Paper on National Transport Policy (2021)	✓	✓	✓	✓	✓	✓
The Green Transport Strategy for South Africa (2018-2050)	✓	✓	✓	✓	✓	✓
Roads Infrastructure Policy for South Africa (2014)	✓	✓	✓	✓	✓	✓
Draft Roads Policy For South Africa (December 2017)	✓	✓	✓	✓	✓	✓

Table 3.3: Summary of policy contribution and targets to environmental and institutional sustainability in the transportation sector (included in the policy = ✓ and not included in the policy = ⊗).

Policy	Environmental sustainability				Institutional sustainability			
	Resilience to climate change	**Improved air quality**	**Mainstreaming ecological connectivity**	**Reduces biodiversity loss**	**Strategic planning & design**	**Integrated impact assessment**	**Across-discipline cooperations**	**Integrated governance/coordination**
White Paper on National Transport Policy (2021)	✓	✓	⊗	✓	✓	✓	✓	✓
The Green Transport Strategy for South Africa (2018-2050)	✓	✓	⊗	✓	✓	✓	✓	✓
Roads Infrastructure Policy for South Africa (2014)	✓	✓	⊗	⊗	✓	✓	✓	✓
Draft Roads Policy For South Africa (December 2017)	✓	✓	⊗	✓	✓	✓	✓	✓

3.4.3. Policy Scenarios for the DPSIR framework

Multiple direct and underlying drivers of the lack of ecological connectivity considerations in green transport strategies and policies in South Africa and their conservation implications for degrading sensitive ecosystems and biodiversity are presented in this section. The DPSIR framework indicates the drivers of poor consideration of ecological connectivity in transportation planning, and the associated impacts of driving forces are highlighted (Fig. 3.2).

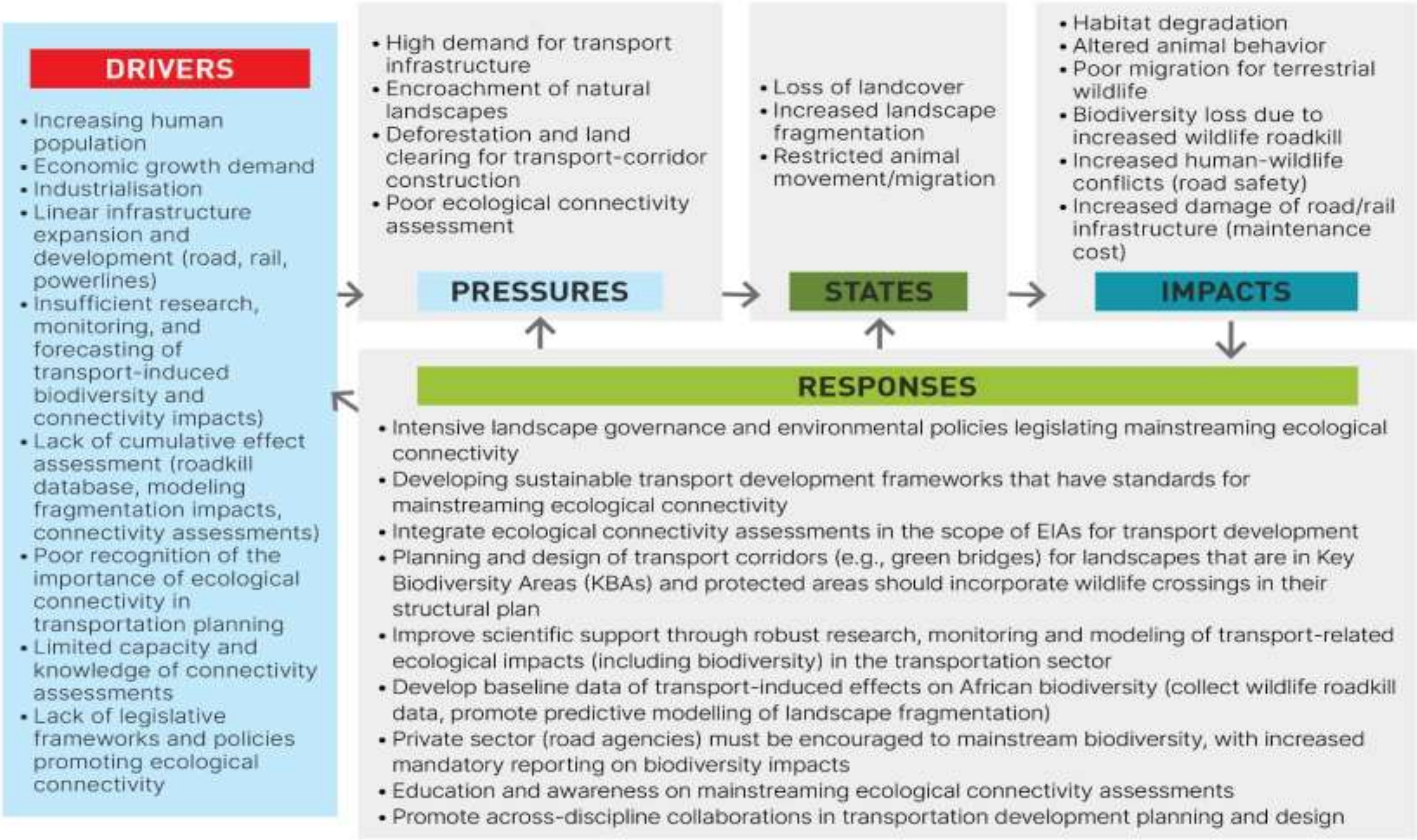

Figure 3.2: Drivers-Pressure-State-Impact-Response (DPSIR) framework of ecological connectivity in transport sustainability in South Africa.

i) Drivers (D)

a. Economic growth demand through linear infrastructure development and expansion

South Africa faces enormous socio-economic changes, such as high rates of poverty and unemployment (Mbanda and Chitiga-Mabugu, 2017). The development of sustainable economic growth through adequate infrastructure development projects plays an important role in enhancing trade and economic growth opportunities in the country. Road infrastructure, in particular, is a key role player in catalysing the country's economy by providing crucial connections between businesses, consumers, and markets. It also connects rural communities to the economic mainstream, ensuring economic productivity. This also ensures that people can easily access opportunities for skill development, employment, healthcare, and education, improving citizens' quality of life. Although the value added to the Gross Domestic Product (GDP) in South Africa by the transport industry has declined drastically in 2020 due to the COVID-19 pandemic travel restrictions, our policy review showed that the transport sector remains a key role player in the country's economy, with its contribution to the GDP showing a recovering trend since 2021 (Fig. 3.3). As the population grows, the demand for land for more linear infrastructure, including transport corridors, continues to increase. As a result, this need will be met by colonising and converting natural landscapes and sensitive ecosystems, often leading to habitat fragmentation, which deteriorates ecosystem quality and species composition.

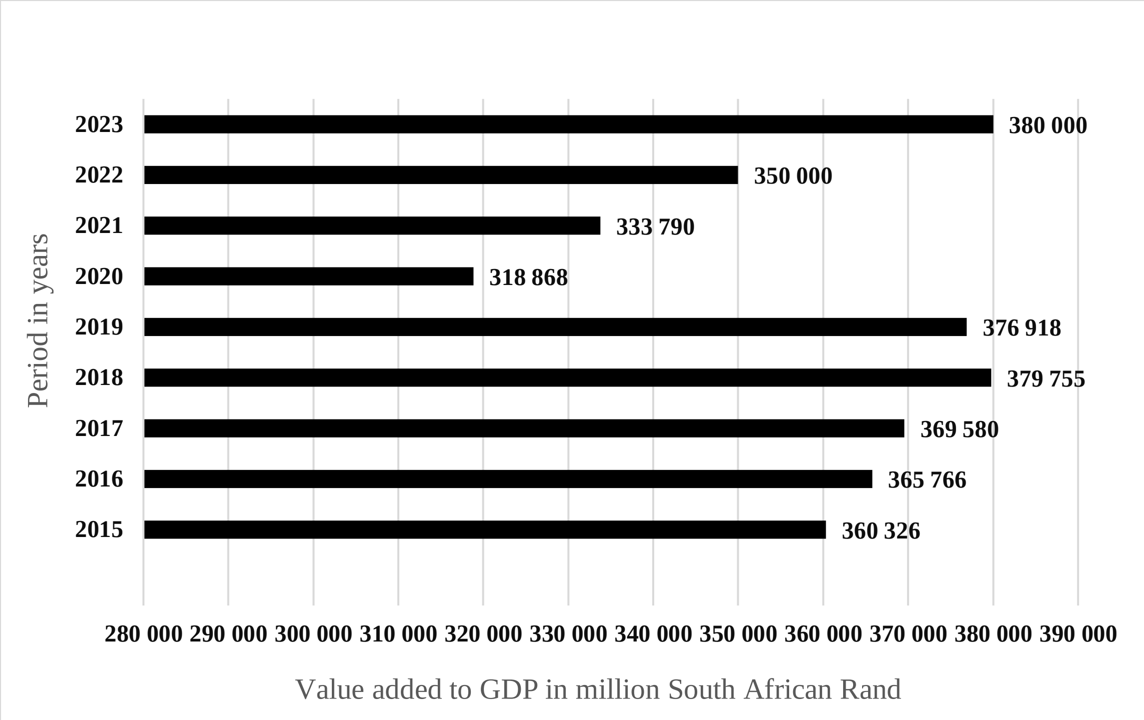

Figure 3.3: Value added to Gross Domestic Product (GDP) by the transport sector in South Africa from 2015 to 2023 (modified from Statistics South Africa, 6 May 2024).

b. Insufficient research, monitoring, and forecasting transport-induced biodiversity and ecological connectivity

Conducting extensive research on transport and climate change as well as robustly forecasting transport-induced emissions, has exerted a critical role in maintaining a low-carbon future in the transport sector. This has contributed meaningfully to combating climate change and its impacts on the transportation sector. However, although a series of empirical studies have shown that transport corridors exacerbate negative impacts on species abundance and composition and further degrade the quality of ecosystems through fragmentation, ecological connectivity remains poorly recognised in South Africa. There has been limited research forecasting, identifying and prioritising where to conserve ecological connectivity. Establishing baseline data of sensitive areas (i.e., hotspot areas) and monitoring wildlife roadkill is important in informing the consideration of ecological connectivity assessments;

these aspects are not considered and remain poorly researched throughout the country. The information appraised from the collated policy documents did not incorporate any commitment to forecasting the effects of transport corridors on isolated wildlife populations as well as modelling wildlife roadkill hotspots for reducing biodiversity threats.

c. Poor recognition of the importance of connectivity in degraded landscapes

Although mainstreaming ecological connectivity helps in guiding future land-use planning that proactively reduces threats to biodiversity, restores ecosystem functioning, and increases opportunities for climate change adaptation, it remains poorly recognised in the frameworks of launching green transport infrastructure in South Africa. The findings of our policy review show that all the collated policy documents did not incorporate any standard or commitment to mainstreaming ecological connectivity, including the Green Transport Strategy document.

d. Limited capacity and knowledge of ecological connectivity assessments (weak Environmental Impact Assessment for transport development projects)

Despite environmental impact assessment legislation having a legal requirement for quantifying the negative ecological impacts of proposed development projects, many environmental impact assessments fail to undertake ecological connectivity assessments strategically (Laurance, 2022). This is mainly because of the lack of capacity during the environmental impact assessment process for transport corridors to provide technical advice regarding ecological assessment procedures, and the lack of data and design expertise that will support innovation through implementing an efficient mitigation hierarchy. Furthermore, there is a lack of cost-benefit analysis relating to mainstreaming biodiversity into green strategies for transport infrastructure development in South Africa.

e. Lack of legislative frameworks and policies promoting ecological connectivity

In striving to respond to the implementation of Agenda 2030 for sustainable development, South Africa has developed several sustainable development green strategies and policies that legislate a just transition to a green economy. Furthermore, the transport sector in South Africa has also launched green strategies and policy documents that demonstrate its commitment to greening the transport industry. However, the mainstreaming of biodiversity and ecological connectivity has lagged far behind the carbon agenda, as evidenced in the Green Transport Strategy for South Africa (2018) and the other reviewed policy documents (Table 3.3). Developing legislative, administrative, and regulatory efforts that provide clear standards regulating mainstreaming ecological connectivity in the transport sector is critical in assisting road agencies and corporations in recognising their dependencies and impacts on nature.

ii) Pressures (P)

Pressures exerted by the driving forces that lead to poor mainstreaming of ecological connectivity in South Africa are exacerbated by the increasing demand for transport infrastructure and other linear infrastructure to support the growing human population. Rapidly developing transport infrastructure has intensified the use and encroachment of natural landscapes in South Africa (Skowno et al., 2021). This has resulted in deforestation, land clearing, and grading that have fragmented the country's landscape. Because these were conducted without effective ecological connectivity assessment and planning, land cover has been degraded, with the ecological connectivity of the landscape jeopardised.

iii) State (S)

The combined consequences of direct and indirect ecological impacts of transport infrastructure continue to cause severe loss to the state of South Africa’s biodiversity.

Expanding transportation corridors was critical in fostering economic growth so striving to reduce economic disparity through infrastructure development as it improved access to economic activities. Clearing natural landscapes for the construction of transport infrastructure contributes to vegetation cover loss, often leading to degraded landscapes. South Africa reportedly lost 0.12% of its natural vegetation cover per year between 1990 and 2018 (Skowno et al., 2021). As a result, transport corridor development and other linear infrastructure projects (e.g., pipelines and powerlines) contribute to landscape fragmentation, hence reducing land cover and connectivity for wildlife. To this end, South Africa has an extensive network of roads, with ~750,000 km of road corridors intersecting natural landscapes (The Green Transport Strategy for South Africa, 2018). Several portions of these road networks stretch through sensitive habitats and wildlife hotspots; as demonstrated in Fig. 3.4, some of the landscapes with threatened species (surveyed by the Endangered Wildlife Trust) are intersected by networks of roads. This reduces ecological connectivity significantly and accelerates biodiversity loss rates in the country's terrestrial ecosystems.

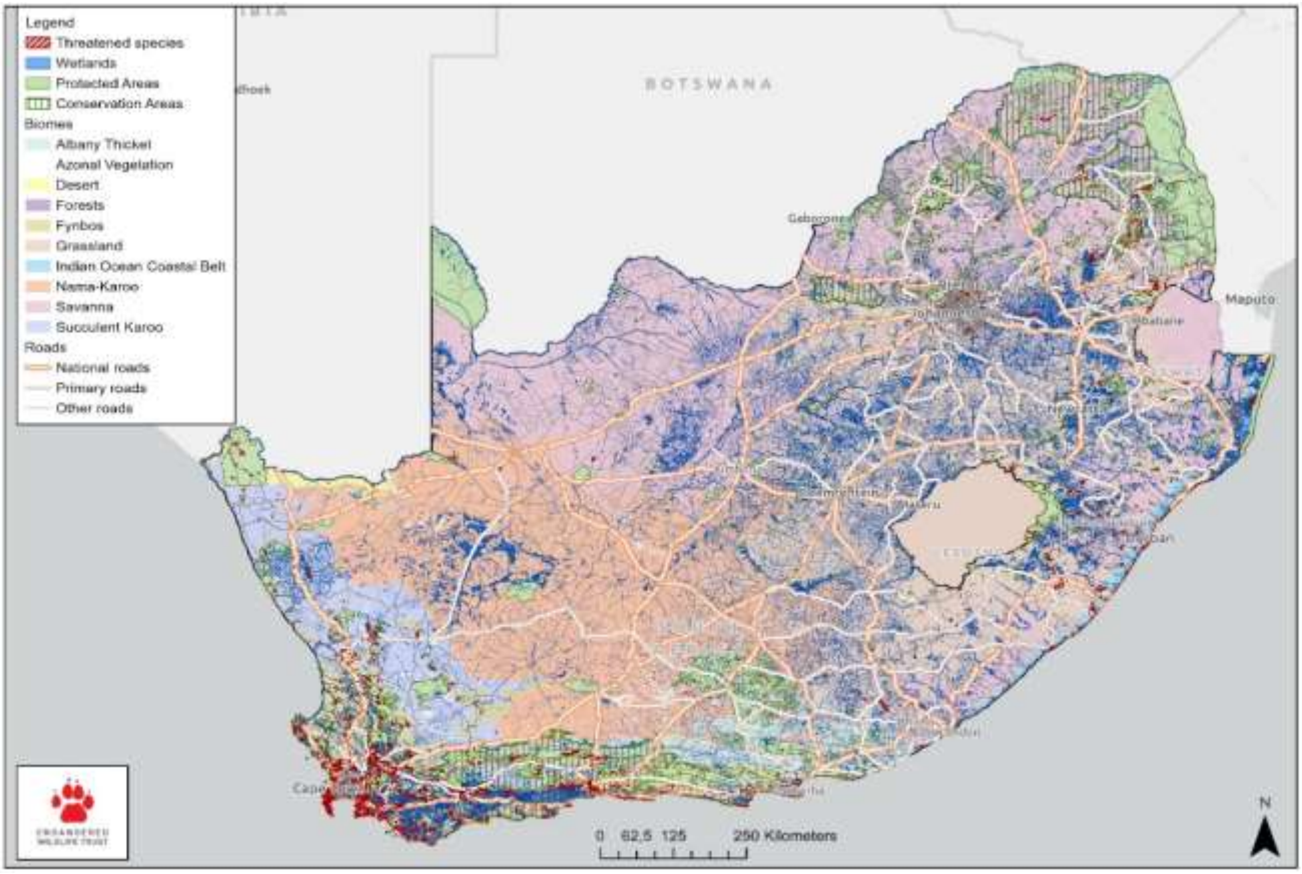

Figure 3.4: A map illustrating landscape fragmentation effects by road networks in South Africa.

iv. Impacts of transport infrastructure on biodiversity and ecosystem when ecological connectivity is not incorporated

The construction and operation of transport corridors (i.e., roads and railways) have a range of both direct and indirect negative impacts on wildlife and natural ecosystems. Transport impacts wildlife, ranging from habitat loss and fragmentation to disruption of animal movement and increasing animal mortality, and combined, these factors continue to drive terrestrial biodiversity and ecosystem services into depletion and great loss. Summarised below are the major impacts transport corridors may have on wildlife when ecological connectivity is not considered in transportation planning, particularly in Africa, where linear infrastructure is rapidly growing.

Road and railway infrastructure expansion takes up considerable land surface area, reducing available habitats and critical resources for wildlife. Habitat loss because of fragmentation is a primary threat to terrestrial biodiversity and could drive species extinction as it affects numerous endemic species. When the landscape is fragmented, animals are subjected to limited migration rates because of the available small patches that only support a small fraction of individuals (Van Der Ree et al., 2011; Ament et al., 2023), increasing the risk of inbreeding depression (Nonaka et al., 2019), which tends to affect gene flow. Poor migration for terrestrial wildlife as a result of isolated habitat patches impacts species population size and further alters animal behavioural patterns such as hunting, foraging, breeding, and home range activities (Collinson et al., 2015; Georgiadis et al., 2020). This also disrupts the distribution patterns of animals and affects the feeding patterns of some species, particularly specialist species, and could, unfortunately, increase the rates of population decline. Habitat loss and fragmentation, because of transport corridors, increase human-wildlife interactions, leading to human-wildlife-conflicts as animals are forced to cross roads for dispersal and migration because of movement barriers created by transport corridors. This further accelerates biodiversity loss through increased wildlife roadkill incidents (Fig. 3.5).

Figure 3.5: Evidence of biodiversity loss from wildlife mortality incidents (A – honey badger (*Mellivora capensis*) and B – Cape clawless otter (*Aonyx capensis*)).

v. Response to driving forces of poor mainstreaming of ecological connectivity in transportation planning

To achieve sustainable implementation of green transport infrastructure in South Africa, several actions to reduce the negative consequences of transport fragmented landscapes on terrestrial biodiversity must be adopted following a collaborative approach. Mainstreaming ecological connectivity to support the conservation of terrestrial ecosystems and their rich biodiversity is critical and should be integrated into the development framework of green transport infrastructure as described below.

a. Regulations and policies promoting mainstreaming ecological connectivity

Laws, regulations, and policies play a fundamental role in advocating and promoting environmental sustainability and the functionality of ecological networks. Although regulations and policies by government that regulate sustainable and green transport corridor development were established in South Africa in the past decade, the existing policy documents have not effectively addressed transport-related biodiversity threats. As indicated in our evaluation analysis, the policy documents lack standards that recognise the importance of habitat connectivity to promote wildlife movement and migration. This indicates an urgent need for South Africa to revise its Green Transport Strategy Policy document and other related sustainability policy documents and frameworks on transport development to ensure that they support spatial and land-use planning that integrates infrastructure development that promotes ecological connectivity and wildlife movement. Policy resolutions for South Africa should recognise the importance of mainstreaming ecological connectivity and include it in the scope of environmental impact assessments for transport development, particularly in biodiversity sensitive areas. Moreover, a national ecological connectivity action plan must be developed as this will promote maintaining habitat corridors that link fragmented landscapes to facilitate wildlife movements.

b. Improve planning and design of transport infrastructure

To combat habitat loss and landscape fragmentation resulting from transport corridor development in South Africa, best management practices and sound engineering design guidelines must be developed. This will produce a mitigation hierarchy framework comprising best-practice design criteria and recommendations for launching wildlife-friendly transport infrastructure that mitigates negative impacts on climate change, biodiversity and ecosystems. This will help produce a mitigation strategy that demonstrates sustainable planning, design, and operation of transportation projects. Furthermore, this process should promote consultation of experts from different disciplines and comprise separate guidelines and recommendations for each respective crossing structure type/design (Ament et al., 2023; Dodd et al., 2024).

c. Improve scientific support and monitoring

South Africa faces increasing pressure of expanding linear infrastructure projects, including transport infrastructure, which causes significant fragmentation of wildlife habitat. Improving connectivity research and monitoring in this country will exert a vital role in gathering data, modelling risks, and establishing baseline data for informing integrated land use planning decisions. There is a need for the country to make it mandatory for road agencies to report on biodiversity impacts by maintaining a database for wildlife roadkill incidences, as this improves data gathering. When wildlife roadkill data are mapped using geographic information systems (GIS) and remote sensing, the exact locations requiring wildlife corridors (i.e., connectivity) can be identified and mapped. This is critical in reducing habitat fragmentation and conservation planning of transport infrastructure development.

d. Education and awareness

Increasing public knowledge of the importance of ecological connectivity in restoring wildlife and their ecosystems improves their recognition and consideration for implementation. Knowledge and skills on mainstreaming ecological connectivity can be shared through environmental education outreach, connectivity assessment workshops, community campaigns, field excursions, and forming advisory forums. This could generate improved conservation knowledge for strengthening wildlife habitat connectivity planning in South Africa.

e. Establishing cross-discipline collaboration

Advocating the conservation agenda of mainstreaming ecological connectivity planning is important and requires establishing interdisciplinary collaborations. Strategic partnerships in connectivity planning are important for achieving integrated planning, research, and policy development that will bolster long-term success in planning road transport corridors that facilitate wildlife movements while responding to climate change impacts. A culture of collaboration should be adopted in South Africa to address ecological connectivity.

3.5. Discussion

Although research on transport sustainability is showing tremendous advancements globally (Sahraoui et al., 2021; Patterson et al., 2022; Ament et al., 2023), major improvements are still required concerning developing national policies that promote integrated spatial and land-use planning in the implementation of green transport infrastructure in South Africa. Our study assessed the performance of four key existing South African policies on road transport infrastructure in promoting wildlife conservation in the sustainable development planning of establishing green-road transport corridors. It also presented an analytical framework for promoting transport infrastructure sustainability and used it as a criterion for assessing the relevance of the identified government policies in addressing sustainability and mainstreaming ecological connectivity in road transport infrastructure planning in South Africa. While the identified policy documents were found to have outlined the majority of the sustainability elements, they all followed the three traditional pillars of the sustainable development model (i.e., social, economic, and environmental). Through this framework of sustainability, clear strategies for addressing the growing ecological impacts of transport infrastructure are lacking, resulting in policy frameworks that are not integrated enough to promote biodiversity conservation (Purvis et al., 2019; Milani et al., 2021). This is an important indication that compels us to demand an even more urgent policy dialogue regarding implementing integrated policies and adhering to international sustainability commitments and standards, particularly now that most African countries are transitioning towards a greener economy.

Our study found that all the assessed national policy documents have clearly articulated sustainability elements for enhancing social and economic justice in the transportation sector; however, they neglected several elements of environmental sustainability. Although both economic and social elements of sustainability form part of the larger ecosystem, the reviewed policies did not explicitly address sustainability standards that promote reducing transport-related biodiversity impacts. Whilst standards that promote climate change resilience and reduction of transport emissions to improve air quality were clearly articulated, transport-related biodiversity impacts such as i) landscape fragmentation effects of roads which impedes wildlife movement among isolated habitat patches (habitat loss) (Gonçalves et al., 2022; Xiao et al., 2024) and ii) wildlife-vehicle collisions that lead to wildlife mortalities and further risk human safety (Collinson et al., 2015; Lala et al., 2021; Hlatshwayo et al., 2023) remained somewhat not included. There is an urgent need to create integrated policy frameworks, as this will illuminate the path to greener, more sustainable road transport infrastructure that strategically promotes mainstreaming ecological connectivity for restoring wildlife habitats (Ament et al., 2019).

Our findings show that the reviewed policy documents entailed important information that promote strategic planning and design, interdisciplinary collaborations and integrated governance. Despite all these elements supporting the strategic involvement of different stakeholders in road planning and design, there is no provision for institutional sustainability in the present sustainability model. We, therefore, propose that strategic cooperation should be recognised and included in the sustainability model to improve the governance, effectiveness of policies, legislations and planning, design and operations of transport corridors, as illustrated in Fig. 3.1.

Although South Africa is a member of PIARC (World Road Association), an international association where road transport sustainability issues are discussed, our results showed that South Africa's policy documents on transport sustainability lacked strategies and standards for protecting vulnerable biodiversity and ecosystems through mainstreaming ecological connectivity. Moreover, from the assessment we have conducted using the DPSIR framework, there seem to be various drivers and pressures that hinder the effective mainstreaming of ecological connectivity in road planning in South Africa (Fig. 3.2). Conducting the DPSIR analysis has allowed several effective responses to be developed to sustainably address poor recognition and mainstreaming ecological connectivity in green transport infrastructure planning in this region. Hence, effective consideration and implementation of the suggested responses will be critical in influencing informed planning and design decisions for road corridor development. The development of an integrated policy framework and strategies that legislate the consideration of mainstreaming connectivity for restoring wildlife habitat and biodiversity in transportation planning is urgently required in South Africa. As illustrated in Fig. 3.5, numerous road corridors in South Africa intersect protected areas, sensitive biomes and habitats that are critical for threatened species; thus, this indicates an urgent need and prioritisation of further research on ecological connectivity assessment in this region. We recommend that the i) Road and Transport, ii) Forestry, Fisheries and Environment departments in South Africa (DFFE), South African biodiversity Institute (SANBI), as well as the South African National Roads Agency Ltd (SANRAL) should collaborate with other qualified stakeholders (research institutions, policy makers, protected area authorities and other Non-Governmental Organisations) in developing a comprehensive national strategy for mainstreaming ecological connectivity conservation for linear infrastructure-fragmented landscapes as this will be significant in establishing integrated land use planning, habitat connectivity, and green infrastructure (eco-friendly infrastructure).

3.6. Conclusions

Noting that laws, regulations, policies, and guidelines are fundamental in promoting sustainable transitioning to a greener economy in road-infrastructure-development planning, our study has comprehensively analysed existing key road transport policies in South Africa. We have assessed the relevance of these national policies in maximising the ecological functionality of road networks through mainstreaming ecological connectivity. Our study further proposed a synthesised analytical framework for promoting transport infrastructure sustainability that presents a user-centric integrated model and establishes road project planning and design that optimises social and economic benefits while minimising negative ecological impacts through strategic collaborations. The proposed analytical framework provides a tool for enshrining national laws that promote the adoption of strategic environmental impact assessments (Cumming and Tavares, 2022; Patterson et al., 2023) and the collaboration of key stakeholders to mainstream ecological connectivity in road planning and design effectively.

The proposed analytical framework has expanded the three traditional pillars of sustainability by incorporating institutional sustainability into the sustainability model. This will create a participatory approach that recognises the involvement and collaboration of qualified stakeholders in road development planning. Furthermore, it emphasises the need to integrate national policies and environmental impact assessments so that they can consider the inclusion of strategic ecological connectivity assessments in their sustainability model (Ament et al., 2023). Lastly, we have applied the DPSIR framework to structure information on the drivers and pressures of transport expansion and poor mainstreaming of connectivity corridors in transport planning in South Africa. We have provided information on the responses that promote collaboration, research interventions and support a consultation process for the formulation of policies that promote sustainable land-use planning by considering wildlife needs in green infrastructure planning frameworks in South Africa.

3.7. Acknowledgements

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3.9. Supplementary information

Supplementary information Table S3.1: Comprehensive synthesis and summary of South Africa's national policy documents and framework promoting Sustainable Road Transport Infrastructure

Policy	**Social effectiveness**		
	Road safety and security	**Accessibility needs**	**Efficiency and Reliability**
White Paper on National Transport Policy (2021)	i) To integrate the safety, security and quality of service of transport infrastructure with international best practice. ii) To optimise road-transport law enforcement and promote and implement efficient, integrated, and coordinated road-traffic management systems. iii) To advance human resource development through iii) To undertake compulsory road-safety audits and reviews every five years in accordance with the policy intent of the Draft Non-Motorised Transport Policy iv) To develop and implement measures for reducing the number of traffic fatalities among vulnerable non-motorised road users.	i) To meet the basic accessibility needs (to work, health care, schools and shops) of all residents of South Africa, ii) To make transport services affordable to the users. iii) To encourage public participation in decision making on important transport issues (formulation of policy and the planning of major projects). iv)To ensure sufficient transportation capacity for all modes of transport that are included in the fully integrated transport system. v) To ensure that the transport needs of persons with disabilities are taken into account when new infrastructure and operations are planned and designed;	i) To determine and provide community and customer transport needs through following a transparent and accountable process ii) To identify inputs from customers and key customer groups through the formation of consultative bodies and assessments of individual needs and how these can best be met. iii). To tailor transport infrastructure to the needs of transport operators and end customers.

The Green Transport Strategy for South Africa (2018-2050)	i) To improve road safety and integrate it into sustainable mobility and transport infrastructure planning design	i) To promote access for all to safe, age- and gender-responsive, affordable, accessible and sustainable urban mobility and land and sea transport systems. This will enable meaningful participation in social and economic activities in cities and human settlements.	i) To improve the National Freight Logistics Strategy so that it identifies long-distance freight and restrict them to rail, ii) To develop (DoT) a national green transport awareness campaign to be rolled out nationally. The awareness campaign will include behaviour change initiatives such as eco-driving.
Roads Infrastructure Policy for South Africa (2014)	i) To improve safer roads for all users ii) To increase mobility, connectivity and access to urban areas	i) To improve access to schools and clinics and other public facilities	i) To improve effective management of the negative impacts of congestion through Transport Demand Management (TDM)
Draft Roads Policy For South Africa (December 2017)	i) To provide an equitable access to a safe, well managed, sustainable road network. ii) To enhance law enforcement so that it would be an adequate deterrent to encourage road users to obey the law. iii) To improve the collection of all crash data, the process for capturing crash data must be reviewed vi) To develop a database of all hazardous locations in South Africa.	i) To improve access and mobility for communities to automatically affords the public improved exposure to health care, education, employment and other opportunities.	i) To integrate more sustainable modes of transport such as public transport, walking and cycling must be included as a key tool. ii) To improve network planning and further promote mass transport options.

	Economic effectiveness		
Policy	**Trade and industry development**	**Opportunities for economic growth**	**Financing sustainable transport infrastructure**

White Paper on National Transport Policy (2021)	i) To improve the safety, security, reliability, quality and speed of transporting goods and people	i) To facilitate the movement of the appropriate type of freight from road to rail and the movement of goods and people ii) To advance human resource development and expand participation through the creation and growth of entrepreneurial opportunities, training and skills development; iii) To better understand and help overcome barriers to entry and the successful operation of SMMEs, and black and women-owned enterprises in transport, in a manner that is grounded in the realities of the marketplace;	i) To build a strong financial base for the creation, maintenance and upgrading of transport infrastructure. ii) To establish investment to build infrastructure in the right places and of the right kind that serves the needs of society and the economy; iii) To protect capital investment in the roads system, and enhance administrative and economic order in the field of road traffic and transport. iii) To encourage, promote and plan for the use of non-motorised transport (NMT) where appropriate.
The Green Transport Strategy for South Africa: (2018-2050)	i) To improve temporal, spatial and economic efficiency in the transport sector. ii) To transfer road freight to rail, for the purpose of reducing road freight traffic and the over-usage of the road infrastructure	i) To establish integrated transport systems that provide equitable access to economic opportunities for all South Africans and support economic growth and development;	i) To improve the development of "Green Corridors" in the road network so that it promote the use of cleaner efficient technologies in the freight industry ii) To increase the capacity to fund maintenance, upgrading and modernisation of the infrastructure
Roads Infrastructure Policy for South Africa: Policy framework (Draft 1)	i) To established streamlined and regulated freight movement ii) To integrate road transport with other transport modes and other economic activities	i) To increase jobs and skills development in the construction/maintenance/operation of roads. ii) To increase the development of technical expertise within delivery authorities/ entities	i) To establish funding mechanisms that enable integrated transport delivery for broad-based road infrastructure projects as part of long-range strategic plans. ii) To enable suitable funding mechanisms for road infrastructure and Transport Demand Management to be comprehensively and holistically implemented. iii) To increase funding levels to match the extent and quality of roads network required for supporting socio-economic growth envisioned for the country.

Draft Roads Policy For South Africa (December 2017)	i) To maximise freight efficiencies. ii) To formulate a framework for the road freight industry (DoT) to align the market cost of road freight activities with the true cost thereof in order to ensure that the road freight industry costs are commensurate with the impact of road freight activities on the existing network. iii) To improve technological advancements and innovation in the road freight industry are to be encouraged and supported by the relevant Road Authorities,	i) To establish sustainable employment opportunities ii) To maximize jobs creation and skills development iii) To invest in the development of technical skills at Road Authorities in order to function effectively iv) To build the capacity to support improvement in the planning, procurement and management of infrastructure delivery at the provincial level	i) To improve the provision of capital investment into new vehicle technologies, in the form of grants or incentives to promote sea and rail freight, as alternative freight modes.

Policy	Environmental effectiveness			
	Resilience to climate change	Improved air quality	Mainstreaming ecological connectivity	Reduces biodiversity loss
White Paper on National Transport Policy (2021)	i) To reduce the impact of transport on climate change by promoting low-carbon modes of transport in the design of transportation systems.	i) To promote Non-motorised transport and be developed with the aim of reducing carbon emissions, promoting a modal shift towards more sustainable modes;	None	i) To reduce negative impact on biodiversity (including wetlands) and air quality in the design, construction or operation of inter-city and intra-city transportation systems and

	ii) To promote compact urban form and eco-mobility in land use and transport planning;	iii)To promotion the harmonisation of emissions and air quality standards ii) To promote fuel efficiency, cleaner fuels and the adoption of fuel-efficient modes of transport;		infrastructure, including highways, pipelines and railways.
The Green Transport Strategy for South Africa: (2018-2050)	i) To promote the construction of low carbon climate resilient (LCR) road infrastructure ii) To replace fossil fuels by vehicle technologies with low or zero tailpipe emissions (electric and fuel cell vehicles) iii) To develop (DoT) best practice guidelines to ensure that integrated, climate-friendly transport options are incorporated into land use and spatial planning - nationally, provincially and locally.	i) To reduce transport GHG emissions to contribute significantly to national efforts aimed at decreasing emissions as agreed to by the South African Government at COP 21 in Paris. ii) To invest in non-motorised transport infrastructure to both reduce harmful air pollution and promoting healthy exercise (eco-mobility mode of transport) iii) To reduce fossil-fuel related emissions in the transport sector by establishing regulations that promote improved efficiency in fossil fuel powered vehicles and improved environmental performance of fossil fuels.	None	i) To reduce the impact of transport infrastructure on the environment; ii) To develop a joint rehabilitation plan focusing on a tree-planting initiative within and around major cities, focusing on replanting trees, especially after the construction of transport infrastructure (facilitated by both the Department of Agriculture, Forestry and Fisheries and DoT).
Roads Infrastructure Policy for South Africa: Policy	i) To move certain freight from road to rail to reduce congestion ii) To reduce the reliance of fossil fuel	None	None	None

framework (Draft 1)				
Draft Roads Policy For South Africa (December 2017)	None	i) To establish a road industry that take measures to actively reduce emissions as it expands transport networks	None	i) To ensure that future road networks do not compromise valuable natural ecosystems, ii) Ensuring the preservation of vital habitats and other requirements for maintaining biodiversity during road construction, operation and maintenance phase.

Institutional effectiveness				
Policy	**Strategic planning & design**	**Integrated impact assessment**	**Across-discipline cooperations**	**Integrated governance/ coordination**
White Paper on National Transport Policy (2021)	i) To integrate land use and transport planning; Land-use planning processes should emphasise compact urban form, reduce urban sprawl, and minimise environmental degradation and loss of agricultural and recreational land. ii) To ensure that the planning for the provision of infrastructure will take place within an integrated environmental	i) To promote environmental protection, resource conservation and the provision of transport infrastructure, with specific reference to all aspects of transporting dangerous substances and goods; ii) To address environmental impacts and corresponding mitigation measures in the planning, construction and operation of transport-related infrastructure;	i) At the national level, the DoT will establish a forum to improve the coordination of infrastructure planning for all modes of transport. ii) To make sure that transport planning by various government agencies and transport-related SOCs gives effect to the vision established by the DoT and should not	i) To improve the institutional, policy and regulatory environment in the transport sector so as to enable investment in transport infrastructure and operations from both public and private sources, ii) To ensure adequate, equitable, efficient, sustainable and dedicated financing and funding

	management approach, and will include, inter alia, the performance of environmental impact assessments (EIAs). iii) To make sure that transport design avoid and reduce travel demand, shifting to more economic and environmentally friendly high-occupancy modes of transport,	iii) To collect, manage and store transport information efficiently to enable data-driven research to inform planning, development and investment.	conflict with that of the relevant provincial departments and municipalities.	for infrastructure, operations and law enforcement; iii) To promote strategies and standards for delivering transport infrastructure
The Green Transport Strategy for South Africa: (2018-2050)	i) To ensure that cooperation between all affected departments in all spheres of Government seeks to achieve Integrated transport planning that actively addresses the spatial planning implications of land use decisions ii) To establish integrated transit planning and systems that build climate resilience in urban and rural communities, whilst minimising the environmental impact of transport infrastructure. iii) To ensure that planning and design of transport infrastructure expansion consider future eco-mobility developments. iv) To ensure that the DoT develops green standards and guidelines for road construction, maintenance and upgrades.	i) To undertake data collection and baseline analysis of the Government fleet and use it as data for the public communication of fleet emissions improvements (engine size, curb weight, footprint, fuel consumption, CO emissions etc.,). ii) To plan for adaptation approaches that have long-term and systemic perspective, as this will also preventing possible lock-ins into unsustainable development paths.	i) To develop best practice guidelines to ensure that integrated, climate- friendly transport options are incorporated into land use and spatial planning at national, provincial and local levels ii) To ensure that the DoT in consultation with National Treasury provide a national team of experts to consult to all spheres of Government as infrastructure expands. The team of green transport integration experts will also consult to the Strategic Integrated Projects throughout their planning and execution. iii) To ensure that the government works with the private sector to expand the current number of electric charging stations powered by renewable energy sources.	i) To ensure that legislative frameworks and smart incentives are introduced to promote uptake of sustainable transport modes and infrastructure. ii) To ensure that the GTS is incorporated into spatial plans, land use schemes and related policies by provinces and municipalities. iii) To assist with developing policy, regulatory norms and standards, fiscal instruments and recommendations essential for achieving a modal shift of passengers from private vehicle use to public transport, and particularly from road to rail.

	This will include standards and guidelines on climate change resilient materials.		These stations will also be accessible to the general public. iv) To promote the engagement of all main stakeholders in the transport sector to enhance both equity and efficiency. v) To make sure that policymakers and researchers make an extra effort to engage stakeholders in their research and information-dissemination activities.	
Roads Infrastructure Policy for South Africa: Policy framework (Draft 1)	i) To prepare specific road infrastructure policies that have been internally ratified by the DOT for each of the focus areas	i) To promote effective monitoring, evaluation and oversight in all functional areas;	i) To promote proper alignment with national developmental priorities ii) To promote the creation of institutional relationships between national, provincial and municipal spheres of government should be strengthened to allow for collaborative planning and implementation	i) To ensure that there is increased transport funding with improved governance ii) To clarify duties and responsibilities across the various spheres of government and agencies iii) To promote policy certainty with clear and concise regulatory framework iv) To enable an environment that will allow the successful implementation of other transport modes and strategies v) To take regulatory actions to reduce the negative impact on infrastructure.

Draft Roads Policy For South Africa (December 2017)	i) To ensure that policy statements therefore prioritise the Integration of road network planning with spatial planning and land use management ii) To robustly and comprehensively monitors and evaluates investments and designs for integrated transport systems across the country, and its social, economic and environmental impact. iii) To establish an Integrated Roads Planning Committee at provincial level to coordinate roads planning, upgrades maintenance, programming and funding cycles and to integrate roads, iv) To review and update current road design guidelines in support of Transit Orientated Developments (TOD), public transport needs, universal access requirements and other national guidelines. v) To ensure that new roads are planned, designed and constructed in accordance with sustainable transport and spatial planning principles taking into consideration the needs of all users. vi) To ensure that engineering standards are constantly be reviewed and improved	i) To Robustly and comprehensively monitor and evaluate investments in infrastructure, and its social, economic and environmental impact. ii) To promote the collection and analysis of more detailed information regarding freight movements, such as weight and content, which should extend across other policies and strategies relating to the road freight industry, must be encouraged. iii) To improve the collection of all crash data, the process for capturing crash data must be reviewed. vi) To develop a database of all hazardous locations in South Africa. v) To develop a national coordinated research programme for road safety involving the universities, research institutions, private industry, the relevant government agencies, insurance companies and other relevant stakeholders.	i) To establish and promote social and physical Integration through participatory planning.	i) To create an environment where institutional relationships are clearly defined and the roles and responsibilities of each authority are unambiguous ii) To ensure that road authorities develop their own Performance Management Plan, implement it and monitor their performance in road service delivery

	to promote the implementation of appropriate designs that will reduce the risk of crashes. vii) To ensure that road safety education for learners are structured and incorporated into the curriculum			

CHAPTER 4

Protecting the unprotected: Monitoring the patterns of terrestrial vertebrate roadkill along a major South African National Highway

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Running header: Patterns of terrestrial vertebrate roadkill along a major South African National Highway

4.1 Abstract

Functionally connected landscapes are a cornerstone for effective biodiversity conservation, particularly in road-fragmented ecosystems. Road corridors cause unprecedented biodiversity loss by forming barriers to animal movement through fragmentation, resulting in wildlife mortality and an increased probability of local extinctions for terrestrial species. Establishing baseline data on wildlife roadkill is significant for improving the understanding of transport-related wildlife impacts and informing mitigation strategies. The present study relied on data collected daily by road patrol staff from 2017 to 2023 to examine the spatiotemporal patterns of terrestrial vertebrate roadkill for six years on the N4 national highway (482.7 km long) in South Africa. It further analysed the effects of landscape and highway characteristics on the distribution of roadkill and hotspot areas, as well as the understanding of seasonality effects on the patterns of fauna roadkill. A total of 1,726 vertebrate roadkill comprising 611 (53.4%) mammalian, 376 (32.9%) avian, and 157 (13.7%) reptilian carcasses were recorded. The carcasses consisted of 111 identifiable species, with 51 avian, 37 mammalian and 23 reptilian species. No significant difference was found in roadkill occurrence between seasons. However, annual vertebrate roadkill rates remained significantly higher throughout the monitoring period, indicating that the distribution of roadkill did not change with changing ecological seasons in the study area. Additionally, a significant difference was found between faunal types, with wildlife showing an average mortality rate of 0.169 carcasses per km and domestic fauna an average mortality rate of 0.062 carcasses per km. Both biome and land-use type significantly influenced vertebrate roadkill distribution, with areas adjacent to natural vegetation cover indicating significantly higher wildlife roadkill rates than any other areas. We emphasise the importance of mitigation interventions along portions of the highway which were identified as roadkill hotspots.

Keywords: Biodiversity loss; habitat fragmentation; national highway; road ecology; transport sustainability; vertebrate roadkill

4.2 Introduction

South Africa is home to iconic wildlife and is ranked among the most biodiverse countries on earth, comprising a wide array of habitats that harbour over 65,000 different species of fauna (SANBI 2013). Functionally connected natural landscapes are critical in promoting ecological connectivity, resulting in effective biodiversity conservation. However, the unprecedented expansion of linear transportation infrastructure (LTI), such as road and rail networks, continues to pose a conflict of interest between the UN's Sustainable Development Goals (SDGs) of improving socio-economics, human well-being and biodiversity protection (Hlatshwayo et al. 2024). Numerous migratory species on land rely on crossing boundaries of diverse terrestrial landscapes for feeding, breeding and dispersal needs. However, networks of roads are increasingly intersecting these key ecosystems that are sustaining high levels of biodiversity, causing barriers to migratory terrestrial species (Lala et al. 2021; Coba-Males et al. 2023; Soanes et al. 2024). As such, when terrestrial wildlife populations timeously migrate to their refuge, breeding, dispersal and feeding habitats, they face enormous challenges and threats along the way because of road corridors that split their natural ecosystems into fragmented patches (Ibisch et al. 2016). Whilst this reduces ecological connectivity for wildlife populations, roads and traffic cause wildlife-road mortalities (known as wildlife roadkill) and animal injuries through wildlife-vehicle collisions (WVCs) (Forman and Alexander 1998; Collinson et al. 2015; Dean et al. 2019; Hlatshwayo et al. 2023; Balčiauskas et al. 2024). The WVCs affect a broad spectrum of vertebrate taxa, including mammals (Périquet et al. 2018; Collinson et al. 2019), birds (Bishop and Brogan 2013; Medrano-Vizcaíno et al. 2022) and herpetofauna (Hastings et al. 2019; Hlatshwayo et al. 2023; Nicolau et al. 2023; Kouris et al. 2024), with impacts on invertebrates challenging to quantify (Reck and van der Ree 2015).

The global extent of road networks is expanding immensely, with an estimation of over 25 million km of road networks projected to be added to the existing global network by 2050 (Thacker et al. 2019), of which the majority of these developments will occur on the African continent (Programme for Infrastructure Development in Africa 2023). Whilst the development of transport corridors impacts biodiversity and ecosystem processes, their profound negative effects are often neglected in transportation planning and design, particularly in the global south regions, including African countries (Hlatshwayo et al. 2024). In the USA, more than a million vertebrates are estimated to be killed daily on roads (Forman and Alexander 1998; Loss et al. 2014). However, the extent of how much biodiversity African countries are losing as a result of WVCs is not quantified because of limited monitoring efforts. Considering the impact of transport-fragmented ecosystems and roadkill on biodiversity, it is critically important to monitor transport impacts on biodiversity as this will enable proper planning for mitigation to prevent biodiversity loss (Collinson et al. 2019). The effects of transport infrastructure on wildlife are still poorly understood in South Africa, with many persisting knowledge gaps. The lack of reliable national baseline information on wildlife roadkill across South Africa limits the understanding of how wildlife populations are affected by transport infrastructure. This further hinders strategic conservation planning, including mitigation measures such as ecological connectivity corridors (green bridges), in the planning and development of new road infrastructure.

Many road ecology studies are focused on monitoring road corridors that are within protected areas because of the key role they play in conservation (Collinson et al. 2019; Cormac et al. 2025; Miranda et al. 2025); this study has opted to survey wildlife roadkill along a road corridor that is outside a protected area. Although the N4 National Highway (N4 toll route,

Figure 4.1) does not bisect formally protected areas, it intersects numerous biodiversity hotspot areas and natural ecosystems critical for biodiversity. All of these contribute to high biodiversity density, and combined with the heavy traffic, they create the potential for increased human-wildlife interaction along the highway. This presents a major barrier to wildlife movement and results in increased levels of vehicle-induced wildlife mortality along the highway.

It is important to intensify initiatives for monitoring incidents of wildlife roadkill to fill this gap, as this will help improve the understanding of the negative impact of transport corridors on wildlife populations. Moreover, this will enhance the generation of standardised baseline data that will form a basis for understanding transport-related wildlife impacts, analysing and mapping hotspots, as well as planning for mitigation measures (Ekstrom et al. 2015; Hlatshwayo et al. 2024). In this regard, our study has relied on data collected by the Trans African Concessions (TRAC N4) road patrol staff as part of their daily road patrols to evaluate the spatial and temporal patterns in the distribution of wildlife roadkill along the N4 National Highway (N4 toll route) in South Africa. We provide a comparison of roadkill occurrence between wildlife and domestic fauna. Furthermore, we evaluated the effect of habitat, vegetation cover, and land-use on the occurrence of vertebrate roadkill along the N4 National Highway. We determined the influence of season on the occurrence and distribution of vertebrate roadkill. We predicted that changing ecological seasons and vegetation cover stratification would influence the occurrence and distribution of vertebrate roadkill along the study road. This study will make a meaningful contribution by demonstrating how successful strategic partnerships between conservation NGOs, researchers, and transport institutions could help establish a reliable database of wildlife roadkill and how these data could inform conservation planning for reducing transport-related wildlife impacts.

4.3 Methods

4.3.1 Study area

Our area of study focused on the N4 toll route (N4 highway), a 482.7 km national highway in South Africa managed by the Trans African Concessions (TRAC) through the South African Road Agency Limited (SANRAL). It extends from Pretoria, South Africa's administrative capital, passes through the city of Mbombela, to the country's border with Mozambique along the southern border of the Kruger National Park (Figure 4.1). As such, the N4 toll route is one of the most critical trade routes in the Southern African region as it stimulates trade and investment in three key economic regions – Gauteng and Mpumalanga (South Africa) and Maputo (Mozambique) (Gelderblom 2021). This makes the highway relatively busy, and it has associated high traffic volumes. Although the N4 highway passes through landscapes that are outside protected areas, it passes adjacent to numerous conservation areas, including the iconic Kruger National Park and large amounts of natural vegetation. In addition, the highway intersects three of the eleven South African biomes, Savanna (Malelane Mountain, Legogote Sour, Pretoriuskop Sour and Undesite Mountain Bushveld), Forest (Northern Mistbelt and Scarp Forest) and Grasslands (Lydernburg Montana, Rand Highveld, Northern Escarpment Dolomite and Eastern Highveld Grassland) (Mucina and Rutherford 2006). Furthermore, it also passes across temperate freshwater and subtropical freshwater wetlands; most of these landscapes are critical habitats for wildlife. Some highway sections intersect landscapes dominated by anthropogenically altered land, including agriculture, mining, and heavily urbanised areas.

The Mean Annual Traffic Volume for the monitored 482.7 km segment of the N4 highway varies, with high daily traffic that ranges between 15,000 and 30,000 vehicles per day (Gelderblom 2021). Whilst the general speed limit is 120 km/h, reduced speed limits are designated for several road sections. As such, sections extending along the Wonderfontein, Elands Valley area (along the tunnel), Elandshoek, Patatanek and Joubert's shop areas, as well as the Malelane area to the Komatipoort urban area were designated as 80 km/h. Thereafter, a 100 km/h speed limit was designated for sections that run along the Karino interchange through the gorge to just before the Nkomazi Toll Plaza. The highway is generally two lanes wide in each direction.

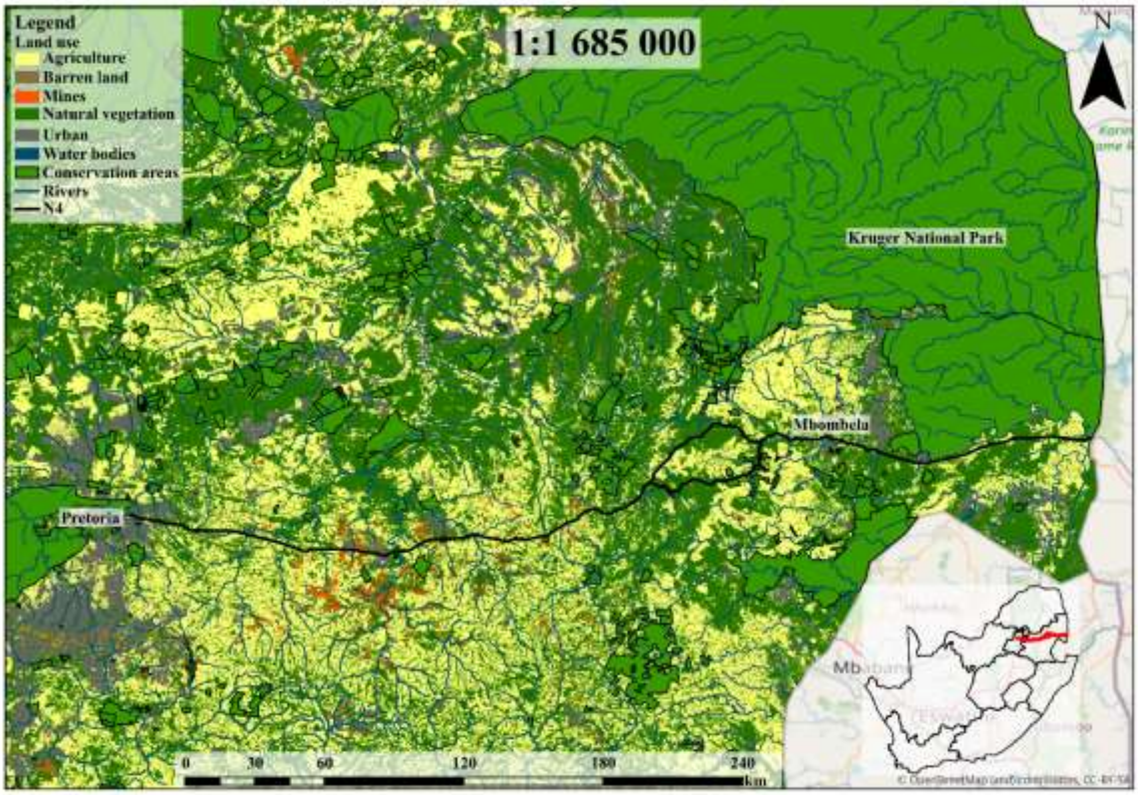

Figure 4.1: Map showing the N4 toll route (N4) from Pretoria to the South African border with Mozambique (Created on ArcGIS Pro 3.0).

4.3.2 Data collection protocol

Annual road ecology training has been facilitated by the Endangered Wildlife Trust (EWT), a South African-based conservation NGO, since 2017. The TRAC road patrol staff involved in the Wildlife and Transport Project are trained on a scientific protocol for gathering and reporting wildlife roadkill data as described by Collison et al. (2015) and on wildlife identification. The day-long training workshop also covered the importance of conservation, an introduction to road ecology, and mitigation for reducing transport-related biodiversity impacts. In addition, each route patroller received a manual and a field guide to identifying animals killed on the road. A field officer (researcher) from the EWT also accompanied route patrol staff on a sample of their patrols to provide additional field training and a deeper understanding of how the patrols work.

After capacitating the route patrol teams through the training, the road patrol staff conducted daily monitoring of the 482.7 km stretch of the N4 toll route. For this study, we relied on mortality data gathered between 1 February 2017 and 31 December 2023. Daily field data on wildlife roadkill incidents were reported, with patrols conducted four times per day (twice in each direction) at a speed of ~60 km/h. Patrol teams mostly consisted of three to four observers for each monitoring trip, each allocated a few short sections of the road to ensure the entire length was covered effectively (Table 4.1). Observers recorded the species of roadkill carcasses encountered, the date and time of the observation, and the carcass location using the nearest route marker, located at 200 m intervals along the road as well as using a geographical positioning system (GPS) to obtain the geographical location. A photograph of the roadkill specimen was taken for verification purposes; thereafter, the carcasses were removed from the road to avoid recounts and secondary roadkill incidents (Collinson et al. 2015; Hlatshwayo et al. 2023).

Table 4.1: Lengths (km) of each road section of the TRAC N4 monitored in the present study.

Section	Start	End	Length (km)
N4/1	9.37	25	15.63
N4/2	0	55.0	55.0
N4/3	0	41.8	41.8
N4/4	0	47.5	47.5
N4/5	0	56.7	56.7
N4/6X	0	43.0	43.0
N4/6Y	0	61.5	61.5
N4/7	0	90.1	90.1
N4/8X	0	7	71.0

*remaining 0.47km comprised by Montrose interchange between section N4/6Y and N4/7

4.3.3. Spatial analyses

For spatial analyses, our study has modified the methods used by Cormac et al. (2025). We made buffers using a 50 m radius before splitting the road into control and kilometre sections. Heat map and hotspot mapping analyses were conducted for wildlife and domestic fauna mortalities following the protocol of Cormac et al. (2025). The analysis of hotspots in this study was defined following three elements relating to the i) intrinsic characteristics of the studied road (traffic volumes, wideness, vehicle speed, topographic variables), ii) landscape attributes (vegetation cover type, land-use type, distance from waterbody, distance from substructures and superstructures as well as ecology of the present species) iii) spatial and temporal distribution of roadkill incidents (daily, monthly and seasonal variation) (Eberhardt et al. 2013). We extracted habitat characteristics for each recorded road mortality using the region's geographical information system (GIS) layers. These included i) distance to running and standing water bodies; ii) road substructures and superstructures; iii) railways and powerlines; iv) elevation; v) surrounding natural vegetation cover type, biome, conservation areas and present land-use. Distance data were extracted using the near tool in ArcGIS Pro 3.0. Elevation data were collected using the extract surface information tool in ArcGIS Pro 3.0. Vegetation and biome information were obtained by spatially joining the most recent national vegetation map (SANBI 2018) with road mortality positions, and land use information was obtained from the most recent land use raster map (DFFE 2022) using the extract values to point tool in ArcGIS Pro. We retrieved river, railway, and conservation area GIS layers using Google Street Map® (HOT 2025).

4.3.4. Statistical analyses

We conducted all statistical analyses using the R (R Core Team 2021) plug-in within Google Collab (Sukhdeve et al. 2023). We used a multiple regression to compare the differences between wildlife and domestic fauna yearly roadkill rates using the lm function in the base R package (R Core Team 2021). A comparison of yearly wet and dry season road mortality rates was then conducted using a paired t-test to determine seasonal significance for both wild and domestic fauna (R Core Team 2021). We used Kruskal-Wallis tests in R (R Core Team 2021) to compare the number of monthly road mortalities by faunal type (wildlife vs domestic) in relation to the surrounding biome and land-use to deduce the significance of each factor subgrouping. We conducted Kruskal-Wallis tests in R (R Core Team 2021) using the dplyr package (Wickham et al. 2023), as the data did not match normality assumptions. We used Mann-Whitney U tests in R (R Core Team 2021) to determine the individual significance of the continuous variables: road chainage (an imaginary line that is used for measuring distance, usually corresponds to the centre of a straight road); elevation; distance to rivers, waterbodies, powerlines, railways, conservation areas, substructures and superstructures, between wildlife and domestic fauna road mortalities. We used a redundancy analysis (RDA) to determine the significance level of the continuous datasets to the monthly number of wildlife and domestic road mortalities. The RDA was conducted using the vegan package (Dixon 2003). Nominal datasets (biome and land use) were excluded as they were assumed to be significant to the system. This is based on the results of the above-stated analyses and previous research findings on the importance of habitat/vegetation cover and land-use on roadkill distribution (Seo et al. 2015; Lala et al. 2021; Carvalho-Roel et al. 2023).

4.4. Results

4.4.1. Roadkill demographics

A total of 1,726 vertebrate road mortalities were recorded on the N4 national highway between 15 February 2017 and 31 December 2023, and this comprised 1,144 wildlife, 416 domestic and 166 unidentified specimens because their carcasses were too damaged for identification. The most commonly recorded taxonomic group was mammalian (611, 53.4%), followed by avian (376, 32.9%) and reptilian (157, 13.7%). The identified carcases were composed of 51 avian, 37 mammalian and 23 reptilian species. Although most of the identified roadkill species had a least concern conservation status according to the IUCN Red List of Threatened Species, several species of conservation priority were found. These included four mammalian species: African wild dog *Lycaon pictus* (Endangered), African clawless otter *Aonyx capensis* (Near Threatened), hippopotamus *Hippopotamus amphibius* (Vulnerable) and African buffalo *Syncerus caffer* (Endangered), two reptilian species: Natal hinged-back tortoise *Kinixys natalensis* and southern African rock python *Python natalensis* both Vulnerable, and an avian species, the African grass owl *Tyto capensis* (Vulnerable), with habitat change/roads listed as a threat to species. The list of identified species is presented in Supplementary Information Table S4.1.

Road mortalities of domestic fauna were made up of 451 carcases (cat, *Felis catus* =130 and dog, *Canis lupus familiaris* = 321) while road mortalities of livestock were least reported, with only ten chickens (*Gallus gallus domesticus*) , five goats (*Capra aegagrus hircus*) and three cows (*Bos taurus*). Wildlife road mortality rates were significantly higher per year ($p = 0.013$) than road mortality rates of domestic fauna (multiple regression, Adjusted R-squared = 0.8665, $F = 29.12$, $df = 10$, $p < 0.001$) (Figure 4.2). No significance was found between seasons within each fauna type (paired t-test, $df = 15.92$; $t = -5.40$; $p = 0.176$), however a significance was again found between fauna types ($p < 0.0001$) where wildlife had an average mortality rate of 0.169 carcass^{-km} and domestic fauna had an average mortality rate of 0.062 (Figure 4.3).

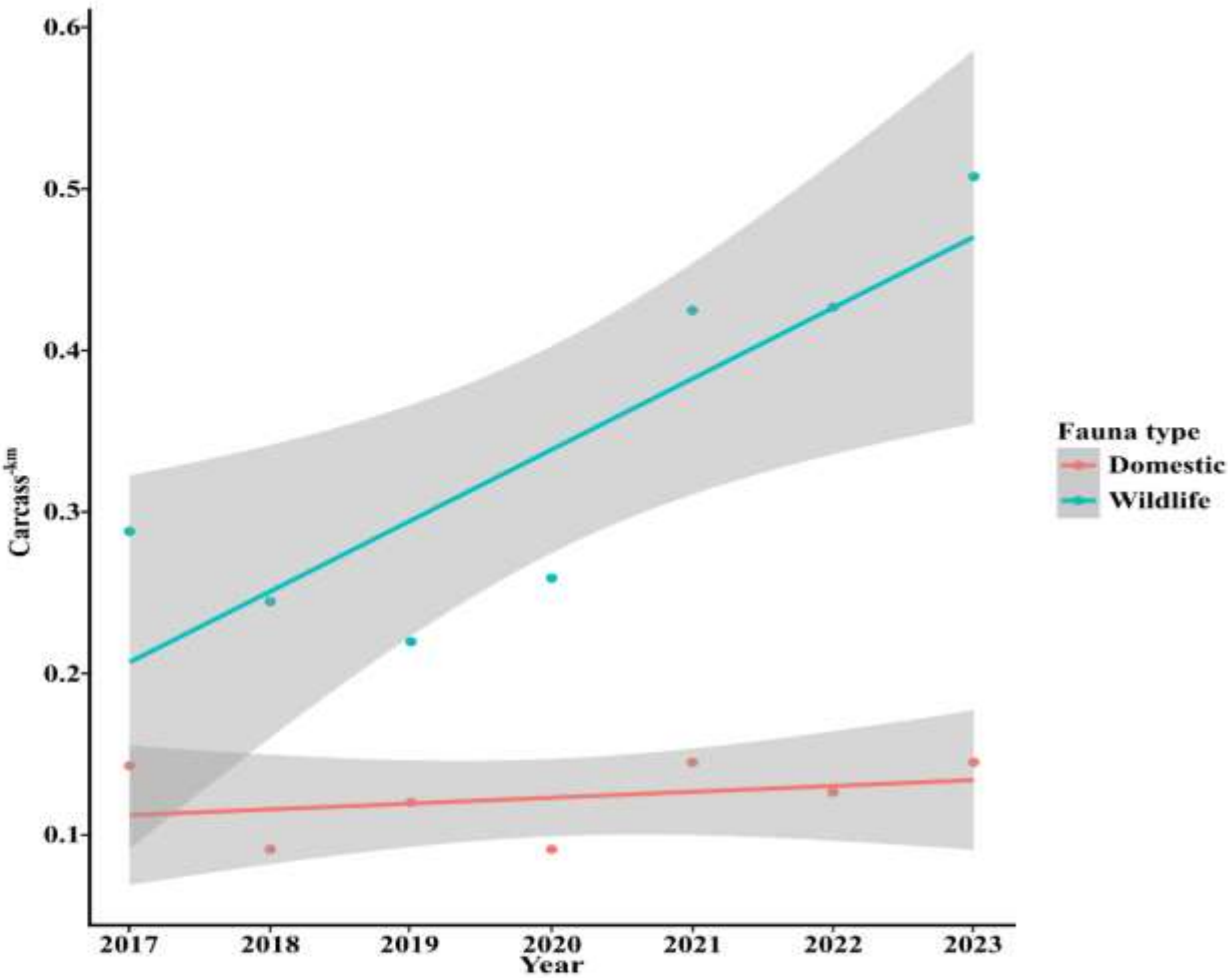

Figure 4.2: Carcass rate per kilometre of faunal road mortalities from 2017 to 2023 along the N4 National Highway (N4 toll route) in South Africa.

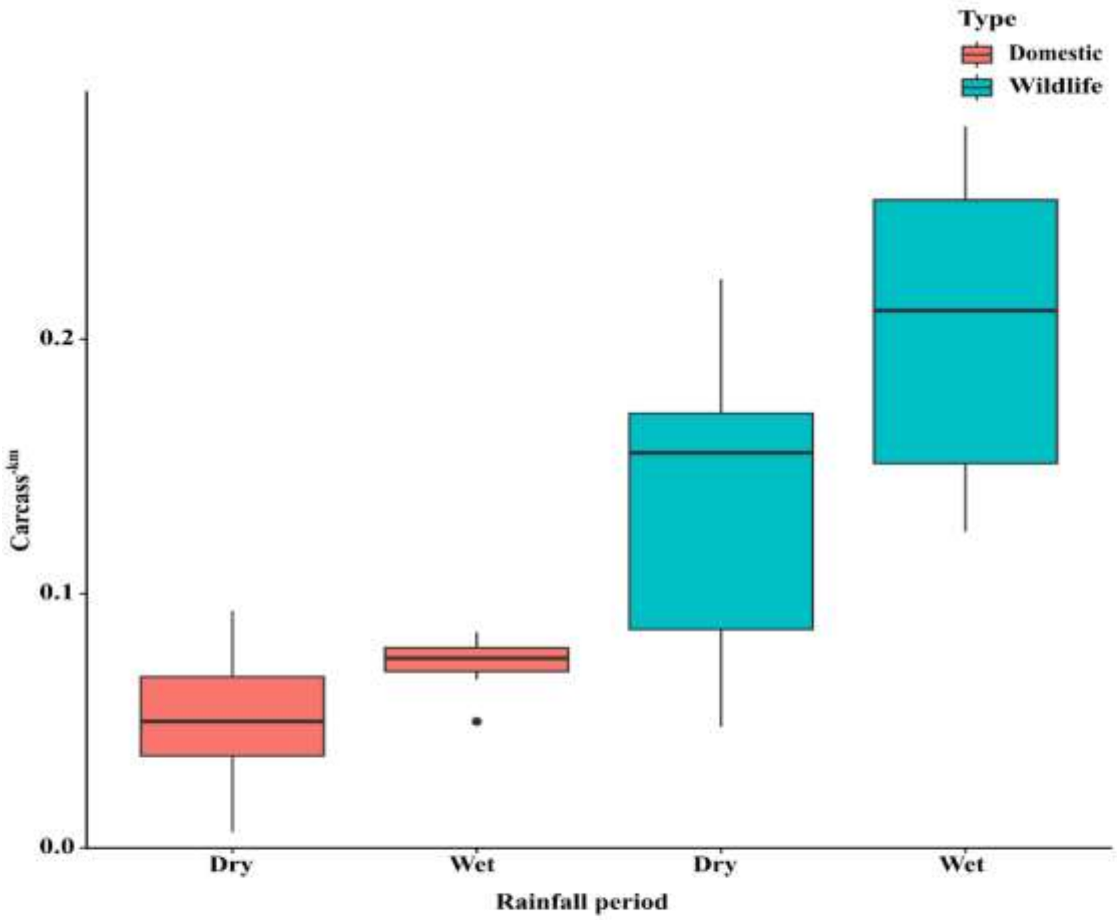

Figure 4.3: Seasonal fauna roadkill rate from 2017 to 2023 along the N4 National Highway (N4 toll route), South Africa.

4.4.2 Spatial analyses on the distribution of vertebrate roadkill

Our analysis of the patterns of wild fauna roadkill along the N4 toll route has identified seven roadkill hotspot areas (Figure 4.4 A). Starting from Pretoria, the first hotspot is in the third kilometre of section two of the N4 toll route (2.3: $z = 2.14$; $p = 0.032$), followed by the one at the 90th kilometre of section seven (7.90: $z = 17.47$; $p < 0.001$) and five hotspot areas at section eight (8.4: $z = 2.59$; $p = 0.009$, 8.20: $z = 1.99$; $p = 0.046$, 8.21: $z = 8.75$; $p < 0.001$, 8.35: $z = 2.59$; $p = 0.009$, 8.60: $z = 1.84$; $p = 0.065$). While analysis of domestic fauna road mortalities found only four mortality hotspots (Figure 4.4 B); one in kilometre 90 of section seven (7.90: $z = 19.58$; $p < 0.001$) and three in section eight (8.5: $z = 2.88$; $p = 0.004$, 8.21: $z = 6.53$; $p < 0.001$, 8.40: $z = 1.84$; $p = 0.066$). Of all the recorded hotspots only two were consistent across fauna type, indicated by *, those being hotspots 7.90 and 8.21, both of which had significance values of $p < 0.001$. The degrees of freedom for all hotspot analyses were 482, and no significant cold spots were identified and an overall similarity of 0.2778 was recorded between hotspot analyses with an expected overall similarity of 0.2285.

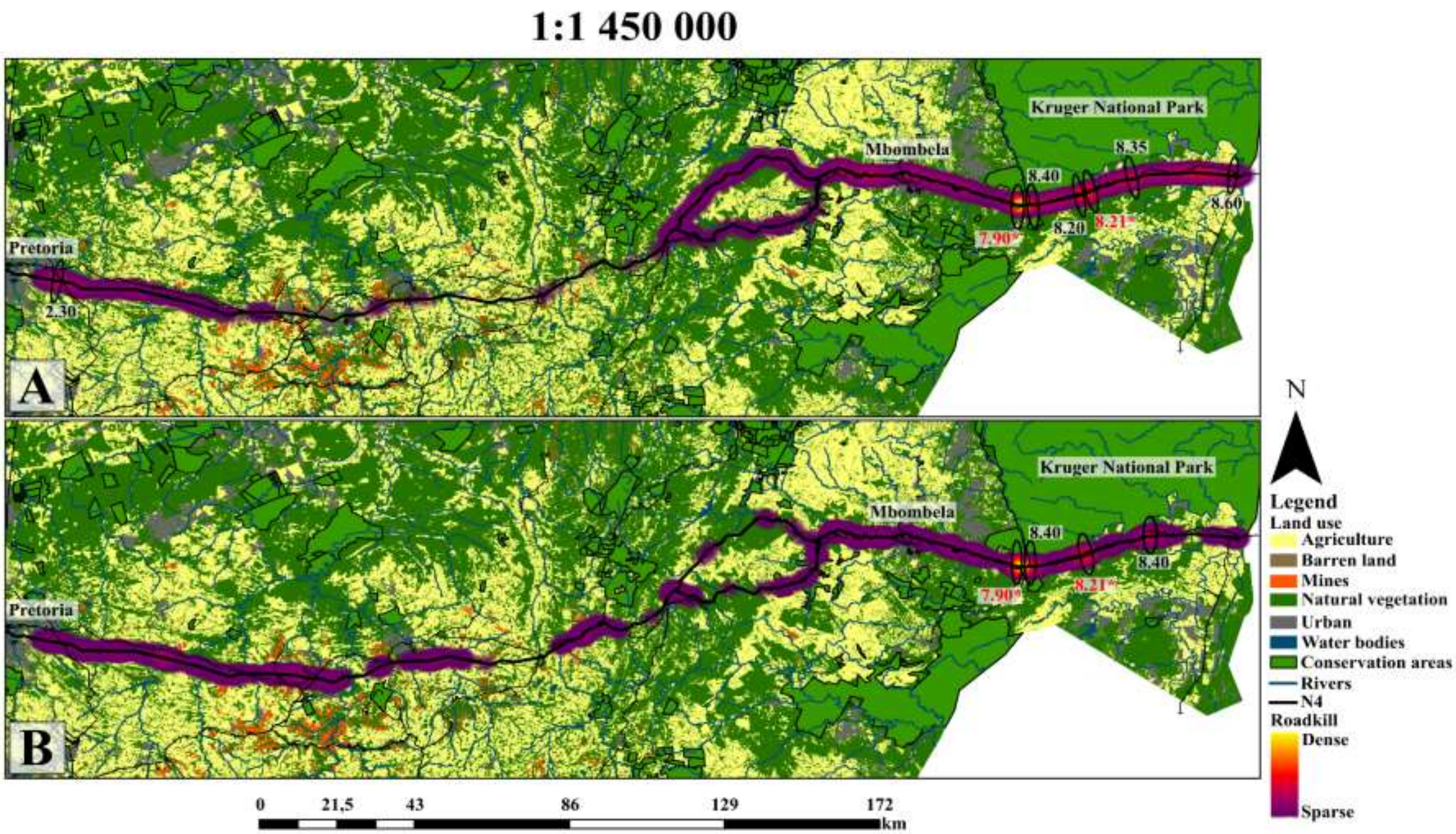

Figure 4.4: Distribution of wildlife (A) and domestic (B) fauna roadkill recorded along the N4 National Highway (N4 toll route) from February 2017 to December 2023. (Note: Black ovals represent significant mortality hotspots, and * represents hotspots present in both groups).

4.4.3. The influence of habitat variables on vertebrate roadkill

The effect of nominal habitat characteristics on the occurrence of domestic and wildlife fauna roadkill incidents indicated a significant difference for biome (Kruskal-Wallis, chi2 = 103.03, df = 5, $p < 0.001$) and land-use type (Kruskal-Wallis, $chi^2 = 153.44$, df = 11, $p < 0.001$). The results of this study further showed that roadkill magnitudes for domestic fauna along forested areas were not significantly different from any other biome/fauna type interaction, whilst in the savanna biome, wildlife roadkill were significantly different to all other biome/fauna type interactions (Table 4.2). Moreover, our results indicated that road sections along the N4 toll route that intersect landscapes with natural vegetation cover showed significantly higher wildlife road mortalities than sections that were human-modified (Table 4.3).

Table 4.2: Kruskal-Wallis test results for multiple interactions between biome and domestic and wildlife road mortality along the N4 toll route, South Africa, in the present study.

	Forest: Domestic	**Grassland: Domestic**	**Savanna: Domestic**	**Forest: Wildlife**	**Grassland: Wildlife**
Grassland: Domestic	1.000	-			
Savanna: Domestic	0.517	0.004***	-		
Forests: Wildlife	1.000	0.316	0.001***	-	
Grassland: Wildlife	0.839	0.275	1.000	0.015**	-
Savanna: Wildlife	0.344	0.000***	0.000***	0.000***	0.000***

Table 4.3: Kruskal-Wallis test results for multiple interactions between land use and domestic and wildlife road mortality along N4, South Africa.

	Agriculture: Domestic	**Barren land: Domestic**	**Natural vegetation: Domestic**	**Urban: Domestic**	**Water: Domestic**	**Agriculture: Wildlife**	**Barren land: Wildlife**	**Natural vegetation: Wildlife**	**Urban: Wildlife**
Barren land: Domestic	0.073	-							
Mines: Domestic	1.000	1.000							
Natural vegetation: Domestic	1.000	0.052	-						
Urban: Domestic	1.000	0.109	1.000	-					
Water: Domestic	0.011**	1.000	0.007***	0.019**	-				
Agriculture: Wildlife	0.001***	0.000***	0.001***	0.022**	0.000***	-			
Barren land: Wildlife	1.000	1.000	1.000	1.000	1.000	0.000***	-		
Mines: Wildlife	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
Natural vegetation: Wildlife	0.000***	0.000***	0.000***	0.000***	0.000***	0.013**	0.000***	-	
Urban: Wildlife	0.011**	0.000***	0.016**	0.111	0.000***	1.000	0.000***	0.028**	-
Water: Wildlife	1.000	1.000	1.000	1.000	0.413	0.000***	1.000	0.000***	0.001***

The effects of continuous habitat characteristics on the occurrence of wildlife and domestic fauna roadkill incidents showed a significant effect for elevation (Mann-Whitney, W = 275893, $p < 0.001$). For the recorded domestic and wildlife roadkill, the variables distance from waterbodies (W = 254222, p = 0.039), powerlines (W = 214770, p = 0.003), substructures (W = 217582, p = 0.010), and superstructures (W = 219908, p = 0.022) showed significant variation, respectively. The RDA test found that the significant continuous variables (constraining variables) only accounted for 25% of the variation, while the remaining 75% of the variation was unconstrained, indicating the need for robust data collection of habitat and climatic variables. The model had an adjusted R^2 score of 0.233 and a model significance of p = 0.01 (F = 49.558; df = 16.49), and Eigenvalues of 16.49 and 49.58 for Axis RDA1 and PC1, respectively. However, despite the low R^2 score and low importance (Supplementary Information Figure S4.2) of variation, a clear separation can still be seen in the distribution of the number of wildlife and domestic road mortalities influenced by the measured factors collectively (Figure 4.6).

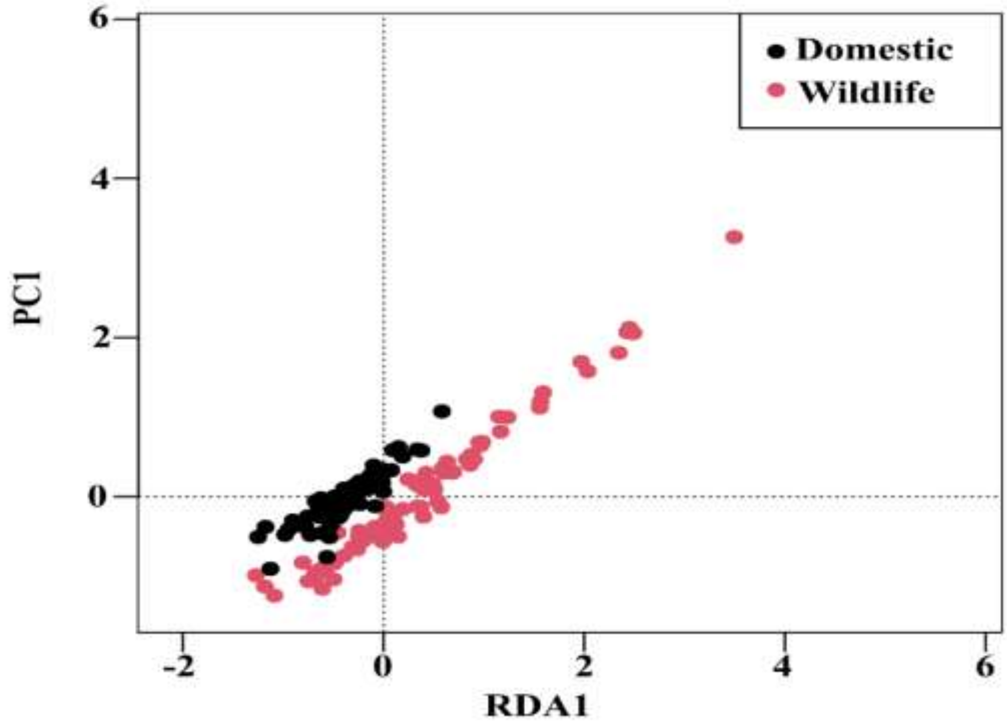

Figure 4.6: Redundancy analyses of continuous variables affecting wildlife and domestic fauna road mortalities along N4 highway, South Africa, in the present study.

4.5 Discussion

This study further confirmed that although the N4 National Highway intersects landscapes outside formally protected areas, over 100 faunal species were reported dead because of wildlife-vehicle collisions. Whilst several wildlife roadkill hotspot areas were identified by examining the spatial structural patterns of vegetation cover and land-use types, the majority of these hotspots emerged along road sections that are adjacent to critical conservation areas, including the Kruger National Park. This emphasises the urgent need for prioritising systematic conservation planning that will address transport-related biodiversity impacts, particularly in critical biodiversity areas in South Africa (Hlatshwayo et al. 2024).

4.5.1 Mortality demographics

While the overall findings of our study showed that mammals were the most abundant vertebrate taxon affected by WVCs (n = 611, 53.4%), in terms of species diversity, birds showed the greatest richness (51 avian species), followed by mammals (37 species) and reptiles (23 species). These findings were expected because the Mpumalanga Province, where the surveyed road extends for longer lengths, is known to have a rich diversity of birds (over 600 species) (BirdLife South Africa 2025). This also supported previous studies that reported that species exhibiting abundant population densities within a wider landscape and their movement patterns across it are more frequently affected by roadkill (Sadleir and Linklater 2016; Miranda et al. 2025). For mammals, we suggest that the high roadkill magnitude could be associated with their daily movements to access essential ecological resources within their individual home ranges, particularly for resident species. Thus, this may include movements for accessing foraging grounds, water sources, or roosting (van der Grift and van der Ree 2015). Furthermore, during annual seasonal migrations, terrestrial mammals often migrate to other habitats for searching breeding mates, wintering grounds, as well as calving areas (Avgar et al. 2014; Leclerc et al. 2021). Whilst these movements are critical for completing the life cycles of species, they often expose them to roadkill casualties as their habitats are fragmented by road corridors. As explained by Van der Grift and van der Ree (2015), animals could attempt crossing highways occasionally when juveniles often undertake long-distance movements to start their own territories. As a result, these roaming species are exposed to networks of road corridors, increasing the potential of wildlife roadkill incidents.

Although only 13.7% of roadkill were reptiles in our study, snakes accounted for the highest roadkill (Supplementary Information Table S4.1). Several factors may contribute to the roadkill casualties of reptiles. Certain ecological traits such as body size, movement speed, thermoregulation, and feeding behaviour are important for the survival and adaptation of reptile and amphibian species; however, these traits may also affect the probability of roadkill casualties for these species (Langen et al. 2009; Rahhal et al. 2023; Kouris et al. 2024). Several studies have reported that for thermoregulation needs, snakes tend to bask on road surfaces for warmth (Andrews et al. 2005; Chyn et al. 2019; Rahhal et al. 2023), making them vulnerable to roadkill casualties. Moreover, incidents of intentional roadkill of snakes are possible (Chyn et al. 2019), and these may be because of existing African myths, phobias and negative attitudes portrayed by people towards them, and could be a source of intentional snake roadkill. Whilst no amphibian roadkill was reported, several studies report that numerous smaller vertebrate fauna, such as frogs and toads, are often underestimated during roadkill surveys as a result of their small body size which causes imperfect detections (Chyn et al. 2019; Hallisey et al. 2022; Pinto et al. 2024), we suggest that this was the case in our study considering the speed at which the surveys were conducted (~60 km/h).

Road infrastructure affects the structure and dynamics of ecosystem functioning and poses direct effects on threatened species and ecosystems. The findings of this study have revealed that a total of seven species of conservation priority were impacted by roadkill. Noting the considerable number of threatened species with declining populations that are vulnerable to roadkill on the studied national highway, efforts for improving biodiversity accounting and compensation in the transportation sector are needed in South Africa (Hlatshwayo et al. 2024). This region comprises a rich biodiversity yet impacted by widespread deforestation (Duku and Hein, 2021), poaching (Minnaar and Herbig, 2018) and habitat exploitation (Skowno et al. 2021). Strategies for combining species vulnerabilities, road mortality and species movement data with existing road maps in South Africa could help identify areas where ecological connectivity could compensate for biodiversity loss (where road infrastructure can result in important loss of biodiversity).

4.5.2 Spatial analyses on the distribution of vertebrate roadkill

The distribution pattern of vertebrate roadkill in our study area showed that roadkill incidents were not randomly distributed across space but rather indicated spatial clustering patterns of roadkill incidents on specific road locations as reported by (Clevenger et al. 2003; Hlatshwayo et al. 2023; Kouris et al. 2024). We suggest that this distribution pattern was influenced by several environmental and ecological factors, such as land-use, habitat and landscape characteristics. Several studies reported that travel restrictions during the COVID-19 pandemic resulted in the reduction of wildlife mortalities on roads (Driessen 2021; Pokorny et al. 2022). Contrary to the findings of our study, the COVID-19 lockdown and its effects on vehicular traffic did not affect the number of vertebrate roadkill during the COVID-19 pandemic period. The multiple regression analysis has indicated that the roadkill rates of wildlife fauna remained significantly higher per year, including during the COVID-19 period (2020-2022). Furthermore, the roadkill rates of domestic fauna were significantly lower than the roadkill rates of wildlife fauna. This suggests that wildlife fauna were more vulnerable to roadkill incidents than domestic fauna, and this pattern could be a result of the abundant wildlife population in this region.

Our results showed that ecological seasons did not have a meaningful effect on the occurrence of fauna roadkill incidents, with no significance found between seasons within each fauna type. Although this was contrary to our prediction, it may indicate that the majority of the reported species are resident and abundant throughout the year within the wider landscape, as different species portray different magnitudes of change and seasonal patterns (Pokorny et al. 2022). Moreover, although season did not significantly influence the occurrence of vertebrate roadkill, a significant difference was found between fauna types, with wildlife fauna indicating an average mortality rate of 0.169 carcass-km and domestic fauna showing an average mortality rate of 0.062.

4.5.3 Environmental, landscape and roadkill hotspots effect

The assessment of the spatial structural patterns of vegetation cover (habitat type), land-use (cropland, settlement areas) and landscape variables adjacent to where wildlife roadkill had occurred is critical for estimating and mapping hotspot areas. Moreover, the assessment of these variables is essential for developing mitigation strategies for reducing wildlife roadkill incidents (van der Grift and van der Ree 2015; Lombardi et al. 2023; Lehnen et al. 2024). The findings of our study showed that vegetation and habitat composition influenced vertebrate roadkill, with significant differences found for biome and land use types in the surroundings where roadkill incidents had occurred. While this supports our prediction, our findings further indicated that the roadkill of wildlife fauna was prominent adjacent to areas with natural vegetation cover along the N4 National Highway. This indicated that adjoining land cover type has an effect on the distribution of wildlife roadkill species and is consistent with several road ecology studies that found a strong association between land cover and roadkill casualties (Seo et al. 2015; Murphy and Xia 2016; Hlatshwayo et al. 2023). The justification of such an association could be that wildlife roadkill incidents are most likely to occur at locations that provide essential resources, such as habitat, refuge, and food, that sustain the needs and interests of the available species.

Topographical variables such as elevation strongly correlated with the occurrence of vertebrate roadkill in our study area. In addition, the distance from the waterbody as an environmental factor and several human-made structures closer to the highway significantly influenced roadkill patterns along the study road. However, the RDA test found that the significant continuous variables (constraining variables) only accounted for 25% of this variation, while the remaining 75% of the variation was unconstrained. This could be a result of missing explanatory variables, such as data on climatic and daily traffic volume variables, indicating the need for further studies that will expand by providing a comprehensive analysis of the effects of traffic volume, habitat, and climatic variables on vertebrate roadkill.

Seven major wildlife roadkill hotspot areas emerged in the study area (Figure 4.4) and a further four hotspots for domestic fauna were identified (Figure 4.5), with all the hotspots emerging along the highest-speed road sections (> 100 km/h), which was expected. The one in the third kilometre of section two occurred along a 120 km/h speed limit zone. The one that emerged in the 90th kilometre of section seven and those that emerged in section eight of the highway were all within a 100 km/h speed limit zone. This supports the findings of previous studies that asserted that wildlife roadkill rates increase with higher speed limits (Hobday 2010; Lester 2015; Collinson et al. 2019). This is mainly because for hotspots that have high posted-speed-limit signage, vehicle drivers may not have enough time to navigate and manoeuvre the vehicle away from the path of an animal when travelling at high speeds, leading to roadkill. No significant cold spots were identified, and an overall similarity of 0.2778 was recorded between hotspot analyses with an expected overall similarity of 0.2285. This suggests that the surveyed highway poses a significant impact on biodiversity and conservation, which motivates the urgent need for mitigation strategies. Our findings of the hotspots offer indications of potential key areas where prioritisation for mitigation strategies should be focused.

4.6 Conclusions

Our study presents an analysis of vertebrate roadkill data that were collected by route patrol staff to present the spatiotemporal patterns of WVCs in a National Highway that is located outside of a formally protected area, yet intersecting areas that are critical for biodiversity. By doing so, the study demonstrated that capacitating route patrol staff through training could help address the lack of a robust database of wildlife roadkill in South Africa, which prevents proper identification of hotspots for the strategic implementation of mitigation measures. This study recommends that such data collection methods are supported and adopted by the i) Roads and Transport, ii) Forestry, Fisheries and the Environment departments, iii) South African Roads Agency Limited (SANRAL) and iv) South African National Biodiversity Institute (SANBI) through a collaborative approach as this will improve biodiversity and transport sustainability mandates in South Africa.

Although the data generated in our study indicated that the seasonal distribution of vertebrate roadkill did not change with changing ecological seasons, wildlife road mortality rates remained significantly higher per year. This indicated that the majority of the species were resident within the wider landscape and interact with the highway throughout the year. This showed that mitigation interventions are needed along certain portions of the highway, particularly along the identified hotspot areas. This could be achieved by improving the landscape connectivity to allow safe animal movement through tunnels connecting the landscape (van der Grift and van der Ree 2015; Hlatshwayo et al. 2024; Cormac et al. 2025). Although several environmental and landscape variables were found to affect roadkill distribution significantly, our study could not get daily traffic volume data for the study road, and this has limited the quantitative analysis of the effects of traffic volume on wildlife roadkill rates. We acknowledge this as one of the study's limitations. Whilst WVCs result in biodiversity loss, they also damage road infrastructure and certainly affect humans. The incidents of WVCs may become a road safety concern when drivers and passengers get injured during these collisions. This highlights a need for further studies to assess the cost-benefit analysis of these collisions, emphasising the need to consider possible mitigations.

CRediT authorship contribution statement

Thabo I. Hlatshwayo: Conceptualisation, Methodology, Data collection, Formal analysis, Data curation, Writing – original draft. Cameron T. Cormac, Manqoba M. Zungu, Wendy J.

Collinson-Jonker: Conceptualisation, Methodology, Formal analysis, Writing – review and editing, Supervision. Colleen T. Downs: Conceptualisation, Methodology, Formal analysis, Writing – review and editing, Funding, Project administration, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this study.

4.7 Acknowledgements

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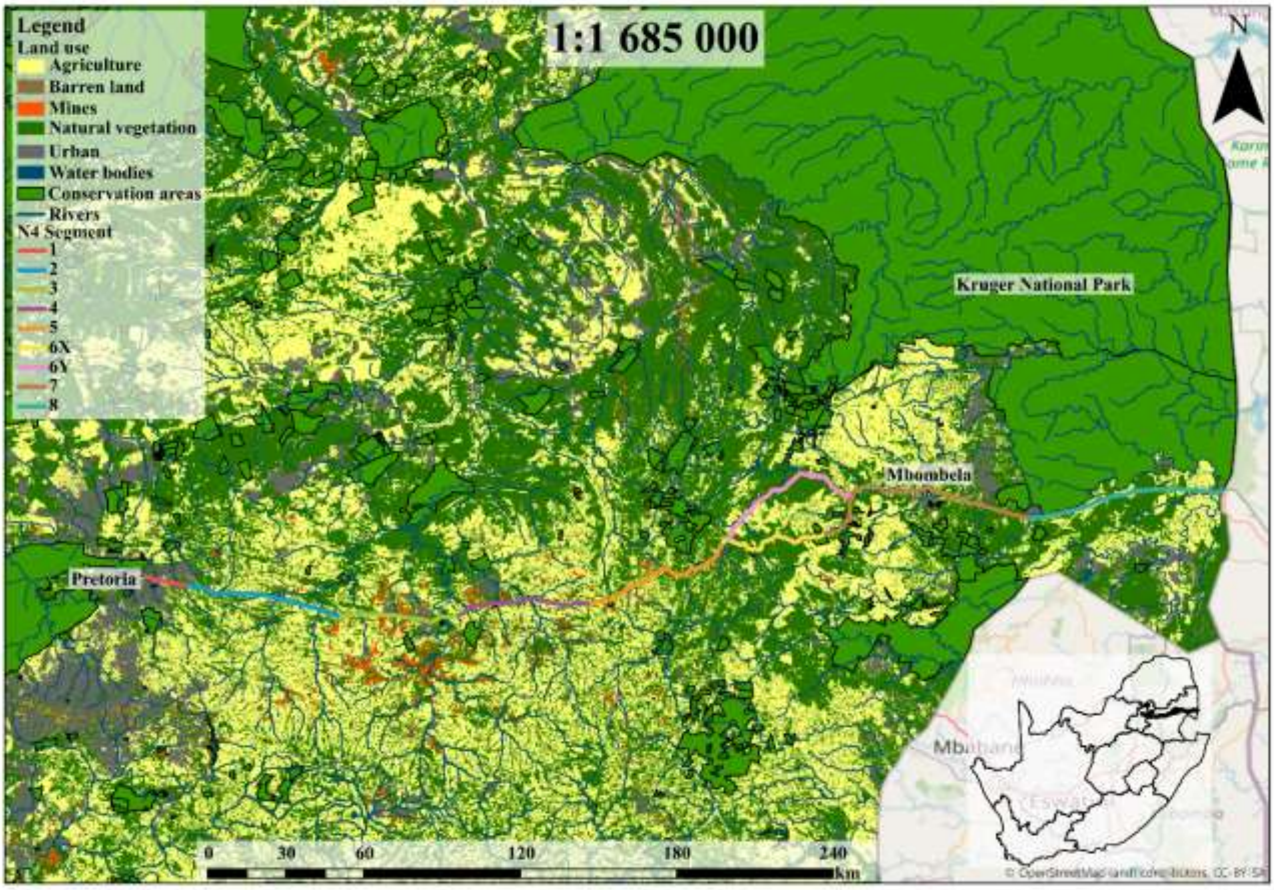
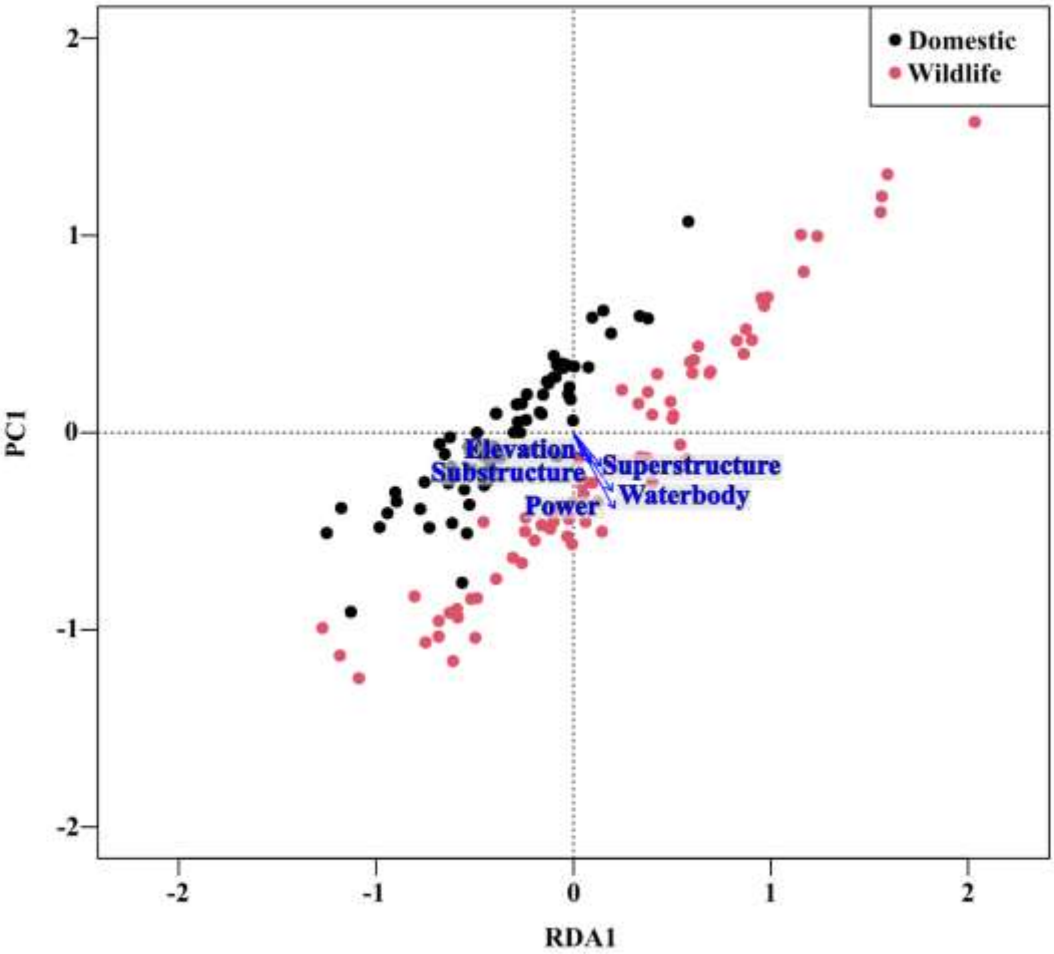
4.9 Supplementary information



Supplementary Information Figure S4.1: South African National Highway Four (N4) road maintenance segments.



Supplementary Information Figure S4.2: Distribution of the effect of measured continuous environmental factors on wildlife and domestic fauna road mortality along N4 highway, South Africa.

Supplementary Information Table S4.1: Vertebrate species identified as reported from road mortalities along the N4 National Highway (N4 Toll route) in South Africa between February 2017 and December 2023. (Activity patterns were modified from Stuart & Stuart 2015)

Scientific name	**Species**	**Activity**	**Conservation Status**	**Number of roadkill**
		Mammalia Wildlife fauna		
Orycteropus afer	Aardvark	Nocturnal	LC	1
Proteles cristata	Aardwolf	Nocturnal	LC	3
Civettictis civetta	African civet	Nocturnal	LC	36
Felis silvestris cafra	African wild cat	Nocturnal	LC	16
Lycaon pictus	African wild dog	Diurnal	CR	1
Thryonomys swinderianus	Cane rat	Nocturnal	LC	48
Vulpes chama	Cape fox	Nocturnal	LC	3
Hystrix africaeaustralis	Cape porcupine	Nocturnal	LC	8
Caracal caracal	Caracal	Nocturnal	LC	3
Papio ursinus	Chacma baboon	Diurnal	LC	4
Aonyx capensis	Cape clawless otter	Diurnal	NT	5
Sylvicapra grimmia	Common duiker	Both	LC	9
Epomophorus wahlbergi	Fruit-bat Wahlberg's epauletted	Nocturnal	LC	4
Genetta maculata	Large-spotted genet	Nocturnal	LC	59
Genetta genetta	Small-spotted genet	Nocturnal	LC	37
Tragelaphus strepsiceros	Greater kudu	Diurnal	LC	1
Mellivora capensis	Honey badger	Diurnal	LC	2
Canis mesomelas	Black-backed Jackal	Both	LC	49
Canis adustus	Side-striped jackal	Both	LC	3
Mungos mungo	Banded mongoose	Diurnal	LC	22
Helogale parvula	Dwarf mongoose	Diurnal	LC	7
Atilax paludinosus	Marsh mongoose / Water mongoose	Nocturnal	LC	17
Herpestes sanguineus	Slender mongoose	Diurnal	LC	17
Ichneumia albicauda	White-tailed mongoose	Diurnal	LC	26
Cynictis penicillata	Yellow Mongoose	Diurnal	LC	2

Procavia capensis	Rock hyrax	Diurnal	LC	3
Lepus saxatilis	Scrub hare	Nocturnal	LC	138
Leptailurus serval	Serval	Nocturnal	LC	48
Redunca arundinum	Southern reedbuck	Nocturnal	LC	2
Crocuta crocuta	Spotted hyaena	Both	LC	1
Xerus inauris	Ground squirrel	Diurnal	LC	1
Paraxerus cepapi	Tree squirrel	Diurnal	LC	2
Ictonyx striatus	Striped polecat	Nocturnal	LC	3
Otolemur crassicaudatus	Thick-tailed greater galago	Nocturnal	LC	49
Galago senegalensis	Lesser galago	Nocturnal	LC	1
Chlorocebus pygerythrus	Vervet monkey	Diurnal	LC	60
Cercopithercus mitis albogularis	Samango Monkey	Diurnal	LC	2
Phacochoerus africanus	Warthog	Diurnal	LC	1
Aepyceros melampus	Impala	Diurnal	LC	1
Cephalophus natalensis	Natal red duiker	Diurnal	LC	1
Hippopotamus amphibius	Hippopotamus	Nocturnal	VU	2
Syncerus caffer	African savanna buffalo	Diurnal	EN	1
Unknown	Unknown Bat	Unknown	Unknown	1
Unknown	Unknown Fox	Nocturnal	Unknown	1
Unknown	Unknown Mongoose	Unknown	Unknown	10
Unknown	Unknown Rabbit	Unknown	Unknown	4
Unknown	Unknown Mammal	Unknown	Unknown	14
Domestic fauna				
Felis catus	Cat	Both	LC	130
Canis lupus familiaris	Dog	Diurnal	LC	321
Livestock				451
Bos taurus	Cow	Diurnal	LC	3
Capra aegagrus hircus	Goat	Diurnal	LC	5
		Aves		
Upupa epops	Common hoopoe	LC	Diurnal	4

Lybius torquatus	Black-collared barbet	LC	Diurnal	2
Tchagra senegalus	Black-crowned tchagra	LC	Diurnal	2
Elanus caeruleus	Black-winged kite	LC	Diurnal	4
Crithagra atrogularis	Black-throated canary	LC	Diurnal	1
Centropus burchelli	Buchell's coucal	LC	Diurnal	32
Bubulcus ibis	Cattle egret	LC	Diurnal	2
Turdus merula	Common blackbird	LC	Diurnal	1
Pycnonotus tricolor	Dark-capped bulbul	LC	Diurnal	8
Streptopelia capicola	Cape Turtle dove	LC	Diurnal	6
Spilopelia senegalensis	Laughing dove	LC	Diurnal	32
Turtur tympanistria	Tambourine dove	LC	Diurnal	1
Nicator gularis	Eastern nicator	LC	Diurnal	1
Corythaixoides concolor	Grey go- away bird	LC	Diurnal	3
Bostrychia hagedash	Hadeda ibis	LC	Diurnal	1
Numida meleagris	Helmeted guineafowl	LC	Diurnal	28
Acridotheres tristis	Common myna	LC	Diurnal	2
Ispidina picta	African pygmy kingfisher	LC	Diurnal	1
Halcyon albiventris	Brown-hooded kingfisher	LC	Diurnal	6
Turdus libonyana	Kurrichane thrush	LC	Diurnal	2
Vanellus senegallus	African wattled lapwing	LC	Diurnal	1
Vanellus coronatus	Crowned lapwing	LC	Diurnal	6
Accipiter badius	Little-banded goshawk (Shrika)	LC	Diurnal	2
Caprimulgus pectoralis	Fiery-necked nightjar	LC	Diurnal	9
Caprimulgus tristigma	Freckled nightjar	LC	Diurnal	1
Tyto capensis	African grass owl	VU	Nocturnal	4
Strix woodfordii	African wood owl	LC	Diurnal	3
Tyto alba	Barn owl	LC	Nocturnal	34
Asio capensis	Owl marsh	LC	Nocturnal	15
Ptilopsis granti	Southern white-faced owl	LC	Nocturnal	2
Bubo africanus	Spotted eagle owl	LC	Nocturnal	65
Otus senegalensis	African scops owl	LC	Nocturnal	2

Glaucidium perlatum	Pearl-spotted owlet	LC	Nocturnal	3
Columba livia	Pigeon feral	LC	Diurnal	4
Treron calvus	African green-pigeon pigeon	LC	Diurnal	5
Gallirex porphyreolophus	Purple-crested turaco	LC	Diurnal	5
Cisticola chiniana	Rattling cisticola	LC	Diurnal	1
Onychognathus morio	Red-winged starling	LC	Diurnal	1
Coracias garrulus	European roller	LC	Diurnal	13
Coracias caudatus	Lilac-breasted roller	LC	Diurnal	5
Anthus brachyurus	Short-tailed pipit	LC	Diurnal	1
Ploceus velatus	Southern masked weaver	LC	Diurnal	8
Passer domesticus	House sparrow	LC	Diurnal	1
Passer diffusus	Southern grey-headed sparrow	LC	Diurnal	1
Astur melanoleucus	Black sparrowhawk	LC	Diurnal	1
Accipiter minullus	Little sparrowhawk	LC	Diurnal	1
Colius striatus	Speckled mousebird	LC	Diurnal	5
Ortygornis sephaena	Crested francolin	LC	Diurnal	2
Pternistis natalensis	Natal spurfowl	LC	Diurnal	5
Pternistis swainsonii	Swainson's spurfowl	LC	Diurnal	1
Apus affinis	Little swift	LC	Diurnal	1
Apus caffer	White-rumped swift	LC	Diurnal	6
Prinia subflava	Tawny-flanked prinia	LC	Diurnal	1
Burhinus capensis	Spotted thick-knee	LC	Diurnal	1
Burhinus vermiculatus	Water thick-knee	LC	Diurnal	4
Uknown	Unknown bee eater	Unknown	Diurnal	1
Uknown	Unknown dove	Unknown	Diurnal	4
Uknown	Unknown eagle	Unknown	Unknown	2
Uknown	Unknown hawk	Unknown	Diurnal	1
Uknown	Unknown nightjar	Unknown	Diurnal	2
Uknown	Unknown owl	Unknown	Unknown	16
Uknown	Unknown roller	Unknown	Diurnal	1
Uknown	Unknown spurfowl	Unknown	Diurnal	1

Uknown	Unknown swift	Unknown	Diurnal	1
Uknown	Unknown raptor	Unknown	Unknown	1
Uknown	Unknown bird	Unknown	Unknown	41
Vanellus armatus	Lapwing blacksmith	LC	Diurnal	1
Dessonornis caffer	Cape robin-chat	LC	Diurnal	1
Fraseria plumbea	Grey tit-flycatcher	LC	Diurnal	1
Cecropis semirufa	Red- breasted swallow	LC	Diurnal	1
Cercotrichas leucophrys	White-browned scrub robin	LC	Diurnal	1
Livestock				
Gallus gallus domesticus	Chicken	LC	Diurnal	10

Reptilia

Chamaeleo dilepis	Flap-necked Chameleon	LC	Diurnal	1
Varanus niloticus	Nile monitor lizard	LC	Diurnal	26
Varanus albigularis	Rock monitor lizard	LC	Diurnal	10
Crocodylus niloticus	Nile crocodile	LC	Diurnal	3
Dendroaspis polylepis	Black mamba	LC	Diurnal	18
Dispholidus typus	Boomslang	LC	Diurnal	1
Boaedon fuliginosus	Brown house snake	LC	Diurnal	3
Telescopus semiannulatus	Common tiger snake	LC	Nocturnal	1
Philothamnus semivariegatus	Green-spotted bush snake	LC	Diurnal	2
Pseudaspis cana	Mole snake	LC	Diurnal	6
Naja mossambica	Mozambique spitting cobra	LC	Diurnal	3
Philothamnus natalensis	Natal green snake	LC	Diurnal	1
Psammophis mossambicus	Olive grass snake	LC	Diurnal	1
Bitis arietans	Puff adder	LC	Nocturnal	8
Dasypeltis scabra	Rhombic egg eater	LC	Nocturnal	2
Naja annulifera	Snouted cobra	LC	Nocturnal	2
Python natalensis	Southern African python	VU	Diurnal	56
Thelotornis capensis	Southern twig snake	LC	Diurnal	3
Psammophylax tritaeniatus	Striped grass snake	LC	Diurnal	1

Pelusios sinuatus	Serrated hinged terrapin	LC	Diurnal	6
Kinixys natalensis	Natal hinged-back tortoise	VU	Diurnal	3
Kinixys spekii	Speke's hinged tortoise	LC	Diurnal	3
Acanthocercus atricollis	Southern tree agama	LC	Diurnal	4
Unknown	Unknown lizard	Unknown	Unknown	4
Unknown	Unknown snake	Unknown	Unknown	8

CHAPTER 5

Evaluating the spatial and temporal patterns of wildlife use of existing road drainage underpass structures along a major South African highway

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Running header: Wildlife use of existing road-underpass culverts for crossing road-fragmented landscapes

5.1 Abstract

Changing climatic conditions influence animal movement patterns, causing numerous faunal species to migrate frequently in search of important ecological resources. In an environment increasingly fragmented by roads, such movements could potentially result in a deathtrap for animals because of wildlife-vehicle collisions and the lack of connectivity corridors. To mitigate the impact of road fragmentation on biodiversity, wildlife crossing structures are increasingly being constructed along identified hotspots, along with associated roadside funnel fencing, to improve connectivity across fragmented landscapes. Noting the urgent demand for promoting ecological connectivity in the planning of eco-friendly transportation infrastructure, we evaluated wildlife use of existing road drainage underpass structures that are not purposely built for wildlife using cameras along a roadkill hotspot area on the N4 highway in South Africa. The underpasses comprised three circular, two rectangular, and one box culverts, as well as one large bridge. These were monitored continuously using mounted camera traps from December 2022 until October 2024. The overall results showed that a total of 1,480 faunal visits were recorded across the monitored culverts, with mammals accounting for the majority of the recorded visits (97.0%, 1,435). The remaining 3% was of non-mammal species (Amphibians – 23, 1.6%; Birds- 21, 1.4%; Reptiles- 1, 0.1%). A total of 30 small-to-medium sized vertebrate species were recorded using the monitored road drainage structures, with *Galerella sanguinea*, *Cynictis penicillata*, *Hystrix africaeastralis* and *Genetta tigrine* indicating the highest crossing index. The Cape clawless otter was the only threatened species detected using the monitored culverts. While the majority of the animal visits were complete crossings, the structure that had a roadside barrier fencing was predominantly used by faunal species. Underpass crossings with a waterbody underneath were less preferred by terrestrial animals, only *Aonyx capensis*, *Atilax paludinosus* and several water birds used them for crossing. Our findings are helpful to (1) guiding monitoring and modifying existing under-road

culverts for reducing road-related biodiversity effects in South Africa and (2) offering insights into the constraining variables that influence crossing structure index by wildlife.

Keywords: Camera trapping, drainage culverts, habitat fragmentation, wildlife crossing structures, wildlife movement, road ecology

5.2 Introduction

Globally, habitat degradation and loss through landscape fragmentation are considered the main drivers of the biodiversity loss crisis (IUCN 1980; Clevenger et al. 2001; Hilty et al. 2020) and have continuously deteriorated the quality of natural habitats inside and outside protected areas. Among other factors, human development needs, particularly linear infrastructure projects such as roads and highways, railways and powerlines, are the major drivers of unsustainable ecosystem fragmentation and deterioration (Forman & Alexander, 1998; Clevenger et al., 2001; Smith et al., 2015; Hlatshwayo et al., 2024). The negative impacts of transport infrastructure on the biological components of the environment disrupt the functionality of the ecological network by fragmenting viable ecosystems. So, habitat patches become isolated, causing barriers to daily wildlife movements and disrupting animal seasonal migration patterns (Forman and Alexander 1998; Coffin 2007; Clevenger and Ford 2010; Gagnon et al. 2015). Thus, they further accelerate wildlife mortalities as a result of wildlife-vehicle collisions (WVCs) (Forman et al. 2003; Collinson et al. 2015; Hlatshwayo et al. 2023; Cormac et al. 2025), and further alter animal behavioural patterns (D'Amico et al. 2015). Poor considerations for a sustainable land-use planning approach during transport corridor planning and development undermine the sustainability mandates of halting biodiversity loss and conserving the quality of the environment through mainstreaming ecological connectivity (Ament et al. 2023; Hlatshwayo et al. 2024; Papp et al. 2024). As such, this results in restricted free movement of wildlife species, making it difficult for faunal species to maintain a functional ecological network in their landscapes.

To minimise the fragmentation of habitat by roads whilst reducing the mortality of fauna because of WVCs, the construction of wildlife crossing structures (in the form of overpasses or underpasses) has become a common part of transport infrastructure development worldwide. Wildlife crossing structures are critical in interconnecting core areas to promote ecological connectivity by linking isolated wildlife populations and improving road safety (Beier and Noss 1998; Hofman et al. 2018). As biodiversity continues to degrade, including wildlife crossing structures in the structural plan and transport infrastructure design has become increasingly relevant in the sustainable development agenda (Hlatshwayo et al. 2024). Thus, correctly placing wildlife passages along wildlife roadkill hotspots significantly improves human safety, enhances ecosystem connectivity, and promotes sustainable animal movements and seasonal migrations (Bhardwaj et al. 2020; Helldin 2022; Hamilton et al. 2024). However, because of the high costs of implementing wildlife crossing structures (Seiler et al. 2016), transportation agencies are not doing enough to compensate biodiversity loss and monitor transport impacts on biodiversity and include strategies for mitigating transport fragmentation impacts. This is prominent in the global south countries, where the concept of incorporating wildlife crossing corridors in road planning is relatively poor, indicating an urgent need for cost-effective alternatives.

Despite global empirical research on the usefulness of drainage culverts in facilitating safe movements for wildlife in road-fragmented ecosystems, an extensive knowledge void persists in Africa. To date, no robust experimental study has extensively explored the potential of existing drainage culverts in supporting animal movements in transport-fragmented ecosystems in Africa. However, a large part of South African transport corridors (roads and railways) intersect large portions of natural landscapes that are critical areas for biodiversity, increasing levels of fragmentation and incidents of WVC. With the rapidly increasing effects of habitat fragmentation and wildlife-vehicle collisions, the inclusion of connectivity structures (wildlife crossings) in transportation planning has received gradual recognition in the global transportation planning frameworks and sustainability agenda (Georgiadis et al. 2020; Ament et al. 2023; Hlatshwayo et al. 2024). However, transportation agencies and conservation practitioners in South Africa have insufficient information to plan for managing or mitigating the effects of transportation infrastructure on wildlife populations. However, the Department of Roads and Transport, in partnership with the South African Road Agency Limited (SANRAL) and several toll companies, have constructed numerous drainage underpasses in almost all South African road networks for channelling stormwater away from roads. Despite these structures not being purposely built to support wildlife, understanding the functionality benefits they could potentially provide in promoting ecological connectivity along fragmented ecosystems is crucial in improving green transport infrastructure strategies in South Africa.

Thus, our study was conducted to understand the effectiveness of existing road drainage underpass structures along one of the most critical highways in South Africa using camera traps. Our objectives were to 1) quantify the temporal trends in the use of existing road underpass structures by vertebrate species, 2) evaluate how passage dimensions, vegetation cover (habitat), human disturbance level, and availability of waterbody influenced the use of the monitored underpasses by vertebrate species and 3) assess if roadside funnel fencing will influence wildlife use of existing underpass structures. We predicted that small vertebrates (<5 kg) would generally use the monitored structures predominantly and that the structure which had a 500 m roadside funnel fencing installed would have a high use and crossing index (CI) by animals, with a wide variety of species. In addition, we predicted that the section of the road with a fenced culvert would have reduced wildlife mortality concentrations as this portion comprised safe passage corridors for wildlife. Lastly, we provided strategies on how non-wildlife underpass structures may be improved and modified to accommodate wildlife use, with a special focus on vertebrate species.

5.3 Methods

5.3.1 Site selection

We surveyed existing non-wildlife underpass drainage culverts built underneath the N4 National Highway (managed by the Trans African Concession, TRAC) in the Bronkhorspruit section, South Africa. The selected underpass culverts were located along section 2 of the N4 National Highway, a road section that has emerged among the hotspot areas as indicated on the Endangered Wildlife Trust's (EWT) database of wildlife roadkill. The surveyed section is dominated by savanna bushlands, patches of open grasses and several waterbodies and wetland habitats. The area is mainly used for agricultural purposes, both crop production and animal grazing, with several portions of the road section traversing human dwelling areas and industries. The average traffic volume along the surveyed road section was ~ 250 vehicles per hour. The underpass culverts were continuous and less than 4 km apart; moreover, they had varying size dimensions, structural shapes/designs and substrate materials (Supplementary information Table S5.1). Lastly, they were not fenced except for culvert structure 2, which was installed with a 600 m stretch of roadside funnel fencing directing fauna towards the road substructure for the purpose of this study (Fig. 5.1).

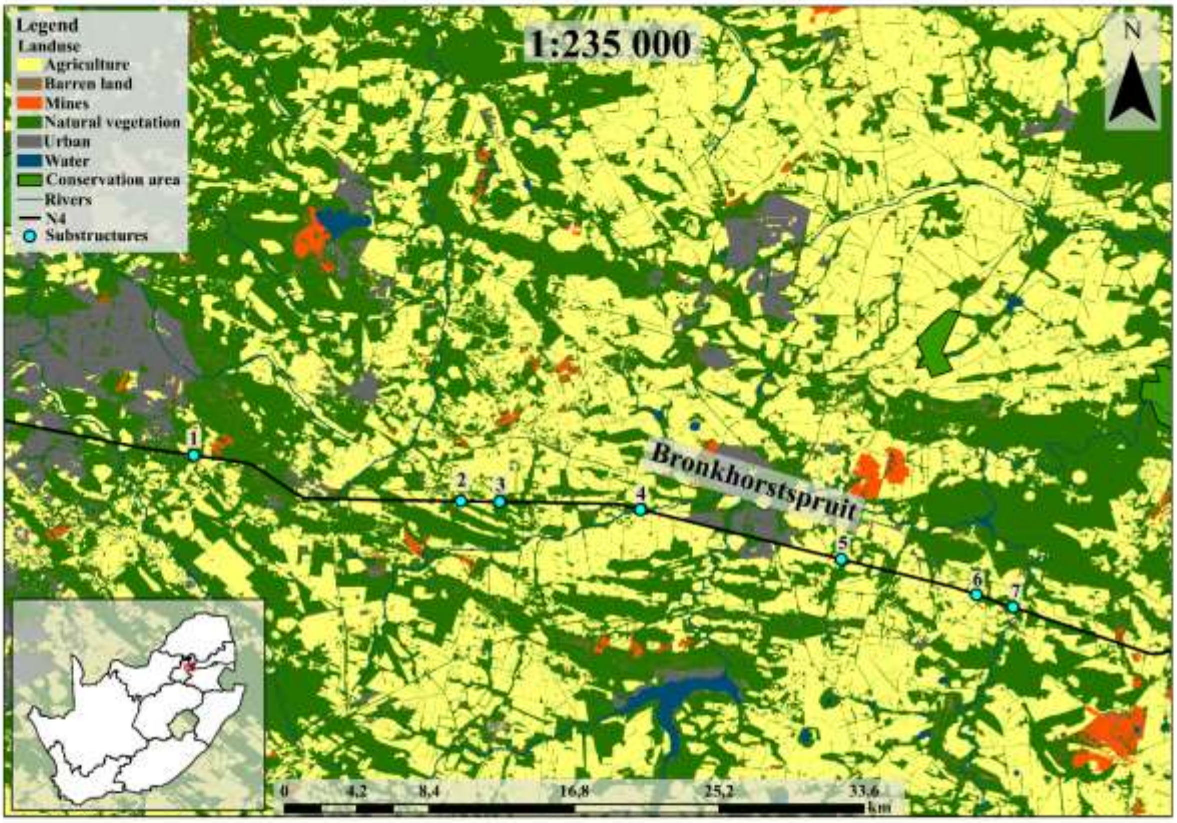

Figure 5.1: Study area map indicating the location of the seven underpass culverts that were monitored for wildlife use using camera traps along section 2 of the N4 National Highway in South Africa

5.3.2 Field method for camera trap monitoring of road underpass culverts

Our method of monitoring animal use of existing road drainage culverts relied on camera trapping as it is generally the most cost-effective method for long-term monitoring (>1 year) of wildlife crossing structures (Ford et al. 2009). D'Amico et al. (2015) argued that camera trapping tools have the advantage of enabling accurate identification of user species for significant analysis and interpretations. The use of camera trapping in this study enabled us to i) establish baseline data of vertebrate use of existing road drainage culverts in a road-fragmented landscape, ii) evaluate trends on the use of existing drainage culverts, iii) compare the factors that influence the crossing Index (CI) and activity of vertebrate species on the monitored underpass culverts.

In this study, infrared motion-detection camera traps (UOVision Green 30 - BLACK FLASH (camo) + built-in viewer) were deployed at each structure at a height of approximately 0.5 m from the ground. The camera placement followed three different techniques depending on the underpass structures' structural design and size dimensions. As such, these included i) placing cameras 4 m away from the culvert, with the camera facing towards the entrances of the crossing structure, 2) attaching the cameras to the walls of the structures and positioning them horizontally at a slight downward angle, to improve detection of small, medium, and large-sized mammals, 3) attaching cameras outside the entrances of the structure against the structure walls, with the camera facing towards the entrances of the crossing structure. We mounted the cameras against a rectangular steel plate that was attached to the walls of the structure or against a rock facing towards the structure using Solidbond QSP quick-set epoxy adhesive. To prevent the risk of camera trap theft, we installed the cameras in metal lockboxes and further pasted laminated notes next to the cameras to inform readers about the scope of our study to discourage vandalism.

At each underpass structure, two camera traps were placed (at each end) to record the activity of animals that approached and exited the underpass, with one bridge structure (B1) that was monitored using four cameras because of its bigger size and openness index. This was to enable the evaluation of 'complete crossing' and 'non-use' of the monitored drainage underpass structures (acceptance/avoidance and rejection behaviour). The camera settings were calibrated to capture a sequence of two images from the detection of the animal by the camera sensor, with an interval of five seconds between sequences, and were kept in full-time operation for the duration of the monitoring period (1064 days from December 2022 to October 2024). We conducted monthly camera trap maintenance fieldwork to download data, change secure digital (SD) memory cards, and replace batteries. In addition to monitoring road underpass structures, data on wildlife roadkill in the study area was gathered since 2017, including during our monitoring period for this study.

5.3.3 Image analytical methods

After processing the camera trap images obtained from the monitored underpass culverts, each camera trap image was carefully screened by the leading researcher and identified to species levels following the field guides of Stuart and Stuart (2015) for mammals, Sinclair et al. (2020) for birds and Alexander and Marais (2013) for reptiles and further assistance in species identification was obtained from various research experts. Each camera trap image depicting an animal was assessed for the following: date, time, temperature, species, number of animals in the group, and direction of movement. During the image screening process, detection events were analysed and recorded; this consisted of either one or more individuals of the same species at a site within specified time intervals. In cases where individual animals of the same species were captured using the culvert together, the event was recorded as a single detection, as their activity was likely to be interdependent (Allen et al. 2013). In a detection event in which images of the same species captured at the same culvert were encountered concurrently, they were only considered independent if they were separated by 30 min. Camera images with an animal that we could not identify to species with certainty were not included in analyses. As two cameras were deployed at each underpass culvert, we relied on imagegraph timestamps to avoid counting a single detection event more than once. The Underpass Crossing Index (UCI) for each species was deduced by adapting the method of Abra et al. (2020):

$$\text{UCI} = \left(\frac{\text{sum of the number of complete and unknown crossings by a given species}}{\text{number of days the structures were monitored}}\right)$$

5.3.4. Analyses

We made heat maps displaying a 50 m radius around each substructure to display the density of visitation of fauna at each of the seven monitored structures, with produced maps displaying wet season (September to April), dry season (May to August), mammalian and non-mammalian terrestrial vertebrate substructure visitation. We extracted habitat characteristics for each record from the region's Geographical Information System (GIS) layers, including the distance to running and standing water bodies, surrounding road substructures, railways, powerlines, and conservation areas. In addition to elevation, surrounding biome, and major land use types, distance data were extracted using the near tool in ArcGIS Pro 3.0 (ESRI 2024). Elevation data were collected using the extract surface information tool in ArcGIS Pro 3.0. Biome information was collected by spatially joining the most recent national vegetation map (SANBI 2018) with records for positions and land use information collected from the most recent land use raster map (DFFE 2022) using the extract values to point tool in ArcGIS Pro. We obtained information on rivers, railways and conservation areas using GIS layers retrieved from Google Street Map® (HOT 2025). We conducted all statistical analyses using the R (R Core Team, 2021) plug-in within Google Collab (Sukhdeve et al. 2023). We conducted Kruskal-Wallis tests to determine the significance of the number of daily visits between substructures, in addition to season and taxa (mammalian and non-mammalian) structure visitation and the effect of fence presence on structure visitation. Additionally, we conducted a Kruskal-Wallis test to determine the significance of the number of each structure usage type (complete, partial, exploratory). These Kruskal-Wallis tests were done using the dplyr package (Wickham et al. 2023) because the data did not match normality assumptions. Dunn’s tests were used to determine the significance of individual structures and structure use types, and were conducted using the FSA package (Ogle 2023). We used redundancy analyses (RDA) to determine the significance level of surrounding habitat characteristics on substructure usage. The RDAs were conducted using the vegan package (Dixon 2003).

5.4 Results

5.4.1. Wildlife crossing detection

A total of 1,480 faunal visits (Table 5.1) were recorded across the seven monitored drainage culverts along section two of the N4 National Highway in Gauteng, South Africa, between December 2022 and October 2024. Mammals were the large majority of the recorded visits, representing 97.0% (n = 1436) of records, while non-mammal vertebrates represented the remaining 3.0% (amphibians = 23, 1.5%; birds = 21, 1.4% and reptiles = 1, 0.1%). A total of 30 species were recorded using the monitored drainage culverts. The majority of the species were individuals with diurnal activity patterns (65.7%, n = 972), followed by nocturnally active species (33.4%, n = 494), and species that are active both during the day and at night were least observed using the drainage culverts (0.7%, n = 10) of records. The drainage culverts were used nearly equally across the day, with 731 (n = 49%) records during AM hours and 751 (n = 51%) records during PM hours. However, most observed movement patterns were of animals moving from east to west, 912 (61.5%), with movement from west to east only making up the remaining 38.5% (570). Low levels of human disturbance were detected at all structures except structure C6. However, only a total of 43 human disturbances were recorded, with structure C1 (17, 39.5%) and B1 (13, 30.2%) having the highest number of human presence records.

The drainage culverts were used by small to medium-sized mammalian species, with slender mongoose (*Galerella sanguinea*), yellow mongoose (*Cynictis penicillata*), Cape porcupine (*Hystrix africaeastralis*) and large spotted genet (*Genetta tigrina*) showing the highest underpass crossing index (Table 5.1). While the majority of the species observed using the drainage culverts have a Least Concern IUCN conservation status on the Red List, only the

Cape clawless otter (*Aonyx capensis*) was listed as Near Threatened because of habitat loss and fragmentation. Although serval (*Leptailurus serval*) is globally listed as Least Concern, it is nationally listed as Near Threatened in South Africa. Whilst the majority of the observed mammal species (73.7%) appear on the roadkill inventory for this road section, eight species (26.7%) that were observed using the drainage culverts were not reported as roadkill in this road section (N4-section 2).

Table 5.1: Vertebrate use of drainage underpass culverts along section 2 of the N4 National Highway, Bronkhorspruit, South Africa. The crossing index was calculated for all the species and structure use categories (complete and incomplete crossings), F-frequency of crossings by a given species and UCI- underpass crossing index, * species not reported as road-kill.

Species	Latin name	Crossing structure monitored							F	UCI
		C1	C2	C3	C4	B1	C5	C6		
*Slender mongoose	*Galerella sanguinea*	121	283	10	38	95	18	0	565	0.53
Yellow mongoose	*Cynictis penicillata*	48	42	0	157	2	16	0	265	0.25
Cape porcupine	*Hystrix africaeastralis*	46	115	0	17	5	52	0	235	0.22
Large-spotted genet	*Genetta tigrina*	33	111	0	9	6	0	0	159	0.15
*Rock hyrax	*Procavia capensis*	1	26	0	0	7	34	0	68	0.06
Marsh mongoose	*Atilax paludinosus*	0	1	29	0	0	0	12	42	0.04
Domestic cat	*Felis catus*	23	2	0	0	4	0	0	29	0.03
Serval	*Leptailurus serval*	0	11	0	0	3	6	0	20	0.02
*Large-grey mongoose	*Herpestes ichneumon*	13	1	0	0	0	0	0	14	0.01
Domestic dog	*Canis lupus familiaris*	1	5	0	1	3	0	0	10	0.01
Common duiker	*Sylvicapra grimmia*	0	1	0	3	2	0	0	6	0.01
*Southern reedbuck	*Redunca arundinum*	0	0	0	0	4	0	0	4	0.004
Scrub hare	*Lepus saxatilis*	2	2	0	0	0	0	0	4	0.004
Rodent	Rodentia	1	0	0	0	0	3	0	4	0.004
Cape clawless otter	*Aonyx capensis*	0	0	1	0	0	0	2	3	0.003
*Banded mongoose	*Mungos mungo*	0	0	0	0	3	0	0	3	0.03
*Domestic cow	*Bos taurus*	0	0	0	0	2	0	0	2	0.002
Honey badger	*Mellivora capensis*	0	1	0	0	0	0	0	1	0.001
Black-backed jackal	*Canis mesomelas*	0	0	0	1	0	0	0	1	0.001
Aves										
*Hamerkop	*Scopus umbretta*	0	0	6	1	0	0	2	9	0.01
African black duck	*Anas sparsa*	0	0	3	0	0	0	0	3	0.003
Black-headed heron	*Ardea melanocephala*	0	0	0	0	0	0	3	3	0.003
Spur-winged goose	*Plectropterus gambensis*	0	0	0	0	1	1	0	2	0.002
Helmeted guineafowl	*Numida meleagris*	0	0	0	0	1	0	0	1	0.001
Natal spurfowl	*Pternistic natalensis*	0	1	0	0	0	0	0	1	0.001
Spotted eagle owl	*Bubo africanus*	1	0	0	0	0	0	0	1	0.001
Domestic goose	*Anser anser*	1	0	0	0	0	0	0	1	0.001
Amphibia										
*Red toad	*Schismaderma carens*	3	1	0	3	0	0	0	7	0.01
Unknown toad	*Sclerophrys species*	0	0	0	15	1	0	0	16	0.02
Reptilia										
Water monitor	*Varanus niloticus*	0	0	0	0	1	0	0	1	0.001
		294	*603*	*49*	*245*	*140*	*130*	*19*	**1480**	

5.4.2 Spatial and temporal patterns of drainage culvert use

Structure two (C2) had the highest overall visitation of all seven substructures, with 603 (40.7%) visits between December 2022 and October 2024, with structures one (C1) and four

(C4) having the second (294, 19.9%) and third (245, 16.6%) highest respectively (Table 5.1). As with the overall distribution of faunal underpass substructure visits, culvert 2 (C2) has indicated the highest number of visitations during the wet season, with substructures one (C1) and four (C4) having the second and third highest, respectively (Fig. 5.2a), with structure two having 407 (41% of wet season visits) records across the duration of survey. The same three structures also had the three highest number of dry season visits (Fig. 5.2b), with structure two again having the highest number at 197 (40% of dry season visits) records during the survey duration. There was also no significant difference in the number of visits at each structure between seasons (Kruskal-Wallis test, chi2 = 41.429, df = 13, p = 0.432).

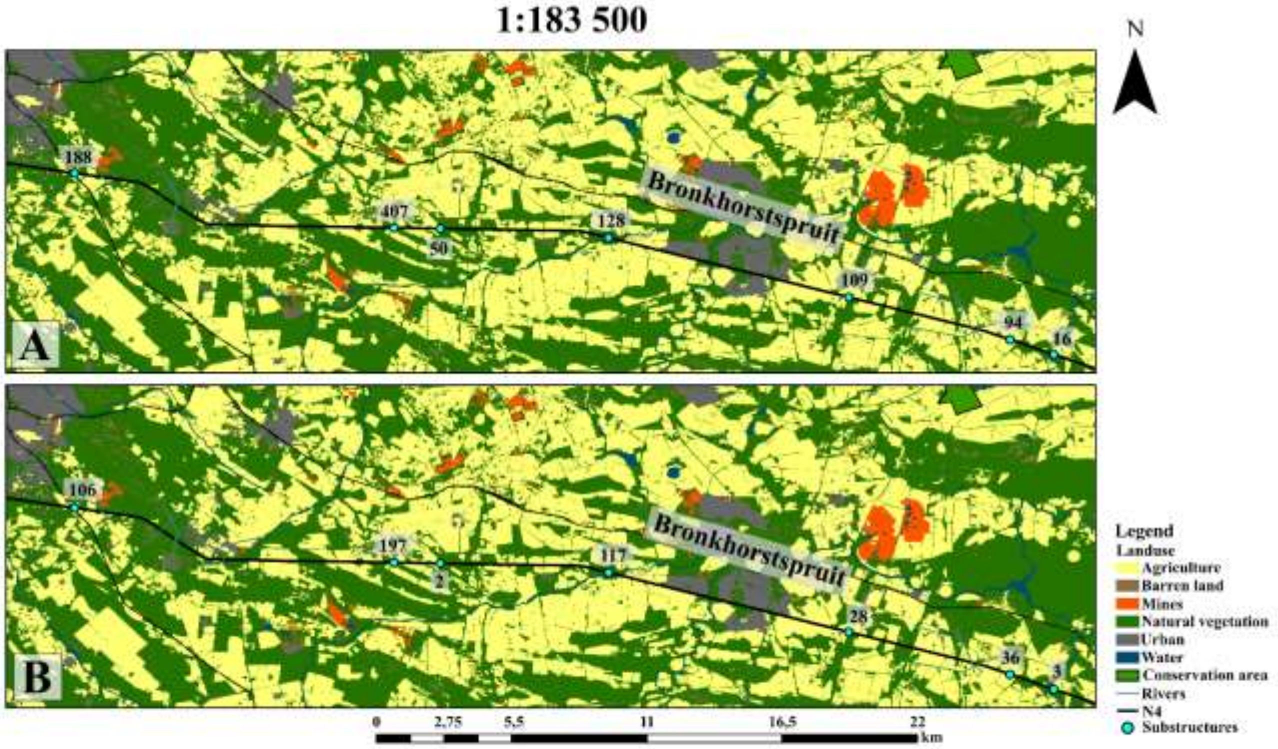

Figure 5.2: Season vertebrate faunal visitation density at monitored substructures along section two of N4 National Highway in Gauteng, South Africa, where A. is the wet season and B. is the dry season.

The seasonal visitation trends indicated that structure two (C2) had the highest mammalian visitation of all the surveyed substructures with 601 (41.8%), followed by structures one (n = 289, 20.1%) and four (n = 226, 15.7%) respectively (Fig. 5.3a). However, non-mammalian visitation was highest at structure four, (n = 19, 42.2%), followed by structure three (n = 9, 20.0%) and structure one (n = 5, 11.1%) (Fig. 5.3b). Furthermore, our results found significant differences between the number of mammal and non-mammal visits at each structure, with an overall significance of $p < 0.01$ (Kruskal-Wallis test, Chi2 = 58.248, df = 13). The p-values of $p = 0.01$ and $p < 0.01$ between the number of mammal visits at structures two (C2) and three (C3), and the number of mammal and non-mammal visits at structures two and five, respectively. Moreover, an additional p-value of $p = 0.03$ was obtained between the number of mammal visits at structures two and five, the number of mammal and non-mammal visits to structures one and five, as well as two and three and four and five.

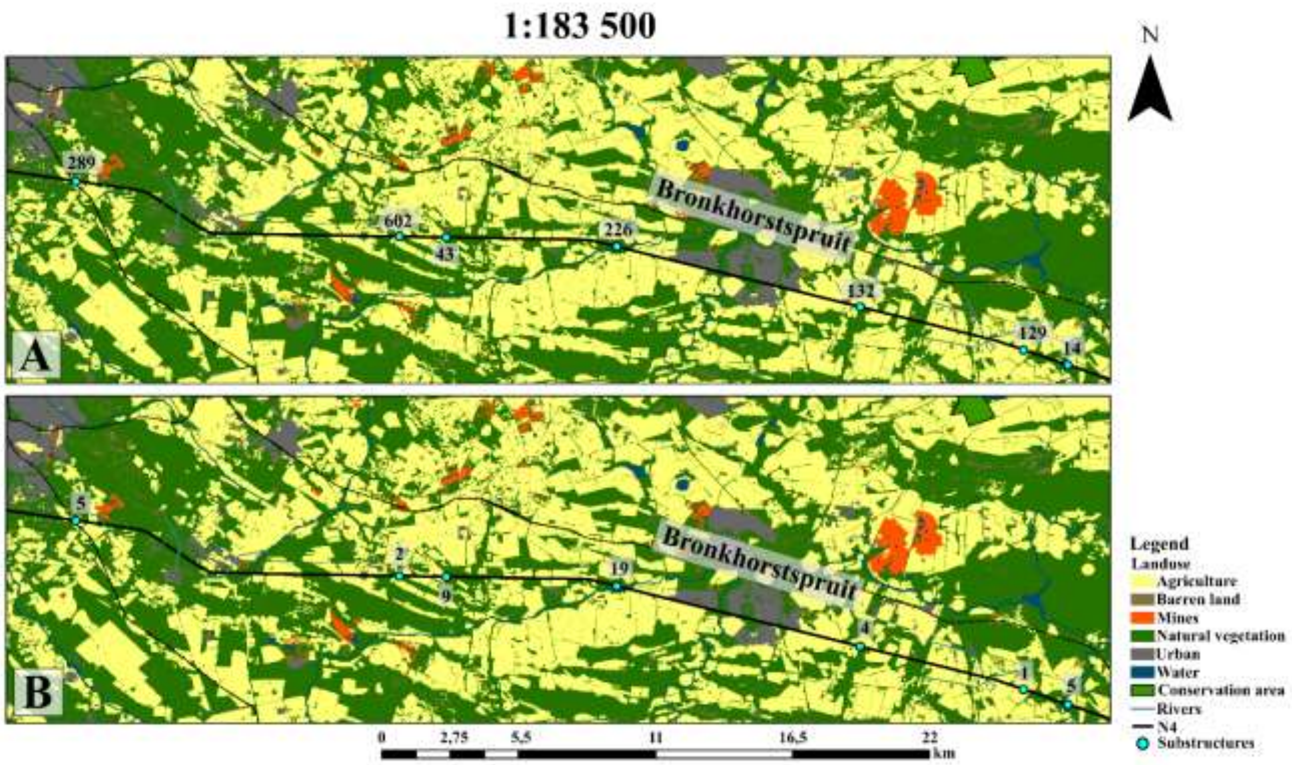

Figure 5.3: Visitation density at monitored substructures along section two of N4 National Highway in Gauteng, South Africa, where a. is mammals and b. non-mammals.

5.4.3. Variables affecting faunal use of monitored substructures

The RDA test found that the significant variables (constraining variables) accounted for 42% of the variation, while the remaining 58% of the variation was unconstrained. The model had an adjusted R^2 score of 0.396 and a model significance of $p = 0.01$ ($F = 13.493$; $df = 8$), and Eigenvalues of 41.60 and 59.35 for Axis RDA1 and PC1, respectively. However, despite the low R^2 score, a clear separation can still be seen in the distribution patterns of faunal use of each structure type (Fig. 5.4), with structure use also showing the only significance as a factor with a p-value of 0.02. No single structure-use was restricted to a single structure (Supplementary information Fig. S5.2). Temperature, the distance to water and the distance to the next substructure, despite being insignificant, were the only recorded variables that showed a non-zero effect on the type of substructure-use and were included in RDA figures.

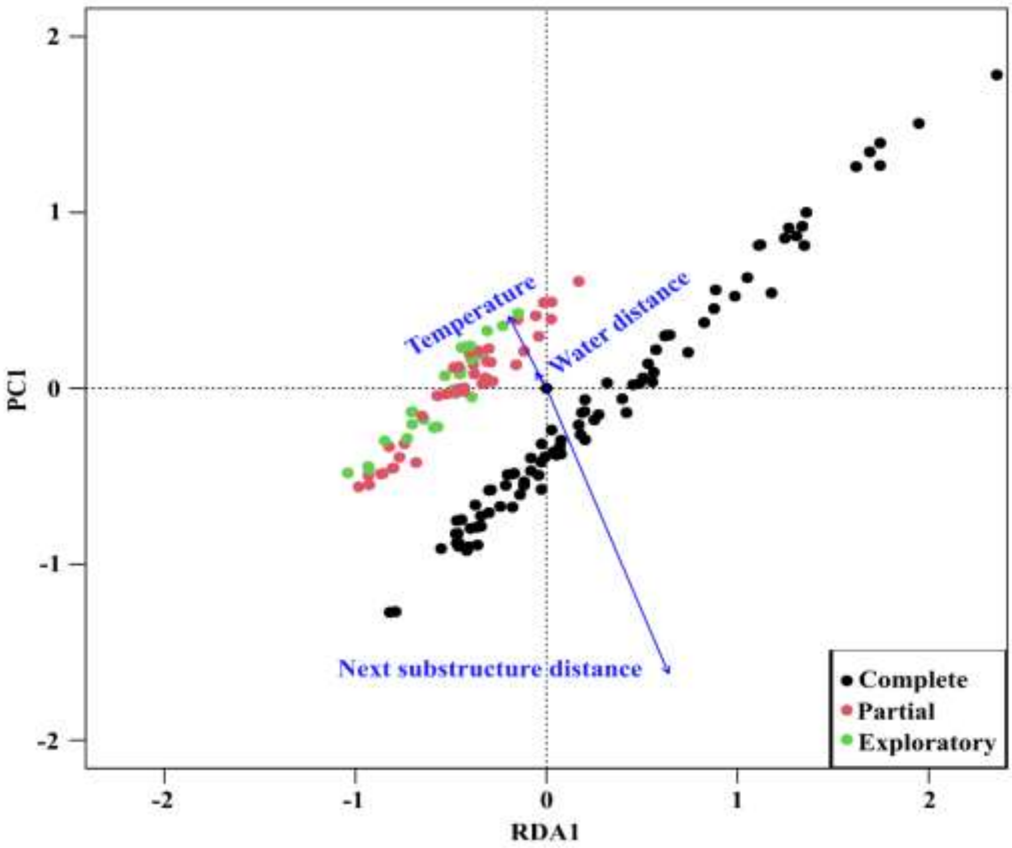

Figure 5.4: Redundancy analyses of determined variables affecting faunal use of monitored substructures along section two of the N4 highway in Gauteng, South Africa.

5.5 Discussion

In the present study, the temporal trends in the use of existing underpasses, such as drainage culverts, were presented. As such, a total of 30 small-to-medium sized vertebrate species were detected using the six monitored underpass drainage culverts and bridge to cross the N4 National Highway over several years. The findings of this study demonstrated that existing road substructures have supported regular animal dispersal movements and seasonal migrations of wildlife species in the study area. These findings are consistent with other road ecology studies that surveyed the usefulness of existing culverts in promoting wildlife movement across road-fragmented landscapes (Clevenger et al. 2001; Ng et al. 2004; Craveiro et al. 2019). This showed that although the drainage underpass structures along the N4 National Highway were not typically designated to accommodate wildlife, if modified accordingly, such structures may be useful in connecting the landscape and further reducing the incidents of wildlife roadkill by allowing safe crossing corridors for wildlife.

Although the roadside fencing along two of the monitored culverts was stolen a day after the installation (leaving only one culvert with fencing), our results showed that the drainage culvert with roadside funnel fencing installed experienced a greater frequency of wildlife visitations than the unfenced segments, with most of the visits being complete crossings. As we acknowledge that these findings are not comparable as it is for only one fenced culvert, to some degree, roadside fencing was successful towards funnelling animals towards the culvert for crossing. We further emphasise the need to replicate roadside fenced culverts when investigating the use of drainage underpasses. This finding supports previous studies that reported on the importance of wildlife barrier fencing in directing faunal species towards the crossing structure, which prevents animal access on the road (McCollister and Van Manen 2010; Young et al. 2023). Several studies assert that in fenced segments, animals tend to follow the fencing away from underpasses, thus causing them to be exposed to the road at the fencing ends and eventually get struck by vehicles when crossing the highway where fencing ends (Clevenger et al. 2001; McCollister and Van Manen 2010). To avoid this risk, the barrier fencing design followed in this study had a 180º curvature at the fence ends to encourage animals to reverse their direction and travel back in the opposite direction towards the underpass structure. In this way, animal exposure to the highway at the fencing ends was reduced, ultimately reducing roadkill incidents. For the duration of our monitoring of underpass culverts, a total of three wildlife roadkill incidents across seven years were reported within 50 m of the monitored culverts.

Although our study showed that the monitored culverts were used by various species, smaller mammals such as slender mongoose, yellow mongoose, Cape porcupine, and large spotted genet accounted for the highest use frequency and underpass crossing index. We suggest that this could be because these species often have smaller home ranges and tend to use underpasses as part of their home ranges (Goldingay et al. 2022). While we found no significant difference in the number of visits to each structure between seasons, the composition of the species that used the drainage culverts varied. Hence, structure two (C2) had the highest mammal visitation of all the surveyed substructures, while structure four (C4) accounted for the highest use by non-mammalian species, followed by structure three (C3) and structure one (C1). Whilst most mammalian species using the structures (73.7%) appeared on the roadkill inventory for this road section, eight species (26.7%) observed using the drainage culverts were never reported as roadkill along the surveyed road section since 2017. This further suggests that the structures have been critical in sustaining safe animal crossings along this route.

Several attributes are reported to influence wildlife use of crossing structures, and these elements vary for each species (Clevenger and Waltho 2005). The design of the crossing structure and the adjacent landscape features were reported to influence the use index of crossing structures (Sołowczuk 2020; Ding et al. 2024). Despite structure 1 (C1) having recorded the highest proportions of human presence (44. 2%), followed by structure five (B1) (30.3%), structure one still recorded the second highest use frequency. However, none of the observed human uses were complete crossing because the structure was a circular culvert with a smaller openness ratio. Although we expected structure five (C5) to have a considerable frequency of use because of its larger openness ratio, presence of flowing water, a dry pathway to facilitate animal movement and a grazing meadow, our study showed that circular culverts were the most frequently used structures. Considering the width and height of this structure and the adjacent agricultural farms, co-use by both animals and humans was possible. Our data showed that human presence and crossing beneath this structure were prevalent, with a 30.2% proportion of human activity. Consequently, this may have made this structure unavailable for wildlife use at certain times or caused some animals to avoid using it because of human activity, as reported in other studies (Clevenger and Waltho 2005; Ding et al. 2024). Moreover, structure seven (C6) was only used by nocturnal mammals, which are both semi-aquatic, such as the marsh mongoose (*Atilax paludinosus*) and the Cape clawless otter. In this study, the significant variables (constraining variables) accounted for 42% of the variation of wildlife use of the monitored culverts, while the remaining 58% of the variation was unconstrained. Despite ambient temperature, distance to water and distance to the next substructure being insignificant, they were the only recorded variables that indicated a non-zero effect on substructure use. However, missing variables may be responsible for incomplete crossings beneath the structures. As such, further comprehensive analysis for understanding how traffic volume, wildlife composition on the roadside habitat, prey-predator dynamics, and co-use of structures by humans and animals, including avoidance-attraction, is needed in South Africa to advance our knowledge on the usefulness of road underpass culvert structures in connecting fragmented landscapes.

5.6 Conclusions

The results of our study show that despite existing underpass structures not being designed to be safe wildlife road crossings, some degree of alterations to these structures can significantly increase their effectiveness as successful wildlife movement pathways. This includes improving existing structures through installing roadside fencing, particularly in roadkill hotspot sections. Our study's findings also provide actionable measures that city planners and road developers could incorporate to further South Africa's sustainable development and wildlife protection goals. However, more extensive studies focusing on all underpass structures along larger portions of the road and detailed investigations on factors affecting artificial pathway-use are necessary to further our understanding of wildlife's use of road substructures. Additional studies should also be conducted to determine differences in wildlife structure-use patterns in natural areas, particularly within protected areas.

5.7 Acknowledgements

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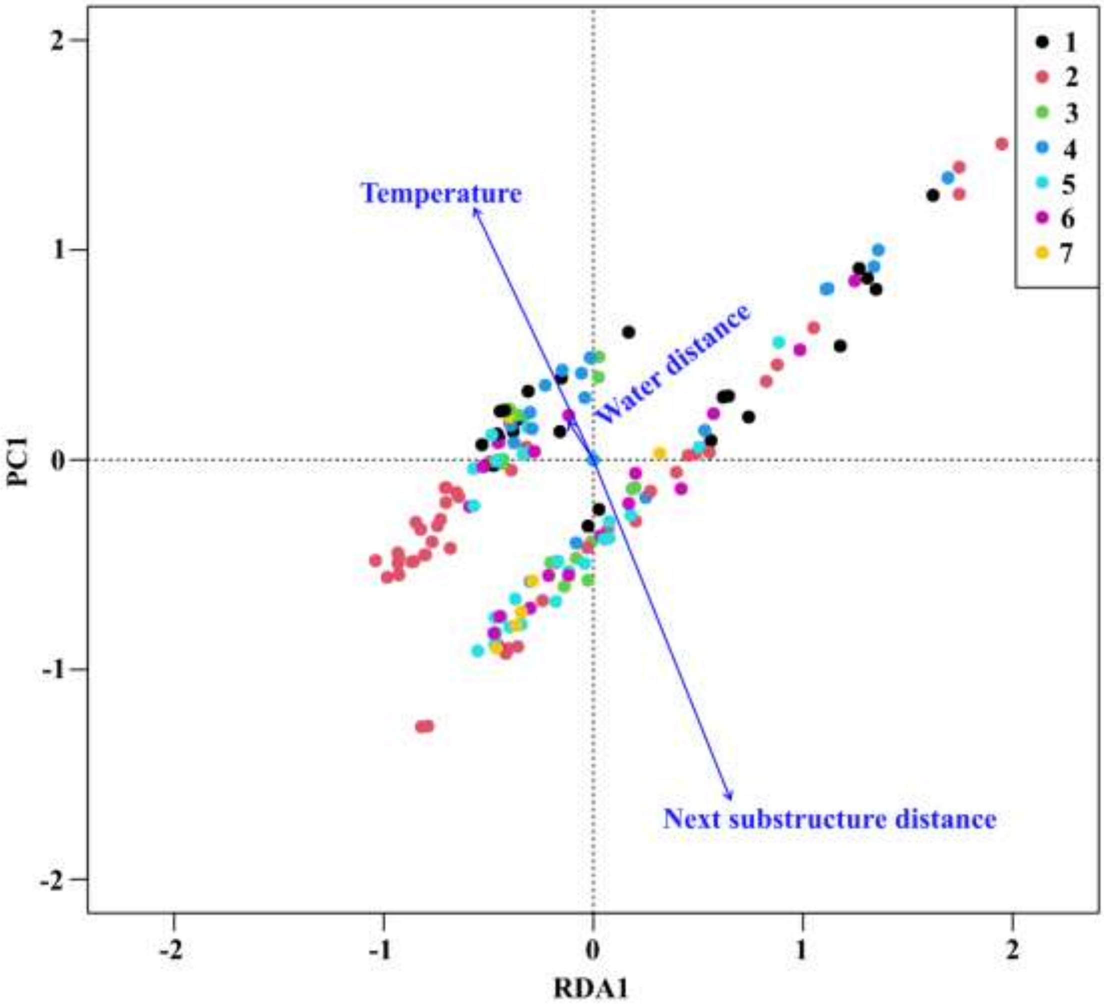
5.9 Supplementary Information



Supplementary Information Figure S5.1: Distribution of the effect of measured environmental factors on faunal substructure use at monitored structures along section two of N4 highway in Gauteng, South Africa.

Supplementary information Table S5.1: Structural characteristics of seven monitored existing road drainage underpasses (Fig. 5.2) underneath the N4 National Highway in Bronkhorspruit, South Africa. Distance to habitat type is the average for the two entrances of the structure

Site ID	Latitude	Longitude	Structure Type	Substrate type	Water presence	Width (m)	Length (m)	Openness Ratio (m)	Height (m)	Distance to adjacent habitat type (m)	Habitat/land-use
N4-2-3,2	-25.4634	28.2718	Circular culvert (C1)	Concrete	No	0.86	45.04	1.43	0.88	10.66	Industrial area, open savanna bushland
N4-2-17,8	-25.4754	28.3437	Circular culvert (C2)	Concrete	No	0.86	61.03	0.04	0.86	9.57	Agricultural area
N4-2-19,8	-25.4755	28.3613	Rectangular culvert (C3)	Concrete, water	Yes	1.81	51.25	6.06	1.20	8.34	Wetland, open grasses
N4-2-27,2	-25.4759	28.3922	Circular culvert (C4)	Concrete	No	1.84	43.61	2.67	1.21	23.31	Open grasses, agricultural area
N4-2-38,0	-25.4943	28.4654	Bridge (B1)	Waterbody, vegetation,	Yes	18.40	43.65	0.37	1.34	61.53	Waterbody, agricultural area
N4-2-45,6	-25.5051	28.5107	Circular Culvert (C5)	Concrete	No	0.61	50.14	0.07	0.69	31.81	Open grasses, agricultural area
N4-2-50,4	-25.5146	28.5352	Box culvert (C6)	Waterbody, concrete	Yes	2.42	41.54	0.08	1.80	20.32	Wetland, stream

Site N4-2-17.8 had a 400m long roadside fencing that was funnelling animals towards the circular drainage culvert, and it was erected for the purpose of this study.

5.10 Supplementary information Table S5.1: List of detected species

Mammalia	
 Slender mongoose (*Galerella sanguinea)*	 Yellow mongoose (*Cynictis penicillata)*
 Cape porcupine (*Hystrix africaeastralis*)	 Large-spotted genet (*Genetta tigrine)*
 Rock hyrax (*Procavia capensis*)	 Marsh mongoose (*Atilax paludinosus*)
 Domestic cat *(Felis catus*)	 Serval (*Leptailurus serval*)


Large-grey mongoose (*Herpestes ichneumon*)


Domestic dog (*Canis lupus familiaris*)


Common duiker (*Sylvicapra grimmia*)


Southern reedbuck (*Redunca arundinum*)


Scrub hare (*Lepus saxatilis*)


Rodent (Rodentia)


Cape clawless otter (*Aonyx capensis*)


Honey badger (Mellivora capensis)

 Black-backed jackal (*Canis mesomelas*)	 Common warthog

Aves

 Hamerkop (*Scopus umbrette*)	 Hadeda ibis (*Bostrychia hagedash*)
 Egyptian goose (*Alopochen aegyptiaca0*	 Black-headed heron (*Ardea melanocephala)*
 Natal spurfowl (*Pternistic natalensis)*	 Spotted eagle owl (*Bubo africanus)*

Amphibia

	
Red toad (*Schismaderma carens*)	Unknown toad (*Sclerophrys species*)

CHAPTER 6

Synthesis, conclusions and recommendations

6.1. Overview

In the absence of safe ecological corridors, the unprecedented rates of transport infrastructure development will accelerate the loss of biological diversity globally (Wang et al., 2022; Hlatshwayo et al., 2024). The rapidity of transport corridor construction and expansion without considering standards and best practices for sustainably compensating the loss of biodiversity by incorporating proper mitigation hierarchy (Ekstrom et al., 2015; Hlatshwayo et al., 2024), has become the biggest hindrance to minimising the negative transport-related biodiversity and habitat fragmentation crisis. By improving the functionality of isolated ecosystems through connectivity corridors, suitable habitats become accessible for wildlife during tough and changing climatic conditions (Littlefield et al., 2024). The purpose of this PhD study was to critically delve into the ecological impacts of road infrastructure on animal movement in a fragmented landscape in South Africa. We highlighted the importance of improving biodiversity loss accounting through monitoring wildlife roadkill incidents. We also emphasised the importance of using the existing data of wildlife roadkill to quantify hotspot areas and examine possible connectivity channels by exploring wildlife's use of existing underpass drainage culverts. In this way, we provided stepping stones for South Africa and the entire African continent to tackle road-related biodiversity impacts by including ecological corridors to facilitate the movement of wildlife and gene flow in fragmented landscapes, as this is deemed to provide “functional connectivity”.

This critical assessment included a review of road ecology studies that deployed camera trap protocol for monitoring animal use of crossing structures in fragmented ecosystems (Chapter 2), a synthesis of key existing South African policies for road infrastructure to assess their implementation and effectiveness in mainstreaming ecological connectivity in their framework of green transport planning (Chapter 3), an evaluation of the spatial and temporal patterns in the distribution of wildlife roadkill on the N4 national highway (Chapter 4), and assessed the effectiveness of existing road drainage underpass structures in one of the most critical highway in South Africa using camera traps (Chapter 5). In this final chapter of the thesis, I have synthesised the key findings and further explored their broader perspectives and implications in a period marked by unprecedented transport linear infrastructure development and biodiversity loss, particularly for developing regions such as Africa. This chapter, therefore, provides (1) an overview of key findings, (2) the importance of these findings, (3) available research gaps and opportunities for further research, and (4) highlights recommendations for advancing ecological connectivity in transport-fragmented landscapes.

6.2. An overview of key findings

Chapter Two: The state and trend of global camera trap studies that explored animal use of crossing structures in road-fragmented landscapes

Wildlife crossing structures, such as overpasses (eco-bridges and canopy bridges) and underpasses (eco-ducts, viaducts, tunnels and culverts), are regarded as important connectivity structures that help animals move across roads safely, including other linear transport infrastructure (railways and canals). This makes these structures known as important ecological corridors promoting the functionality of transport-fragmented landscapes. The study in the first data chapter assessed the camera trap protocol used by 84 peer-reviewed global studies to examine if the value of existing drainage culverts not specifically designed for wildlife usage is realised, and evaluated the camera trap protocol for monitoring crossing structures. As such, this has enabled the researcher to collate critical information regarding the method of setting the camera traps so that they are applied effectively when monitoring crossing structures.

Moreover, it provided an opportunity to improve some of the existing disparities that weaken the camera trapping reliability in monitoring wildlife crossings.

The findings of our review have revealed that the design and methods of each evaluated study differed in how they deployed camera traps. This suggests that the differences that exist among structures in terms of their structural design, size, target species, landscape and road characteristics variables are critical elements to consider during crossing structure monitoring surveys. Of greater importance, such disparities in the camera trap protocol make it difficult for studies to successfully evaluate whether species are avoiding the structures or are successfully using them. Whilst the findings of our review indicated that the temporal trend of camera trap studies that monitored animal use of wildlife crossing structures using camera trapping is increasing, the majority of these studies were conducted in the global north regions. The global north regions have shown the least interest in exploring animal use of crossing structures, although a considerable number of studies have been conducted in Asia. Moreover, only two studies were found to be conducted in Africa; one was conducted in South Africa in 2014, and the other was conducted in Kenya in 2018. In this chapter, we emphasised the urgent need to develop a harmonised camera trap protocol and guidelines for surveying crossing structures' use and effectiveness, depending on their structural design, size, aims, and target species or animal group. We provided a recommendation that countries in developing regions should consider intensifying efforts for road agencies to account for biodiversity loss and explore existing road underpass structures, such as culverts, on how they could facilitate wildlife dispersal movements in fragmented landscapes.

Chapter Three: mainstreaming ecological connectivity and wildlife needs in transportation planning

The research in Chapter 3 urges that poorly planned transport infrastructure development can severely impact ecological connectivity and species survival. Roads can create barriers to wildlife movement, limiting terrestrial wildlife's ability to find water, food, and mates (van der Grift & van der Ree, 2015; Pinto et al., 2024; Xiong et al., 2025). Furthermore, road-fragmented landscapes accelerate incidents of wildlife-vehicle collisions; whilst these incidents almost always result in wildlife mortality, they also impact populations of threatened and endangered species (Oliveira Gonçalves et al., 2022; Hlatshwayo et al., 2024). Moreover, these impacts are particularly relevant in South Africa, which has diverse wildlife populations and is still transitioning to a green economy. Therefore, the work in this chapter expands on previous research by emphasising the urgent need for adopting road development projects that optimise social and economic benefits while safeguarding biodiversity and ecosystems through the inclusion of ecological connectivity.

In this chapter, key existing South African policies for road infrastructure were synthesised to assess and evaluate their effectiveness in promoting ecological connectivity and wildlife needs in their framework of green transportation planning. An analytical framework for advancing the sustainability of transport infrastructure development was developed and used to review the identified policies. The findings of the policy review showed that the reviewed policies articulated sustainability standards for developing road infrastructure that is climate change-resilient with reduced emissions, but did not have provisions for mainstreaming ecological connectivity for restoring key ecosystems and threatened species. The Drivers, Pressures, State, Impact, Response (DPSIR) analysis has identified a lack of policy interventions that promote ecological connectivity among the pressures that exacerbate the ecological impacts of transport corridors on biodiversity ecosystems. This clearly showed that the policy for sustainable road transport development in South Africa lacked integration.

We recommended that a comprehensive national ecological connectivity conservation strategy be developed for linear infrastructure fragmented landscapes in South Africa to promote integrated land use planning and mainstreaming ecological connectivity for wildlife. Secondly, we developed and proposed a synthesised analytical framework for promoting transport infrastructure sustainability; this analytical framework presents a user-centric integrated model and establishes road project planning and design that optimises social and economic benefits while minimising negative ecological impacts through promoting strategic and multi-sectoral collaborations in transport development projects. Lastly, we provided policy recommendations for mainstreaming ecological connectivity to conserve biodiversity in national policy frameworks, as we believe this will improve sustainable development mandates and strengthen future research regarding transport sustainability in South Africa.

Chapter Four: Protecting the unprotected: Monitoring the patterns of terrestrial vertebrate roadkill along a major South African National Highway

In recent years, wildlife has been under increased pressure due to reduced habitat and demands for linear infrastructure development. Linear transport infrastructure (roads and railways) plays a significant role in enhancing sustainable human economic development and society (Ruiz and Guevara, 2020; Paul, 2023). However, despite transport corridors having a vital role in the economy and mobility of South Africa, when they are not built following the bounds of sustainability, they may result in a rapid decline in biodiversity (Eliasson and Proost, 2015; Oliveira Gonçalves et al., 2022; Xiong et al., 2025). As such, this will degrade ecosystem functions, resilience, and ultimately threaten human well-being and the United Nation's Sustainable Development goals (SDGs). Therefore, in this chapter, we elaborate on the importance of monitoring incidents of wildlife roadkill, as this will help improve the understanding of the negative impact of transport corridors on wildlife populations in South Africa. Furthermore, we demonstrated how successful strategic partnerships between conservation NGOs, research and transport institutions could help establish standardised monitoring of transport-related wildlife impacts. We used data collected by the Trans African Concessions (TRAC N4) road patrol staff to evaluate the spatial and temporal patterns in the distribution of wildlife roadkill along the TRAC N4 highway. The effects of landscape and highway characteristics on the distribution of roadkill and hotspot areas were analysed, as well as the understanding of seasonality effects on the patterns of roadkill.

The data generated in this chapter of the research indicated that although the seasonal distribution of vertebrate roadkill along the N4 National Highway did not change with changing ecological seasons, wildlife road mortality rates remained significantly higher per year ($p = 0.013$). This suggests that most of the species reported as roadkill are resident within the wider landscape and interact with the highway periodically throughout the year. Through analysing the patterns of vertebrate roadkill along the N4 National Highway, several major wildlife roadkill hotspot areas were identified, with all the hotspots emerging along the highest-speed road sections, which was expected. This significant pattern showed that mitigation interventions are needed along certain portions of the highway, particularly along the identified hotspot areas. Lastly, we recommended that studies that will explore the effect of daily traffic volume on wildlife roadkill rates and monitor the wildlife composition on roadside habitat be conducted across South Africa to improve our understanding of transport-related biodiversity impacts.

Chapter Five: Evaluating the spatial and temporal patterns of wildlife use of existing road drainage underpass structures along a major South African highway

Numerous studies have demonstrated the significance of wildlife crossing structures in facilitating the ecological functionality of fragmented ecosystems, significantly reducing the impact of roads and railways on wildlife. Crossing structures have proven highly effective in connecting isolated habitat patches for numerous wildlife species, thus allowing animals to cross above or below linear transport infrastructure (Bissonette & Cramer, 2008; Clevenger & Waltho, 2003; Mysłajek et al., 2020; Tay et al., 2024). When used together with roadside funnel fencing, wildlife crossing structures could reduce the incidence of wildlife road mortality by as much as 98% (Clevenger et al., 2001; Gagnon et al., 2017).

With the massive development of linear transport infrastructure across Africa, the fragmentation of natural ecosystems is rapidly increasing, and this has become a key ecological concern for biodiversity conservation and sustainable development. The inclusion of connectivity structures (wildlife crossings) in transportation planning has received gradual recognition in the global transportation planning frameworks and sustainability agenda (Ament et al., 2023; Dodd et al., 2024; Hlatshwayo et al., 2024). However, transportation agencies and conservation practitioners in South Africa have insufficient information to plan for the management or mitigation of the effects of transportation infrastructure on wildlife populations.

This doctoral study in this chapter has investigated the usefulness of existing under-road culvert structures (bridges, culverts, viaducts and tunnels) in helping animals to move across the N4 national highway so we can reduce roadkill incidents and improve landscape ecological functionality. Through undertaking surveys of existing road structures using camera traps on the N4 National Highway, this study has determined how wildlife road-side fences are used in combination with such passages to benefit wildlife and assist in roadkill reduction, although they were not purposely built for wildlife. Of greater importance, there was no road-kill incident recorded near the drainage culvert that had a roadside fencing for the duration of our monitoring; this structure also had a higher animal crossing index.

6.3. Conclusions and recommendations

The findings of this thesis have offered insights into the ecological impact of transportation corridors on wildlife movement, which is an emerging environmental problem in South Africa's terrestrial ecosystems and biodiversity. Whilst current road ecology global studies have demonstrated that human anthropogenic activities have altered terrestrial ecosystems through landscape fragmentation, this thesis has provided critical information regarding how road infrastructure development has led to habitat fragmentation in South Africa. Furthermore, it has indicated how poor planning and design of transport infrastructure affect biodiversity, ecosystem functioning and stability. As such, recommendations that could enhance proper transport infrastructure planning that recognises mechanisms for sustainable land-use practices were provided.

The study findings have revealed that the surveyed highway poses a significant impact on biodiversity and conservation, and we therefore recommend the urgent need for South Africa to prioritise strategies for improving biodiversity loss accounting and compensation in the transportation sector. Our findings of the hotspots offered an indication of potential key areas where prioritisation for mitigation strategies should be focused, as such, we recommend that further studies for evaluating animal use of drainage culvert and wildlife roadside fences be used in combination with such passages. Furthermore, we recommend integrating national policies and environmental impact assessments so that they can consider including strategic ecological connectivity assessments in their sustainability model. Lastly, we recommend that the departments of i) Road and Transport, ii) Forestry, Fisheries and Environment departments in South Africa (DFFE), South African biodiversity Institute (SANBI), as well as the South African National Roads Agency Ltd (SANRAL) should collaborate with other qualified stakeholders (research institutions, policy makers, protected area authorities and other Non-Governmental Organisations) to develop a comprehensive national strategy for mainstreaming ecological connectivity conservation for linear infrastructure-fragmented landscapes. This strategy will be significant in establishing integrated land use planning, habitat connectivity, and green infrastructure (eco-friendly infrastructure).

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