Seasonal use and mortalities of mammals along the Phalaborwa – Hoedspruit railway line in Balule Nature Reserve, South Africa.

BY

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DECLERATION

I, Siboniso Khulekane Thela, hereby declare that this thesis (*Seasonal use and mortalities of mammals along the Phalaborwa – Hoedspruit railway line in Balule Nature Reserve, South Africa*) is my own work, and have not been previously submitted for any degree at any at this university or any other institution. All design, execution, and all reference materials contained therein have been well acknowledged.

07 – Dec – 21

Signature

Date

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DEDICATION

I wish to dedicate this study to everyone who lost their loved ones, jobs, and businesses due to Covid-19 pandemic. I hope that you find strength and courage to heal and flourish again. I also dedicate this study to all the Non-Government Organisations in the conservation sector that were or still heavily affected by the Covid-19 and continue to do everything possible to protect our precious biodiversity.

ABSTRACT

Railways are essential transportation corridors that facilitate the movement of goods and people with important environmental and economic benefits. Despite these benefits, railways and trains can negatively affect wildlife through mortalities, barrier effects, disturbances, and habitat loss. There is growing evidence that human activity negatively affects the spatial distribution of wildlife in relation to the distance from the infrastructure and wildlife also adjust their spatiotemporal activity to avoid or minimize encounters of human activity. Moreover, wildlife mortalities due to collision with trains are a major conservation concern which can jeopardize the persistence of wildlife populations as wildlife-train collisions are non-specific with regard the species, age and sex of the animal affected.

In this study, I assessed the activity patterns of six medium-large sized mammals (≥ 10 kg) and monitored the mortalities of wildlife from four different taxonomic groups on the landscape bisected by the railway line in Balule Nature Reserve. Impala and giraffe occurrences on the railway line is mostly diurnal. Meanwhile, lion occurrence on the railway line is mostly nocturnal. Four of my focal species moderately overlapped with train activity, with no seasonal differences in their degree of activity overlap. African buffalo and elephant activity decreased with increasing distance from the railway line. Giraffe, impala, and lions are less active around the railway line in the wet season than the dry season. Spotted hyaena are more active around the railway in both open grassland and woodland compared to mixed shrubland habitat intersecting the railway.

I recorded a total of 99 rail-kills from a total of 450 km surveyed over a 90-day period. Of these rail-kills, mammals were recorded more often (29.29%), followed by birds (26.26%), reptiles (26.26%) and amphibians (18.18%). There was no significant difference in the frequency of mortalities on the railway line between seasons (U = 286.5, n = 49, p = 0.421). The rail mortalities of diurnal did not differ significantly from nocturnal species (x^2 = 0.55, df = 1, p = 0.458). However, there were significantly more mortalities of diurnal species than nocturnal species on the railway line during the dry season ($p < 0.05$). Most encountered deaths on the railway line occurred in a mixed shrubland section but there was no significant association in the frequency of rail mortalities and rail-side habitat type (H = 0.84, df = 2, p = 0.657).

Keywords: Railway, medium-large, wildlife, activity, mortality, rail-kill, collision

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ABBREVIATIONS

IUCN – International Union for Conservation of Nature

BNR – Balule Nature Reserve

WTC – Wildlife-Train Collision

APNR – Associated Private Nature Reserve

KNP – Kruger National Park

OWNR – Olifants West Nature Reserve

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CHAPTER ONE: INTRODUCTION

1.1. RAILWAY HISTORY AND DEVELOPMENT

Railway is defined as “a prepared track which so guides the vehicles running on it that they cannot leave the track” (Borda-de-Água *et al.*, 2017). Today, we understand the railway as a parallel track that is made up of steel rails to provide safe passage of trains. The origin of railways can be traced back as far as the 17th century (Paaswell, 2009). Prior to 1830, railway networks consisted of isolated lines to and from the mines and were dependent on horses and often manpower to translocate wagons that carried heavy goods (Paaswell, 2009). It was only in the early 19th century which saw a success for the railways when they were completely operated by the steam engine locomotives – an invention by George Stephenson (Paaswell, 2009). Currently, there are more than 1.3 million km of railway networks globally (Morelli *et al.*, 2014) and there is an expected increase of 45% by 2050 (Popp & Boyle, 2017). The dependency on railway networks is increasing as they are more economically, environmentally friendly, and safer for humans (Borda-de-Água *et al.*, 2017; Blumenfeld *et al.*, 2019).

Rail networks on the African continent made their appearance in the late 19th century or early 20th century (Jerome, 1999). Many of the networks were built by the European colonial powers to aid with military movements and the transportation of mining and agricultural goods (African Development Bank, 2015). By 2007, African rail networks covered a total length of approximately 82 000 (African Development Bank, 2015). Most of the African rail tracks are now degraded and out of service as the result of poor investment for repairs and maintenance (Arewa, 2016). Several factors such as wars, political and economic challenges may have led to the deterioration of African railway infrastructure and upgrading the existing and building of new railways in Africa will require an investment of more than $100 billion (African Development Bank, 2015).

The expansion of rail networks on the African continent is linked with the anticipated population growth, urbanization, and the development of new mines that will produce large volumes of bulk goods (African Development Bank, 2015). African population size is projected to rise by 70% with an expected increase in urban population from 450 million to 1 billion by 2040 (African Development Bank, 2015). China has a long-standing history and relationship with African countries through financing the development of African railway networks and the first involvement by China on the African rail industry was the construction of Tanzania-Zambia railway line in the 1970’s (Richter & Wang, n.d.). The Chinese government is expected to invest over $1.3 trillion by 2027 in the Belt and Road Initiative which include existing plans to develop more miles of railway networks in Africa and Asia (www.sierraclub.org/sierra/2020-1-january-february/feature/chinas-belt-and-road-initiative-threatens-pave-planet).

In South Africa, the partnership of the Cape and Natal colonial governments led to the development of first railway lines of about 110 km heading inland from ports at Cape Town and Durban between 1860 and 1867 (Perkins *et al.*, 2005). Substantial development of the rail lines occurred during the period of 1875 – 1930 following the discoveries of diamonds at Kimberley in 1867 and gold on the Witwatersrand in 1886

(Perkins *et al.*, 2005; Fourie & Herranz-Loncan, 2015) and this was illustrated by a remarkable growth of up to 18 445 km by 1930 (Perkins *et al*., 2005). Railways played an important role in connecting the mining centers with the global economy and allowed the establishment of industrial and urban areas through low transport services (Fourie & Herranz-Loncan, 2015). Between 1870 and 1909, the actual Gross Domestic Product of the Cape rose at the annual rate of 4.77% as the result of railway construction to link Kimberley with the global economy (Fourie & Herranz-Loncan, 2015). In 1910, all railways from the four British colonies were amalgamated into the Union of South Africa, a self-governing supremacy of the British Empire, and became a state-owned network (Havenga *et al.*, 2014).

After 1930, the growth in length of the South African railway tracks was too little as roads became a dominant mode of transport for movement of goods and people (Fedderke *et al.*, 2006). As the country's infrastructure investments prioritised on improving the national and provincial roads, the growth in road transport far exceeded the growth of rail transport throughout the century (Fedderke *et al.*, 2006). This saw a rise in the truck fleet from 20 000 vehicles in 1950 to 340 000 vehicles in 2012 (Havenga *et al.*, 2014). Although there was a slow progress in the growth of railways, the rolling stock kept on rising (Fedderke *et al.*, 2006) and the network still made a fairly contribution towards the growth of the economy and transportation of both freight and passengers (Perkins *et al.*, 2005).

Compared to other African countries, South Africa has the largest density of railway lines which are still at better conditions despite low investments on railway infrastructure for more than three decades (Cheteni, 2013). As of 2013, the rail network was estimated to be more than 20 800 km of which 8 931 km were powered by electricity (Cheteni, 2013). The network had already constituted over 17 200 km single tract and 3 400 double tracks of railways (Perkins *et al.*, 2005). The country's rail networks are operated by two state owned enterprises: Transnet Limited and Passenger Rail Agency of South Africa (PRASA) (George *et al.*, 2018). Transnet responsibility is to manage, maintain, and operate the national freight rail networks (George *et al.*, 2018).

1.2. STUDY BACKGROUND

Railways are important transportation corridors that facilitate the movement of goods and people and the increase in the economic fortune in some countries may necessitate their extension (Dulac, 2013). Undoubtedly, railways can have both positive and negative effects on wildlife and the habitats through which they traverse. For instance, wildlife frequently uses railway corridors as travel routes (e.g., Popp *et al.*, 2018; Popp & Hamr, 2018) and provide important food sources (e.g., Pollock *et al.*, 2017; Murray *et al.*, 2017), shelter (e.g., Vandevelde *et al.*, 2014; Price & Banks, 2018) and nesting sites (e.g., Li *et al.*, 2010; Malo *et al.*, 2016). Despite all these viable services, railways and trains are also known to negatively affect wildlife through mortalities, barrier effects, disturbances, and habitat loss and fragmentation (Barrientos *et al.*, 2019). This can pose a serious threat on wildlife, especially to species of conservation concern and species with large territories and low productive rate (Santos *et al.*, 2017).

Wildlife mortalities that occur because of train collisions are the most obvious impacts of railway that can jeopardize the persistence of population. For instance, Popp & Boyle (2017) reported that moose (*Alces alces*) population in Alaska declined by 35% between 1989–1990 of which more than 60% of deaths were due to train collisions. Several factors can likely influence the use of the railway by wildlife and the occurrence of wildlife-train collisions including season, train volume, habitat, train speed, railway design as well as species abundance and behaviour. Kušta *et al.* (2014) recorded the highest number of roe deer (*Capreolus capreolus*) train collisions during the winter period as they tend to move over large distances in winter to find food or snow-free places. Popp & Hamr (2018) also found a greater use of the railway by mammals in summer than autumn, spring, and winter seasons. Train volume may affect the interval for wildlife to successful cross the railway without collision from moving trains. Wildlife that prefers habitat closer to the railway corridor or where railway bisects their habitat may use the railway more frequent and face greater risks of train collision. The frequency of trains influenced the probability of roe deer-train collisions with the highest number of collisions occurring at the field or meadow habitat type that had higher densities of roe deer (Kušta *et al.*, 2014).

The high train speed reduces the reaction time for the animal to notice and escape from the oncoming train (Dorsey *et al.*, 2017) and the more animals are present on the railway line, the higher the risk of train collision (Dorsey, 2011). The risk of eastern grey kangaroo (*Macropus giganteus*) collisions increased considerably with increasing train speed of above 85 km/h (Visintin *et al.*, 2018). A peak in the number Asian elephant (*Elaphus maximus*) collisions with trains was likely due to the increase in their local population which were more than doubled (Roy & Sukumar, 2017), suggesting that species abundance attributes to the risk of train collision. The daily activity patterns of wildlife may also be closely associated with the risk of train-collisions. For instance, moose had greater risk of train collisions at night, morning, or evening than the daytime due to their high activity in those periods (Gundersen & Andreassen, 1998). Accidents involving train collisions with Asian elephants occurred more (80%) at night (18:00 – 06:00) than during the day (06:00 – 18:00), but only 35% of trains operated at night because elephants tend to rest during daytime periods (Roy & Sukumar, 2017). Although railways are likely to affect wildlife in a similar way as roads, there is much less research on the effects of railways on wildlife than the effects of roads on wildlife (Popp & Boyle, 2017; Popp & Hamr, 2018). Popp & Boyle (2017) found only 17 railway-ecology related published studies which is 15 times less than road-ecology studies. The impacts of railways on wildlife may be understudied due to the remoteness of railways which makes data collection difficult (Hamr *et al.*, 2019), and the lack of financial support as wildlife-train collisions are less threatening to humans than wildlife-vehicle collisions (Popp & Boyle, 2017). Given the projected growth of railway networks in across the globe (Popp & Boyle, 2017), it is imperative that the effects of railways on wildlife are studied and considered during the planning stage before the construction of new or maintaining the existing railways.

1.3. RESEARCH PROBLEM

Balule Nature Reserve is a home to a diverse range of terrestrial wildlife but collisions of wildlife with trains have been a pressing concern for both wildlife management and conservation with more than 500 animals reportedly killed on the railway line by trains over the past 25 years (Elliott *et al.*, 2019; Appendix A). This includes species that are of conservation priority such as the black rhinoceros (*Diceros bicornis*), African wild dog (*Lycaon pictus*), and African elephant (*Loxodonta africana*) (IUCN, 2021). Therefore, wildlife mortalities due to collision with trains can have negative effects on the local populations and biodiversity as wildlife-train collision is non-specific with respect to the species, age and sex of the animal affected. Moreover, rail mortalities of wildlife due to collision with trains have been detrimental to several species of birds (e.g., Garcia de la Morena *et al.*, 2017; Godinho *et al.*, 2017), reptiles (e.g., Heske, 2015; Kumar & Kumar, 2020), and amphibians (e.g., Budzik & Budzik, 2014; Heske, 2015). In Balule Nature Reserve (hereafter “BNR”), there is a lack of evidence that other terrestrial vertebrate groups are killed on the railway line by trains as all the reported wildlife-train collisions (hereafter “WTC”) in the study area only focused on medium-large sized mammals (see Appendix A). This has serious wildlife management implications and represent a conservation challenge as it limits our understanding on the possible mitigation strategies for other species from smaller mammals and taxon groups which are likely to be prone to collision with trains and require conservation efforts.

1.4. RESEARCH JUSTIFICATION

Transport infrastructure is considered a major threat for biodiversity loss (Benítez-López *et al.*, 2010; Sharma *et al.*, 2018). Specifically, railways that bisect important wildlife habitats contribute to wildlife mortality because of rail entrapment, electrocution with overhead wires and collision with trains (Santos *et al.*, 2017). As the conservation status of many species decline globally, studies addressing the threats posed by railways and trains on wildlife are very much needed, more especially in protected areas that accommodates several species of conservation priority, such as BNR (Mwakiwa, 2011). In addition, the effects of railway and trains on wildlife are not yet fully understood due to the scarcity of rail ecology studies (Popp & Boyle, 2017). This limits our knowledge and possible measures that could be implemented to reduce WTC. Therefore, this study will not only provide important information of risk related to train collision and baseline data of rail mortalities of African wildlife to the body of research on rail ecology but also contribute to the awareness of the threat caused by railways and trains on wildlife populations, more especially on the African continent that have railways intersecting protected areas and proposed railway development (Sloan *et al.*, 2017).

1.5. RESEARCH AIMS AND OBJECTIVES

The aims of this study are to assess:

I. the activity of medium-large mammals (≥ 10 kg) on the landscape bisected by the railway line in BNR.
II. the mortalities of wildlife from four different taxonomic groups (mammals, birds, reptiles, and amphibians) on the railway intersecting the landscape of BNR.

The objectives from my first study aim were to determine:

- the daily activity patterns for each mammal species in the occurrence on the railway line.
- the degree of seasonal overlap in the activity of each mammal species with trains.
- the effects of distance, seasons, and habitats in the activity patterns of each mammal species around the railway line.

From my second study aim, the objectives were to determine:

- the seasonal patterns in the mortality of wildlife on the railway line.
- the daily activity patterns of wildlife in mortality on the railway line.
- the effect of surrounding habitat along the railway line in the mortality of wildlife.

1.6. RESEARCH HYPOTHESIS

The study conducted two case studies were with different aims and objectives, as such, several hypotheses were formulated (more details explained for each case study in Chapter 4 and 5). From the case study which assess the activity of medium-large mammals (≥ 10 kg) around the railway line in BNR, I hypothesised that:

- the degree of overlap in the activity of mammal species and trains will differ between seasons.
- the distance to the railway line will negatively affect the activity of mammal species.
- The activity of mammal species around the railway line will be influenced by season and surrounding rail-side habitat.

In a case study which examine the mortalities of different taxon groups on the railway line bisecting BNR, I hypothesised that:

- the rail mortalities of wildlife will differ between seasons.
- there will be differences in the daily activity patterns of wildlife killed on the railway line.
- the rail-side habitat will influence the rail mortalities of wildlife.

CHAPTER 2: LITERATURE REVIEW ON THE IMPACT OF RAILWAYS ON WILDLIFE

Railway networks are most preferred mode of transport over roads due to their capacity to move large volumes of goods and people in an energy efficient, economical, and environmentally sustainable way (Borda-de-Água *et al.*, 2017; Blumenfeld *et al.*, 2019). The transportation of goods and people by railways can reduce the external costs by at least 47.5% passenger per km and 75.5% per tonne km in comparison to road transport regardless of whether the railway is diesel or electric powered (Blumenfeld *et al.*, 2019). Moreover, cargo transport by trucks causes between 75% and 80% more greenhouse gas emissions per transport unit than the rail freight (Blumenfeld *et al.*, 2019). Although railways provide considerable environmental benefits when compared to roads, their impacts on wildlife cannot be overemphasized; more especially when there is still little scientific knowledge concerning their effects to wildlife (Popp & Boyle, 2017). Therefore, it is important that the negative effects of railways are recognised to help identify mitigation strategies. This chapter aims to evaluate our current understanding of the impacts associated with railways on wildlife.

I conducted a literature search from Google Scholar in March 2021 to compile existing studies assessing the effects of the railway on wildlife using a combination of key terms: “rail-mortality”, “train-collisions”, “railway impacts” and “railroad barrier”. During the search, I did not limit my search to a specific time-period and both peer-reviewed and non-peer-reviewed studies (such as journal papers, book chapters and technical reports) were analysed due to the scarcity of studies focused only on impacts of railway on wildlife (Popp & Boyle, 2017). Additionally, studies that assessed the effects of railways together with road infrastructure on wildlife were included. Other similar studies assessing the impacts of linear infrastructure on wildlife (e.g., power lines) were used to provide support on the potential effects of railways on wildlife. However, these studies were not included on the compiled list of reviewed studies because were not specifically investigating railway effects on wildlife. All the compiled studies were assessed in terms of (1) the kind of impact that was investigated, (2) the species or taxa that was investigated, and (3) the country where the study was conducted. The negative impacts caused by the railway on wildlife were classified into: (1) mortality, (2) barrier, (3) habitat loss, and (4) disturbances as shown on Table 1.

Overall, 56 studies published between 1991 and 2020 examining the impacts of railways on wildlife were obtained. Out of the 56 compiled studies, 36 studies examined mortalities and 9 studies examining barrier effects of the railway on wildlife. Studies investigating habitat loss and disturbances of wildlife on the railway line were 6 and 5, respectively. From the literature review, 28 of the 36 rail mortality studies on wildlife focused only on large mammal species with the greatest number of studies fixed specifically on moose-train collision (7 of 28 studies). A predominant focus of rail mortality studies to larger mammals may be the results of their economic importance or conservation concern, cause serious train damage, and interrupts train operations resulting to substantial financial losses (Barrientos & Borda-de-Água, 2017; Santos *et al.*, 2017). Researchers may also give more attention to large mammals because of longer persistence of their carcasses and have greater probability of detection by the researcher due to their large body size (Barrientos *et al.*, 2019).

From the 56 studies compiled, a total of 347 species were documented on the effects of the railway. When the number of different species pooled together in terms of their taxonomic groups, this consist of birds (48%), mammals (35%), amphibians (6%), reptiles (6%) and invertebrates (5%). However, it is worth pointing out that these results underestimate the number of different species negatively affected on railways due to difficulties identify rail mortalities of wildlife into species level or distinguish between species of the same genus (e.g., Godinho *et al.*, 2017; Garcia de la Morena *et al.*, 2017; Pop *et al.*, 2020). Reviewed studies were carried out on rail tracks of 18 different countries, 2 studies were conducted on an international railway of 2 countries (China – Russia) and only 1 study was unspecified. From the literature review, Canada (*n* = 6) and the United States of America (*n* = 6) were the nations with the higher number of reviewed studies on the impact of railways on wildlife.

2.1. MORTALITY

Wildlife collision with trains is the obvious source of mortality on the railway line (Santos *et al.*, 2017). Rail mortalities of wildlife due to train collisions have been significant to a wide variety of species from different taxonomic groups, ranging from mammals (Hamr *et al.*, 2019; Nezval & Bíl, 2020), birds (Garcia de la Morena *et al.*, 2017; Godinho *et al.*, 2017), reptiles (Kumar & Kumar, 2020), amphibians (Budzik & Budzik, 2014) and, more recently, for invertebrates (Pop *et al.*, (2020). At least a minimum of 245 different species have been reportedly killed by trains, including species vulnerable to local extinction (e.g., leopards, *Panthera pardus*; Joshi, 2010), species considered to play a vital ecological role for the management of ecosystems (e.g., Asian elephants; Joshi & Puri, 2019) and species with considerable economic value both for ecotourism and hunting (eg., moose, and elk, *Cervus elaphus*; Hamr *et al.*, 2019). WTC have also been shown to cause considerable financial loss. In Norway, the economic cost of train collision with one moose was approximately $ 3 169 (Jaren *et al.*, 1991). This estimated cost was based on train-related costs (such as train repairs, etc.) and the economic value for hunting a moose (Jaren *et al.*, 1991). On average, 87 moose are killed each year along the 240 km railway in Norway, totalling to a socio-economic loss of approximately $ 250 000 (Gundersen & Andreassen, 1998). Similarly, the revenue loss due to elephant-train collisions in India was estimated at Rs. 69 700.00 cores from freight and Rs. 28 700.00 cores (Roy & Sukumar, 2017).

Studies that have quantified wildlife mortality due to collisions with both trains and vehicles found that proportion of mortality on railways to be almost similar and, sometimes, even exceed mortality on roads. In Croatia, 73 brown bears (*Ursus arctos*) were killed by traffic of which 70% of deaths were the results of colliding with trains (Huber *et al.*, 1998). In Germany, the rate (accident/km) of train-related deaths for European hare (*Lepus europaeus*) was nearly as high as roads (Reck & Schmüser, 2019). This suggest that wildlife mortality caused by colliding with trains is as concerning as collisions with vehicles on roads, which obvious needs attention despite the knowledge that the global footprint of railway network is far less developed when compared with roads (Popp & Boyle, 2017).

The factors affecting the risk of WTC have been reported from different studies, with several studies revealing that the existence of railway curves influence mortality rate as it limits the ability for wildlife to detect oncoming trains (Popp *et al*, 2018; Clair *et al.*, 2020). In Canada, the majority of train collisions with elk occurred at locations closer to the bends in the railway than on straighter sections (Popp *et al.*, 2018). Rail curvature also increased the chances of train collisions for roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) in Poland (Jasińska *et al.*, 2019). Seasonal migration of wildlife is also shown as a major factor contributing to WTC. For instance, Budzik & Budzik (2014) recorded high mortalities of amphibians (87%) during spring due to their seasonal migration towards feeding grounds in that period. Moose-train collision in Norway occurred mainly during winter periods when moose seasonally migrate to areas of low snow cover closer to the railway (Jaren *et al.*, 1991; Gundersen *et al.*, 1998). Wildlife displays a certain behaviour toward approaching trains which likely increases their risk of collision. Rea *et al.*, (2010) observed video footages of moose, elk and deer running down the rail track to escape collision from oncoming train instead of moving away from the railway. Better understanding wildlife seasonal patterns and their behavioural aspects with train interactions can provide valuable information to improve mitigation strategies.

The availability of food resources on and along the railway corridor affects the rate mortality as the time spend by wildlife feeding on the railway likely increases the risk of train collision (Dorsey, 2011). Granivores may search for grain spills from train wagon (Gangadharan *et al.*, 2017), while scavengers search for dismembered carcasses from train collision and herbivores are attracted to the rail-side vegetation (Pollock *et al.*, 2017; Dean *et al.*, 2018). Railway edges promote the growth of forage plants for grizzly bears (*Ursus arctos horribilis*), potentially increasing their risk to train collision (Pollock *et al.*, 2017). The browse preferred by moose tend to grow along the railway and encourages them to spend more time close to the railway which increases their chances to be run over by trains (Jaren *et al.*, 1991). This suggest that the diet or feeding habits of wildlife play a large part on use of the railway and mortalities by wildlife and, therefore, food sources on railway corridors need to be directly monitored and removed to reduce the risk of WTC. For example, vegetation clearing from 20 – 30 m distance at both sides of the railway on sections with high accident risk resulted to a reduction in the number of moose mortalities by 56% in Norway (Jaren *et al.*, 1991).

Apart from risk of train collision, entrapment is another cause of wildlife mortalities on railway corridors because wildlife that become trapped die of dehydration and hunger (Santos *et al.*, 2017). Budzik & Budzik (2014) observed rail mortalities of Common Toads (*Bufo bufo*) that were trapped between the rails and probably died of desiccation. Malo *et al.* (2016) also recorded a total of 162 carcasses of nesting birds trapped on uncapped tubular poles that support overhead wires on a high-speed railway in Spain. These pole structures functioned as pitfall traps since they prevented birds from flying out when inside them and a problem that can simply be solved by using capped poles (Malo *et al.*, 2016). Therefore, monitoring of mortalities on railway corridors is needed for species vulnerable to entrapment and should focus on both active and inactive railways. The presence of overhead power lines on the railway lines also represents a source of wildlife mortality, particularly for birds, due to collision and electrocution (Santos *et al.*, 2017; Godinho *et al.*, 2017). From my literature review, there is no study that specifically assess the mortalities of birds related to overhead lines on the railway infrastructure. Nevertheless, bird mortalities through electrocution and collision with power lines has been documented elsewhere (e.g., Bevanger & Brøseth, 2004; Barrientos *et al.*, 2012). More than 350 bird species are reportedly killed by power lines and other electric utility structures (Barrientos *et al.*, 2012). Moreover, Bernardino *et al.* (2018) reported that the collision of birds with power lines can even modify their migration patterns and flight paths. This suggest that existing power lines and other related structures on railways represent a potentially serious threat for bird species at risk to collision and studies are necessary to provide important guidelines to planners on the construction power lines on railway corridors.

2.2. BARRIER

Railway corridors can act as a barrier to wildlife by disrupting their movements to access crucial resources. Barrientos & Borda-de-Água (2017) recognizes two kinds of barrier caused by the railway on wildlife; physical barrier which occurs when a species is physically incapable to cross the railway and behavioural barrier when a species avoids crossing the railway despite being physical capable to cross it due to unfavourable surrounding conditions or perceived risk. The physical barrier caused by railways on wildlife have been shown to be a concern for species with small body size and short limb size suggesting that the physical characteristic of the species is the essential factor that allows for successful crossing over the rails. For instance, Kornilev *et al*. (2006) carried out an experiment by placing Eastern Box Turtles (*Terrapene Carolina*) between the rails and found that the turtles are physically unable to climb over the rails except on railway crossings. A similar study found that the railway represents a physical barrier for Gopher Tortoises (*Gopherus polyphemus*) as none of the habituated (familiar with the railway) and naïve (unfamiliar with the railway) tortoises managed to escape from the rails after several attempts (Rautsaw *et al.*, 2018). The movement behaviour of wildlife has also been investigated to demonstrate how railways can be a behavioural barrier. Mongolian gazelles (*Procapra gutturosa*) are considered highly mobile species and had no obstacles preventing crossing, yet the radio collared gazelles only exploited one side of the railway (Ito *et al.*, 2005). Bhattacharya *et al*. (2003) discovered that the marked bumblebees (*Bombus sp.*) seldom crossed the railway despite being physically capable to cross it. They found that only two individuals of 80 marked bees from the north side moved on the south side of the railway due to the decline of forage resources (Bhattacharya *et al*., 2003).

The bumblebees perceived the railway as a landmark and tend to return to their foraging site when they reach the edge of the railway (Bhattacharya *et al.*, 2003).

On the other hand, a similar experiment carried out in France observed many marked Gate-keeper Butterflies (*Pyronia tithonus*) crossing the railway (31%) and suggesting that the high-speed railways are not a behavioural barrier on these butterflies (Vandevelde *et al.*, 2012). This implies that the barrier effects created by railways on wildlife may differ between species and within species and can be a most pressing concern for species with limited physical traits and species that frequently cover large areas to access important resources. The consequences of railway barrier can result to serious implications on the genetic diversity and structure of wildlife populations due to reduced gene flow. A study in the United States of America found a significant genetic difference within a geographical close population of Marbled Salamanders (*Ambystoma opacum*) that were isolated by the railway track (Bartoszek & Greenwald, 2009). In the Netherlands, railways (and roads) resulted to the reduced genetic exchange among the populations of Moor Frog (*Rana arvalis*) (Vos *et al.*, 2001). Yu *et al.* (2017) also found the genetic differences on the endangered przewalski's gazelle (*Procapra przewalskii*) populations along the fenced railway line in China. Without any interventions, wildlife populations impacted by barrier effects on railways may face a greater threat of local extinction due to restricted movements and exchange of gene pools.

2.3. HABITAT LOSS

Railway infrastructure can present conditions for several species that provides important habitats as shelter, foraging and nesting places. For example, railway verges may support sheltering a same abundance of common bats as other habitats (Vandevelde *et al.*, 2014). Penone *et al.* (2012) also found that the railway edge can provide valuable habitats for bush crickets (*Tettigoniidae* sp.) and they even assert that the rail edges can play an essential part for the protection of insects in urban landscapes. However, the transformation of the landscape following the development of railway is directly associated with the reduction of available habitat for wildlife and the altered habitat becomes unfavourable for some species (Barrientos *et al.*, 2019). Habitat loss contributes to the decline of species richness, population abundance, distribution, and growth rate (Fahrig, 2003), suggesting that the permanent replacement of habitats by railway lines can represent a major threat on wildlife populations. For instance, A study carried out in France on the potential effects of the high-speed railway in the distribution of the endangered European Tree Frog (*Hyla arborea*) found a decline in their occupancy closer from the railway (0.5 km) than further away from the railway (3.5 km) due to fragmented habitat patches (Clauzel *et al.*, 2013). Another study in Portugal found a decrease in the abundance of breeding and wintering of shorebirds in impacted saltpans habitat which are considered as important for these birds after the construction of the railway line (Múrias *et al.*, 2017).

Conversely, a study assessing aquatic birds on the railway traversing wetland habitats found no differences in the species richness and abundances of aquatic birds closer to (<500 m) and further away from the railway (>500 m) (Godinho *et al.*, 2017). This suggests that the impact of habitat changes due to the development of railways may differ depending on the species affected since some species are tolerant of habitat conditions on the railway. Therefore, assessment of the potential effects of transformed habitats on wildlife related to railway development is necessary for the protection of prime habitats for species impacted. The introduction of alien invasive species that may be accidental dispersed by trains can also poses a severe threat to wildlife populations (Ascensão & Capinha, 2017). Rutkovska *et al*. (2013) observed more than 35 different alien plant species alongside the railway in Daugavpils City. Several factors determine the establishment of non-native species on a landscape, including competition and predation (White *et al.*, 2008). The non-native species outcompetes the native species for resources due to their competitive advantages of superior life history traits, thereby threatening the continued survival of native species (Peh, 2010). There is no work from my literature review that assessed the negative effects of alien invasive species on wildlife habitats bisected by the railway. However, it becomes clear that invasion of non-native species on the landscape due to railway development can be a serious concern for conservation of wildlife population. As such, studies on potential impacts of alien invasive species on wildlife caused to railway lines are needed to help find mitigation strategies.

2.4. DISTURBANCE

Disturbances that occur during the construction and operation of railways often negatively affects wildlife populations by causing shift in species richness and abundance (Lucas *et al.*, 2017). Railway disturbances on wildlife can contributes to habitat loss and barrier effects since certain species that are intolerance to disturbances may be excluded from habitats closer to the railway. Pollutions (noise, soil, water, and air pollution) arising from railway operations and human activities connected with the construction and maintenance work of railways are considered as main sources of disturbances to wildlife (Lucas *et al.*, 2017). Waterman *et al.*, (2020) found that noise created by passing trains negatively affected the densities of all meadow birds. Tibetan antelopes (*Pantholops hodgsonii*) successful used the underpass from their wintering range to calving ground but avoided using it during construction of the railway near the underpass because of uncleared machinery and debris (Xia *et al.*, 2007). However, they further argued that the use of the underpass by the tibetan antelopes will be improved after all machinery and debris have been removed (Xia *et al.*, 2007), suggesting that the wildlife disturbance due to human activities on railways may be temporary. Additionally, some species either disregard or adapt to human disturbances on railways. For example, a study in China found higher species richness and abundance of seven ground dwelling birds close to railway than away from the railway because these birds were accustomed to human activities (Li *et al.*, 2010). Similarly, a study in Poland found high diversity and abundance of birds near the railway line (30 m) than further away from it (530 m), despite the decrease of noise levels with increasing distance from the railway track (Wiącek *et al.*, 2015). Despite this, disturbances of wildlife on railways cannot be neglected because it can affect the reproductive success, foraging and communication behaviour of wildlife. For instance, noise pollution obstructs communication among species that produce sounds to acquire mates, defend territories, and give warning of danger from predators (Chen & Koprowsk, 2015). Therefore, understanding the disturbances associated with railways on wildlife is important for effective management and conservation of species that are susceptible to disturbances on railways.

Table 1: Reviewed papers (both peer-reviewed and non-peer-reviewed studies) on the impacts of railways on wildlife.

Impact	Species/Group	Scientific name	Country	Reference
Mortality	Eastern grey kangaroo	*Macropus giganteus*	Australia	Visintin *et al.*, (2018)
	Moose	*Alces alces*	Canada	Child *et al.*, (1991)
	American black bear	*Ursus americanus*		Dorsey *et al.*, (2017)
	Grizzly bear	*Ursus arctos*		
	Elk	*Cervus elaphus*		
	Deer	*Odocoileus* spp.		
	Elk	*Cervus elaphus*		Popp *et al.*, (2018)
	Moose	*Alces alces*		Hamr *et al.*, (2019)
	Elk	*Cervus elaphus*		
	Mammals (bears, carnivores & ungulates)			Clair *et al.*, (2020)
	Mammals (ungulates & carnivores)			Gilhooly *et al.*, (2019)
	Mongolian gazelle	*Procapra gutturosa*	China - Russia	Ito *et al.*, (2008)
	Brown bear	*Ursus arctos*	Croatia	Huber *et al.*, (1998)
	Mammals (large)		Czech Republic	Kušta *et al.*, (2011)
	Roe deer	*Capreolus capreolus*		Kušta *et al.*, (2014)
	Mammals			Nezval & Bíl, (2020)
	European hare	*Lepus europaeus*	Germany	Reck & Schmüser, (2019)
	Roe deer	*Capreolus capreolus*	Hungary	Cserkesz & Farkas, (2015)
	Red deer	*Cervus elaphus*		
	Wild boar	*Sus scrofa*		
	Leopard	*Panthera pardus*	India	Joshi, (2010)
	Asian elephant	*Elephas maximus*		Roy & Sukumar, (2017)
	Asian elephant	*Elephas maximus*		Joshi & Puri, (2019)
	Mugger Crocodile	*Crocodylus palustris*		Vyas & Vasava, (2019)

	Common Krait	*Bungarus caeruleus*		Kumar & Kumar, (2020)
	Indian Rat Snake	*Ptyas mucosa*		
	Sika deer	*Cervus nippon*	Japan	Onoyama *et al.*, (1998)
	Sika deer	*Cervus nippon*		Ando, (2003)
	Mammals (large)			Nishi *et al.*, (2012)
	Moose	*Alces alces*	Norway	Jaren *et al.*, (1991)
	Moose	*Alces alces*		Gundersen & Andreassen (1998)
	Moose	*Alces alces*		Gundersen *et al.*, (1998)
	Moose	*Alces alces*		Andreassen *et al.*, (2005)
	Amphibians		Poland	Budzik & Budzik (2014)
	Mammals (ungulates)			Krauze-Gryz *et al.*, (2017)
	Mammals (ungulates)			Jasińska *et al.*, (2019)
	Birds (wetland birds)		Portugal	Godinho *et al.*, (2017)
	Mammals, birds, reptiles, amphibians, invertebrates		Romania	Pop *et al.*, (2020)
	Birds		Spain	Melo *et al.*, (2016)
	Birds			Garcia de la Morena *et al.*, (2017)
	Moose	*Alces alces*	United States of America	Belant, (1995)
	Mammals, birds, reptiles & amphibians			Heske, (2015)
	Moose	*Alces alces*	Unknown	Rea *et al.*, (2010)
Barrier	Toad-headed Lizard	*Phrynocephalus vlangalii*	China	Hu *et al.*, (2012)
	Przewalski's gazelle	*Procapra przewalskii*		Yu *et al.*, (2017)
	Mongolian gazelle	*Procapra gutturosa*	China - Russia	Ito *et al.*, (2005)
	Gate-keeper Butterfly	*Pyronia tithonus*	France	Vandevelde *et al.*, (2012)
	Moor Frog	*Rana arvalis*	Netherlands	Vos *et al.*, (2001)
	Invertebrates (bumblebee)	*Bombus impatiens* *Bombus affinis*	United States of America	Bhattacharya *et al.*, (2003)
	Eastern Box Turtle	*Terrapene carolina*		Kornilev *et al.*, (2006)

	Marbled Salamander	*Ambystoma opacum*		Bartoszek & Greenwald, (2009)
	Gopher tortoise	*Gopherus polyphemus*		Rautsaw *et al.*, (2018)
Habitat loss	Black rat	*Rattus rattus*	Australia	Price & Banks, (2018)
	Invertebrates (bush crickets)	*Tettigoniidae* sp.	France	Penone *et al*., (2012)
	Mammals (common bats)			Vandevelde *et al.*, (2014)
	European Tree Frog	*Hyla arborea*		Clauzel *et al.*, (2013)
	Birds (Wetland birds)		Portugal	Godinho *et al.*, (2017)
	Birds (Shorebirds)			Múrias *et al.*, (2017)
Disturbance	Mammals (small)		Brazil	Cerboncini *et al.*, (2016)
	Tibetan antelope	*Pantholops hodgsonii*	China	Xia *et al.*, (2007)
	Birds (ground-dwelling birds)			Li *et al.*, (2010)
	Birds (meadow birds)		Netherlands	Waterman *et al.*, (2002)
	Birds		Poland	Wiącek *et al.*, (2015)

CHAPTER 3: ECOLOGICAL SETTINGS OF THE STUDY AREA

3.1. LOCATION

BNR is situated in the western part of the Kruger National Park, Limpopo Province of South Africa. The reserve is one of Associated Private Nature Reserve (APNR) of the Greater Kruger Park, which is a group of privately-owned nature reserves with no boundary fence between them and adjoins Kruger National Park (hereafter "KNP") to form Greater Kruger Park (Figure 1). The fence removal initiative between BNR and neighbouring reserve (Klaserie Nature Reserve) was aimed at expanding habitats for local wildlife through creating a large open system that allows wildlife to move freely across the landscape. This means that animals able to move from the world famous KNP until they reach the Western boundary fence of BNR.

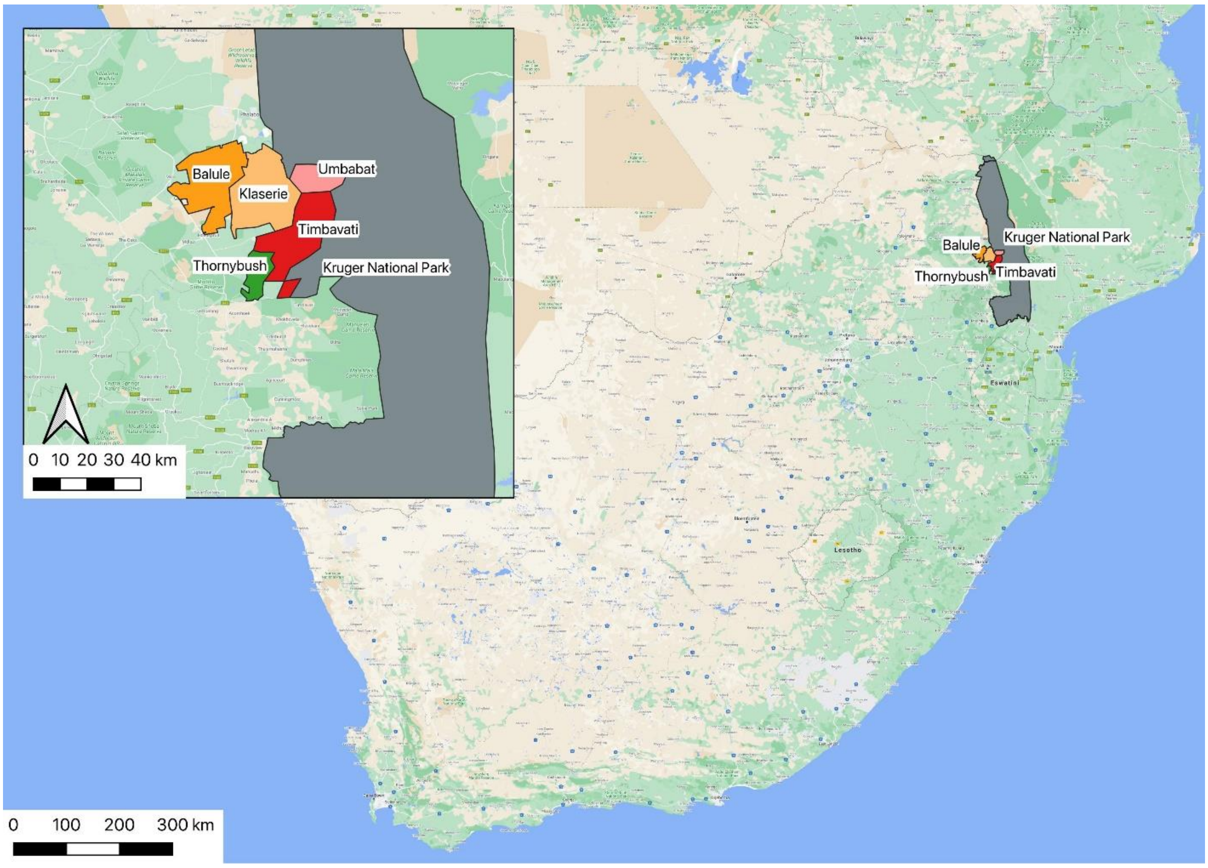


Figure 1: Location of BNR in relation to other APNR and KNP.

BNR is primarily made up of several properties from privately-owned farms which were previously fenced. It was established in 1993 following the dropping of internal fences and official secured a nature reserve status in 2005. The reserve expands regularly as landowners voluntarily decide to integrate their land into the reserve. Currently, the reserve covers a total surface area of 56 000 hectares and consist of nature reserves which are subdivided into management regions (Figure 2).

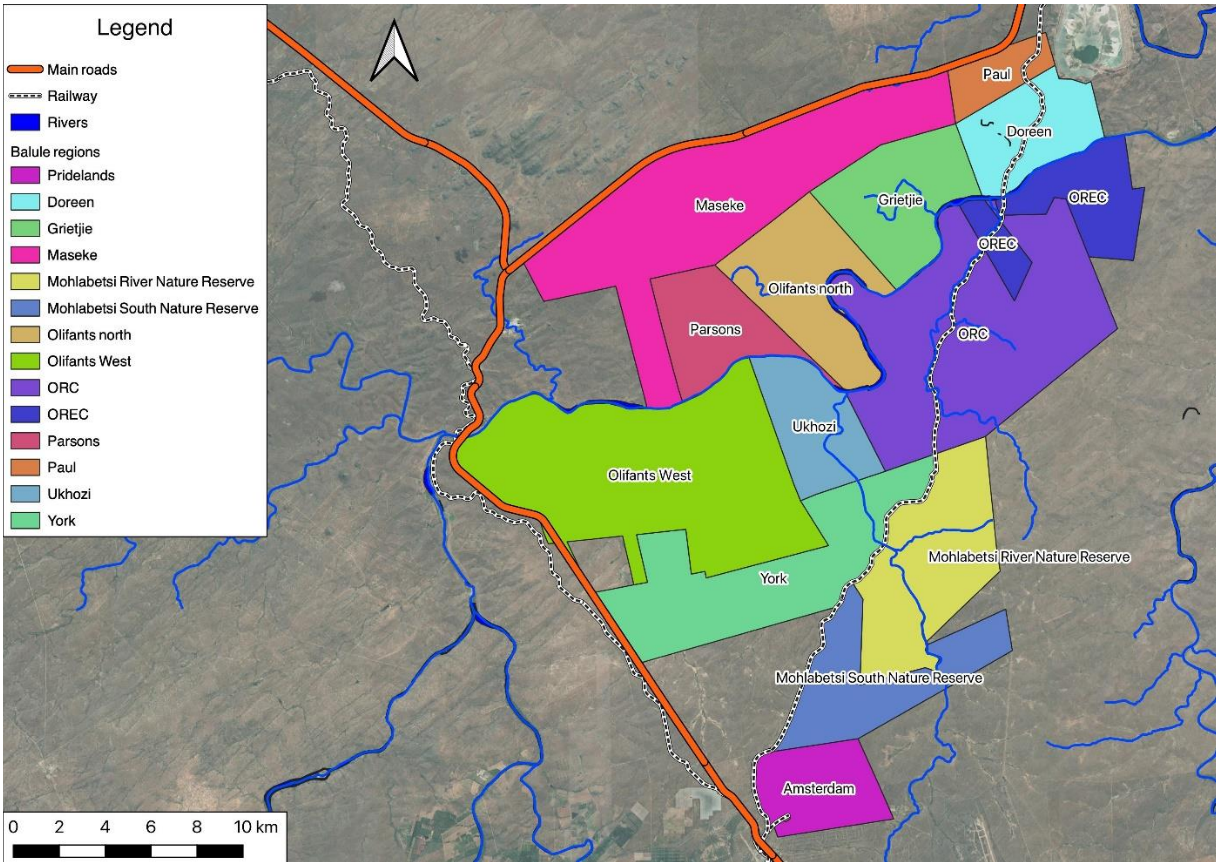
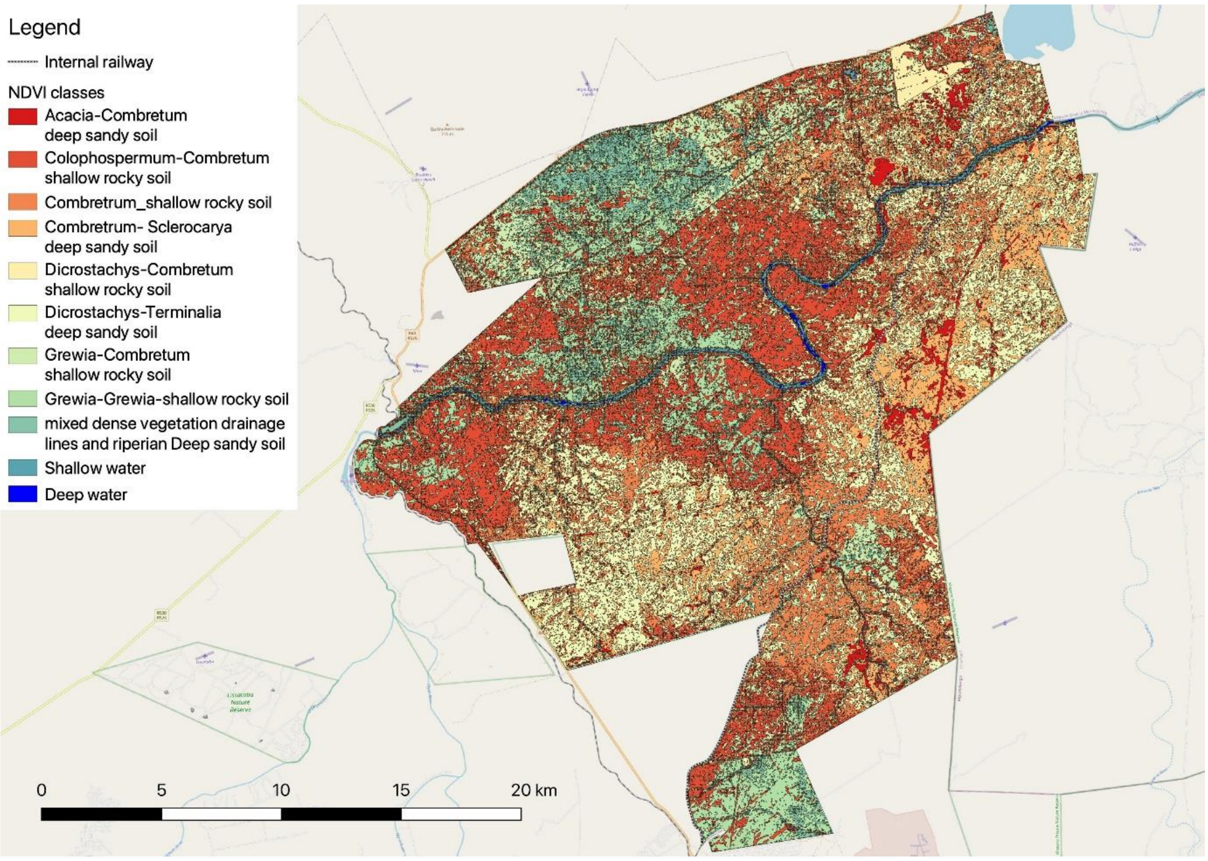


Figure 2: Different management regions that form part of BNR.

3.2. FLORA AND FAUNA

BNR completely falls under the savanna biome within the dry savanna subregion (M'marete, 2003; Mucina & Rutherford, 2006). The vegetation in the study area is recognised by the Lowveld Rugged Mopaneveld and Granite Lowveld vegetation units of the Mopane and Lowveld Bioregions (Mucina & Rutherford (2006), ranging from open grass layer and scattered trees to dense woodlands (Peel *et al.*, 2021).

The reserve is part of the large open system that adjoins the KNP, which is well known for its highly diverse range of species (Mwakiwa, 2011). As such, BNR provides a home to a diverse array of species, with more than 140 species of mammals, 450 species of birds, 100 species of reptiles and 30 species of amphibians (Mwakiwa, 2011). This includes the "Big Five"; African elephant, black rhinoceros, African buffalo (*Syncerus caffer*), leopard (*Panthera pardus*), and lion (*Panthera leo*), and many other species that are vulnerable (e.g., cheetah, *Acinonyx jubatus*), endangered (e.g., African wild dog, and critically endangered (e.g., White-backed Vulture, *Gyps africanus*) (IUCN, 2021). Moreover, the Olifants River running through the reserve is a home to water associated animals, such as the hippopotamus (*Hippopotamus amphibious*) and Nile Crocodiles (*Crocodylus niloticus*).



3.3: Vegetation map showing the composition of woody plant communities in BNR.

3.3. CLIMATE

The climate in the savanna biome is characterised by a very distinct seasonal rainfall pattern of wet summers and dry winters (Mucina & Rutherford, 2006). Around 90% of annual rains occurs during the summer months in the province (M'marete, 2003). In the study area, the wet summer months are experienced between November – April and the dry winters occurs from May - October (Lagendijk *et al.*, 2015). According to the long-term monitoring data accessed from the reserve, BNR receives the annual seasonal rainfall of 200 – 600 mm with the mean rainfall of 406 mm (Figure 3). The climatic condition in the region is characterised by extremely hot summer and cool winter periods (M'marete, 2003). The temperatures in the reserve ranges from 4 – 45°C (Lagendijk *et al.*, 2015), with the mean annual temperature of round 21°C (Mucina & Rutherford, 2006).

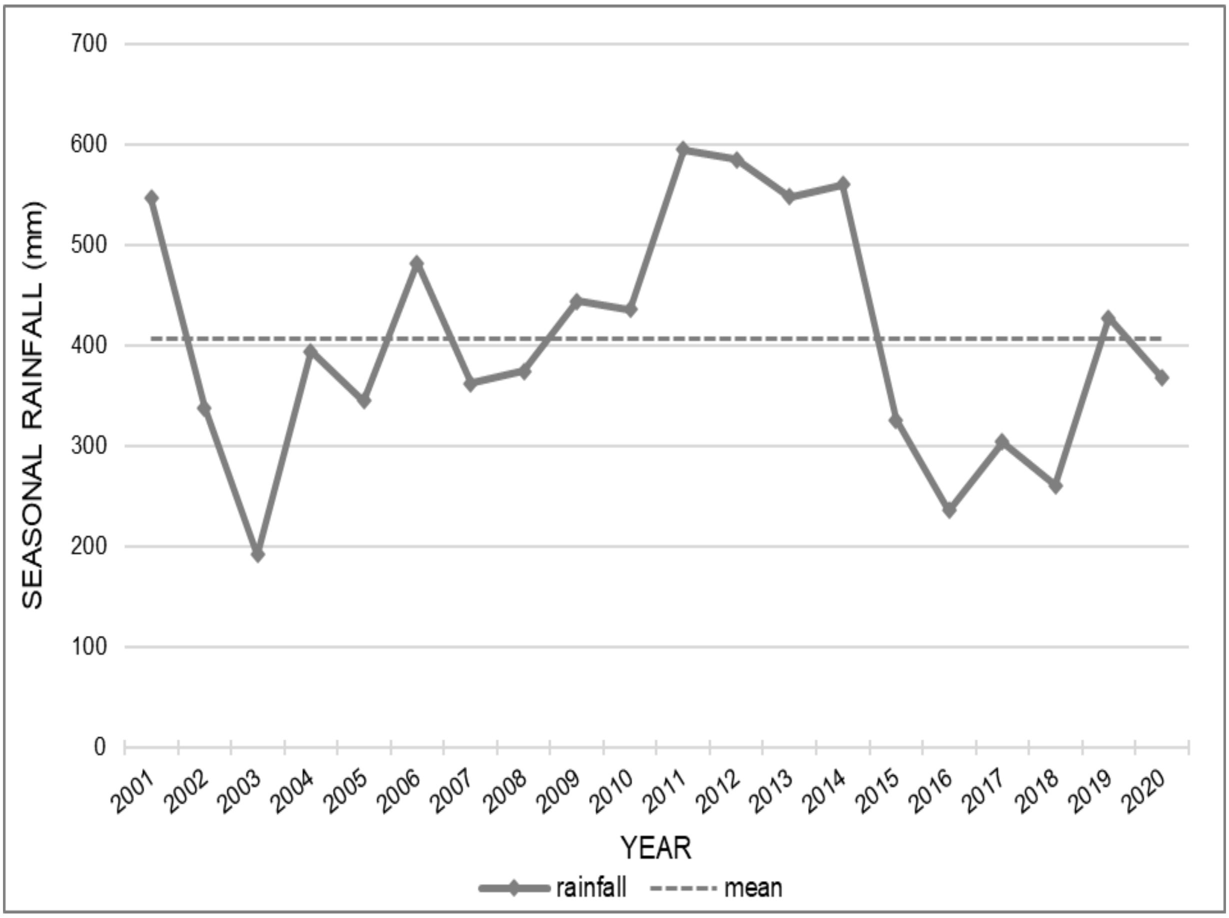


Figure 3: Seasonal rainfall (mm) received in the study area over the past 20 years. (Accessed from OWNR weather station).

3.4. TOPOGRAPHY AND GEOLOGY

The topography throughout the study area is relatively undulating with elevation of between 340 – 450 meters above sea level (Lagendijk *et al.*, 2015). The underlying geology in the study area is Goudplaats and Makhutswi Gneiss which weathers into clay soils of high sodium content in the granite lowveld (Mucina & Rutherford, 2006). Hutton, Mispah and Glenrosa are the predominantly soil forms in the mopane lowveld, producing red-yellow apedal, shallow and freely drained soils (Mucina & Rutherford, 2006).

3.5. STUDY SITE

The railway line bisecting the reserve from Phalaborwa to Hoedspruit town was established in 1963 to facilitate in the transportation of rich phosphate and copper deposits from the mines (Stephan, 1967). The 45.3 km line on the landscape of BNR is predominantly a single lane with two right-of-way stations at the center and further south of the reserve. Of the 45.3 km stretch, 14 km is inaccessible for most wildlife because it is fenced off with a Kruger Standard Fence, unless animals walk directly along the rail line. Thus, 31.3 km stretch was considered for this study (Figure 4).

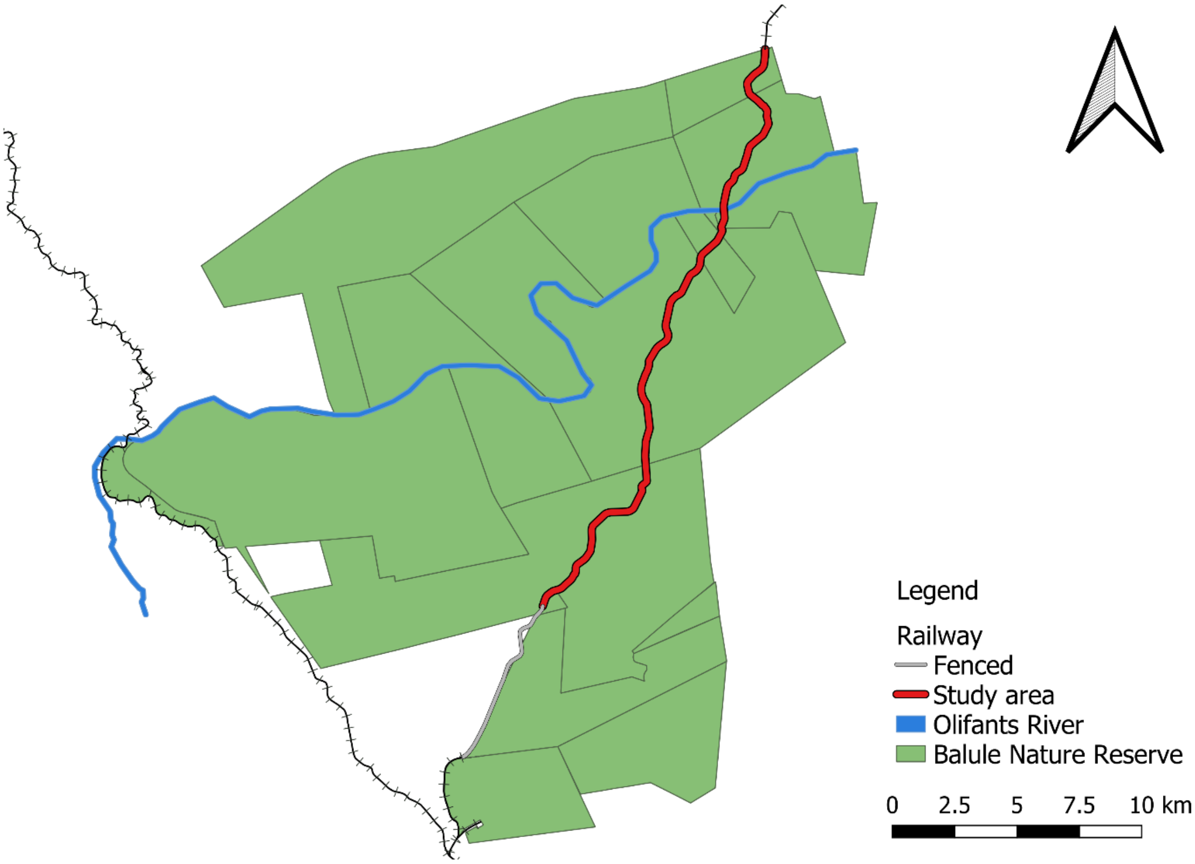


Figure 4: The stretch of the railway line monitored for this study (unfenced stretch).

The trains running through the landscape of BNR were previously electric powered and later changed to diesel locomotives (P. Allin, *pers. comm.*). Although the trains are currently operated with diesel engines, overhead wires with other supporting structures (steel poles) can still be noticed on the railway line as were not removed (*pers. obs*). Because there was no available data monitoring the train traffic, this study recorded approximately 13 trains per day on average, ranging from a minimum of 5 trains per day to a maximum of 23 trains per day. The train frequency on the reserve largely dependent on the schedule operations from the railway authority (Transnet Limited) as there were often consecutive days without a single train running through the landscape of BNR. The railway track consists of more than 65 underpasses of varying sizes, ranging from small (≤ 1 m) to very large (≥ 5 m) sizes from both sides of the railway (*pers. obs*). These underpasses may have originally been built without considering the safe passage of wildlife since entire stretch of the railway line on the reserve was previously fenced-off from both sides. However, several mammal and bird species have been recorded using the underpasses (*Unpublished data*).

CHAPTER 4: ACTIVITY PATTERNS OF MEDIUM-LARGE MAMMALS ON AND AROUND THE RAILWAY LINE.

4.1. INTRODUCTION

The rapid increase of human population and economic growth necessitate the expansion of transport infrastructure for passenger travel and movement of goods (Dulac, 2013). As of 2014, there were more than 1.3 million km of railway globally (Morelli *et al.*, 2014), and there is a projected increase of 45% by 2050 (Popp & Boyle, 2017). In Africa, railway expansion is associated with the anticipated population growth, urbanization, and the development of new mines (African Development Bank, 2015). The development of transport infrastructure is considered as one of leading threat for biodiversity loss (Benítez-López *et al.*, 2010; Torres *et al.*, 2016; Sharma *et al.*, 2018) and rail ecology studies have shown that wildlife are negatively affected by human activity following the development and operation of railways as it result in wildlife mortalities (e.g., Heske, 2015), barrier effects (e.g., Rautsaw *et al.*, 2018), habitat loss (e.g., Múrias *et al.*, 2017), and disturbances (e.g., Waterman *et al.*, 2020). This represents serious concerns for the management of wildlife populations in areas where railways bisect their habitats, like BNR, as sensitive species avoids exploiting areas adjacent to railways due to intolerance of human-induced disturbances (Lucas *et al.*, 2017).

There is growing evidence that human-induced disturbances influence the behaviour of wildlife and wild animals may adjust their spatiotemporal activity to avoid or minimize encounters of human activity (Neumann *et al.*, 2013; Carter *et al.*, 2015; Gaynor *et al.*, 2018; Cremonesi *et al.*, 2021; Larm *et al.*, 2021). For instance, moose (*Alces alces*) were found more often closer to roads from 18:00 in the evening until 06:00 in the morning when traffic volume is low (Neumann *et al.*, 2013). Changes in wildlife activity patterns may contribute to physiological stress which in turn affects the survival and reproductive success of wildlife population (Houngbégnon *et al.*, 2020). Moreover, human activity can negatively affect the spatial distribution of wildlife populations in relation to the distance from the infrastructure (Rost & Bailey, 1979; Reijnen *et al.*, 1995; Benítez-López *et al.*, 2010; Rashidi *et al.*, 2019; Waterman *et al.*, 2020). Deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) kept away from roads within 200 m distance (Rost & Bailey, 1979). Train traffic resulted to the reduction of meadow birds close to the railway (Waterman *et al.*, 2020). Similarly, Rashidi *et al.*, (2019) found a decline in bird abundance and diversity closer to the roads (65 m) due to traffic noise. The completely lack of data on the activity patterns of wildlife on and proximity to the railway line limits our understanding on the potential disturbance effects of human activity associated with railway operations (e.g., train operations) on wildlife.

Rail ecology studies have shown that the risks of rail mortality vary temporally as collisions of wildlife with trains can be more frequent at distinct times of the day and seasons in relation to their daily their daily activity patterns (e.g., Gundersen & Andreassen, 1998; Roy & Sukumar, 2017), seasonal dispersal or migration (e.g., Gundersen *et al.*, 1998; Krauze-Gryz *et al.*, 2017), and changes in forage availability (e.g., Pollock *et al.*, 2019). In addition, spatial variation of rail mortality has also been shown, with more risk of train collision occurring at certain areas or sections of the railway bisecting important habitat preferred by wildlife (e.g., Kušta *et al.*, 2014). How an animal selects a particular habitat on the landscape can be influenced by several factors, including resource availability, cover, competition, and predation (Krausman, 1999). For example, herbivores might select habitats with low vegetation cover to minimise the risk of predation by carnivores (Hopcraft *et al.*, 2005; Riginos & Grace, 2008; Burkepile *et al.*, 2013). Consequently, this could affect how the activity of wildlife are pronounced between surrounding habitats on the railway line. It becomes clear that the activity of wildlife on the railway line are influenced temporal and spatial factors and affects their risk of train collision. Therefore, information on spatiotemporal activity patterns of wildlife around the railway line is necessary to advance our knowledge on the risks related to WTC and guide for management decisions for possible mitigation measures to reduce chances of WTC.

In this study, I investigate the activity patterns, both spatial and temporal, of medium-large sized mammals (≥ 10 kg) on a landscape bisected by the railway line in BNR. Medium-large mammals were selected for this study because their carcasses arising from train collisions are likely to attract scavengers to spend more time on the railway than carcasses of smaller animals, thereby increasing the chances of further wildlife-train collisions (Cserkesz & Farkas, 2015). Specifically, I assess the activity of mammals (≥ 10 kg) utilizing the railway line to determine their daily activity patterns of occurrence on the railway line. Secondly, I explore temporal overlap in the activity of mammals (≥ 10 kg) utilizing the railway with that of train activity to determine whether the degree of activity overlap differs between seasons. Finally, I examine the activity of mammals (≥ 10 kg) in proximity to the railway line to determine whether the distance from the railway line, season and rail-side habitat affects the activity of mammals around the railway line.

I hypothesised that the degree of activity overlap between mammals (≥ 10 kg) and trains will vary between seasons, with a degree of overlap in the dry season (May – Oct) than the wet season (Nov – Apr) because they are more likely to cover large distances in the dry season searching for food and water (Ogutu *et al.*, 2008; Owen-Smith & Ogutu, 2012; Venter *et al.*, 2015), and thereby increasing their chances to interact with train activity. Based on existing studies that documented a decline in the distribution of wildlife in proximity to infrastructure (Benítez-López *et al.*, 2010; Rashidi *et al.*, 2019; Waterman *et al.*, 2020), I hypothesised that the activity of mammals (≥ 10 kg) will be negatively affected by the distance from the railway line, with more activity of mammals at increasing distance from the railway. I hypothesised that season would influence the activity patterns of mammals (≥ 10 kg) around the railway line because seasons influence the dispersal cycles of wildlife (Ogutu *et al.*, 2008), thereby affecting their movements around the railway line. Additionally, I hypothesised that activity patterns of mammals (≥ 10 kg) will be influenced by the surrounding habitat on the railway because an animal is likely to spend increasingly amount of time from one habitat compared to other habitat types (Krausman, 1999), thereby resulting to disproportional in activity patterns between rail-side habitats.

4.2. METHODOLOGY

4.2.1. Target species

The body weight (small, medium & large) is frequently used in mammals as practical categories that require different methods but not as taxonomic groupings (Hoffmann *et al.*, 2010). For this study, I focused on six medium-large sized mammal species whose body weight is greater than or equal to 10 kg (Table 2). These medium-large mammal species were selected because they are amongst the frequently reported species in wildlife-train collision in the study area (see appendix A).

Table 2: Selected medium-large mammal species for this study.

#	Common name	Scientific name	Body weight (kg) (Apps, 2012)	Status (IUCN, 2021)
1	African buffalo	*Syncerus caffer*	530	Near Threatened
2	African elephant	*Loxodonta africana*	3 200	Endangered
3	Giraffe	*Giraffa camelopardalis*	828	Vulnerable
4	Impala	*Aepyceros melampus melampus*	41	Least Concern
5	Lion	*Panthera leo*	153	Vulnerable
6	Spotted hyaena	*Crocuta crocuta*	60	Least Concern

4.2.2. Study period and site

African savanna ecosystem is generally classified into wet season and dry season that differs according to the rainfall (Young *et al.*, 2009**;** Table 3). In this ecosystem, the seasonal variations in rainfall can result in dramatic changes in wildlife behaviour as it affects their migration, dispersal, foraging as well as the reproduction cycles (Ogutu *et al.*, 2008). Therefore, the behavioural cycles of wildlife between these seasons are likely to influence the activity patterns of target mammals on and along the railway line.

Table 3: Sampling period of the study according to the seasonal rainfall experienced in the study area classified by Lagendijk *et al.*, (2015).

SEASON	RANGE	SAMPLING PERIOD
Dry	May - October	mid-May - October
Wet	November - April	mid-November - early April

I conducted the study on the railway sections bisected by three broad habitat types found on the reserve (Figure 5). These habitat types were classified through a satellite image, Normalized Difference Vegetation Index (NDVI) and validated with the data of woody vegetation surveys collected from randomly selected sites across the reserve (1327 plots), which was made available by the reserve before the commencement of this study. I grouped NDVI class codes with similar averages of woody plant density and structure (tree height & stem) into a single broad habitat type. I therefore distinguished habitat types bisecting the railway based on variation in vegetation cover of woody plants as follows:

- Open grassland: woody plant density of less than 10%, and dominated by single-stemmed trees with a height of less than 1.5 m.
- Open woodland: woody plant density ranging from 25 – 30%, and dominated by single-stemmed trees with a height of more 4 m.
- Mixed shrubland: woody plant density of about 50 – 55%, and dominated by multi-stemmed trees of more than 1.5 m and less than 4 m.

4.2.3. Data collection

To monitor the activity of target species on the landscape bisected by the railway line, as well as on the railway line, I deployed 54 number of camera traps wildlife camera traps (Cuddeback, Infrared model 1354 and strobe model 1347; https://www.cuddeback.com/products/professional-no-flash). In each habitat type, I deployed six camera trap sites and facing along the railway, where the camera traps were approximately 160 – 170 m apart. From each of these camera sites, I further deployed 48 camera traps in a grid layout, starting close to the railway and moving perpendicular away to the railway line (Figure 5). The grid layout was repeated on both sides of the railway line stretch and the distribution of camera traps away from the rail line was based on the number of available camera traps and access to site.

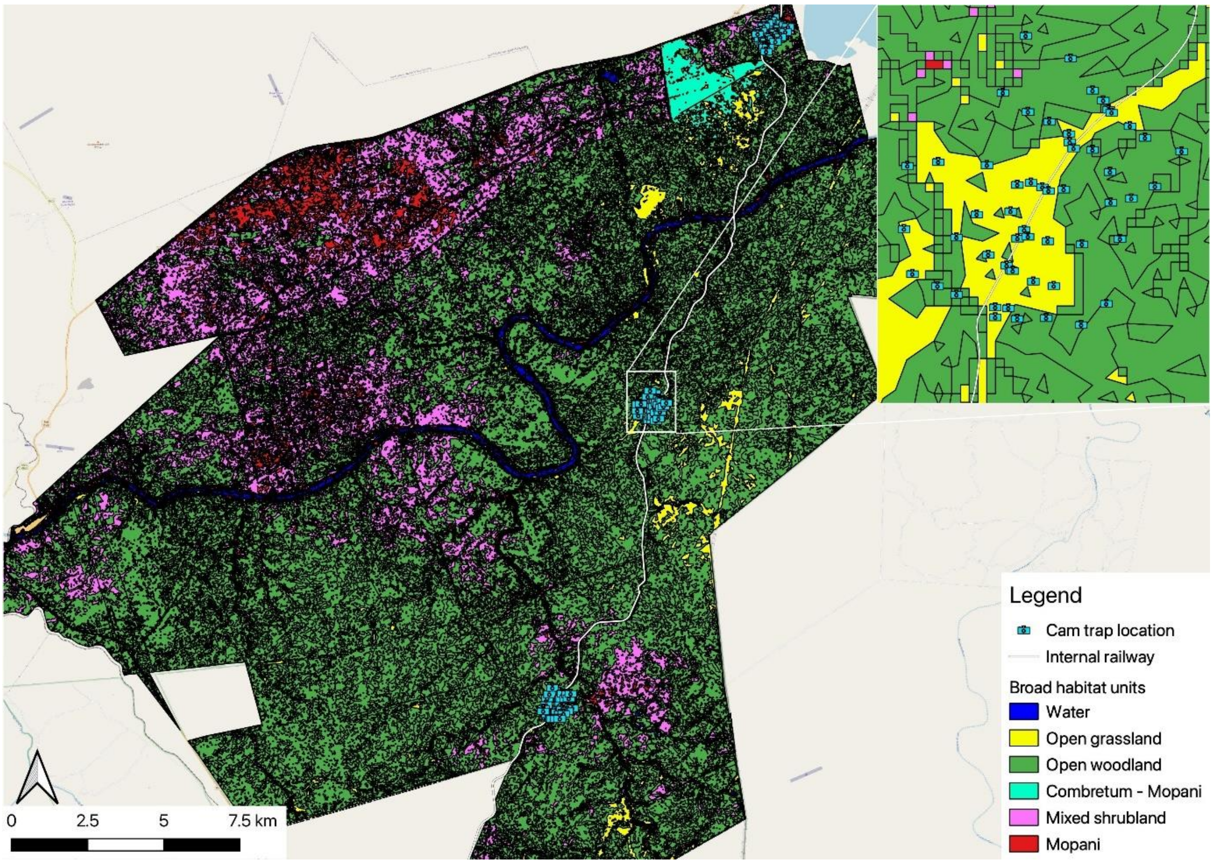


Figure 5: Location of camera traps on and along the railway during the study period.

To collect data across all habitat types and seasons, I sampled each habitat type bisected by the railway for 6 weeks within the two seasons due to the limited number of camera traps. Because of variation in habitat with increasing distances from the railway line, the habitat type for each camera trap at distances away from the railway was noted during the deployment. The camera traps on the railway line were secured on the rail post structures, while camera traps in proximity of the railway were secured on tree trunks. All the camera traps were set at the height of ≤ 75 cm above ground and operated for the entire day cycle. I used wildlife trails in the selection of the location of camera traps to maximise the likelihood of detection, and the vegetation or any other object that could obstruct the camera was removed (Rovero & Zimmermann, 2016).

I programmed all the camera traps to take one photo when motion is detected with a one-minute time delay to prevent storage of large number of similar images, especially for camera traps placed along the railway line which also recorded the movement of passing trains. The initial operating date and time of all camera traps as well as their location was recorded on the data sheet when they were deployed in the field (Appendix B). I revisited the camera traps after three weeks to check for possible camera malfunction, replace memory cards and batteries if needed and a check-up data sheet was used when the cameras were visited (Appendix C).

4.3. DATA ANALYSIS

4.3.1. Data preparation and processing

Prior to the analysis of camera trap data, I manually checked all photographs to identify the content of each photo and the information was recorded on an Excel spreadsheet (Microsoft Excel 365; Microsoft Inc., Redmont, USA). A full list of all mammal species captured on and along the railway during the study period is found in Appendix D. I considered an image as a single capture event regardless of the number of conspecific individuals on the image as some targeted species, such as Impala, live in social groups (Skinner & chimimba, 2005**;** Apps, 2012). To reduce pseudoreplication of capture events with the same individuals, images from the same camera trap location within 15-minute intervals from the initial picture captured were excluded from the data set. To explore how each species' activity changes with proximity to the railway, I explored the changes in frequency of their occurrence on each camera trap.

4.3.2. Daily activity patterns

To determine the daily activity patterns of target species on the railway line, I used the time at which a species was captured on the railway line. Firstly, I obtained the time of sunrise and sunset in the study area from the website (www.sunsetsunrisetime.com) to categorise each capture event on the railway as either diurnal, nocturnal or crepuscular (Ogurtsov *et al.*, 2018; Houngbégnon *et al.*, 2020). Following similar the procedure used by Ross *et al.* (2013); Monterroso *et al.* (2014), and Houngbégnon *et al.* (2020), the time intervals for each period were as follows:

- crepuscular period: one hour before and after sunrise and sunset.
- diurnal period: one hour after sunrise until one hour before sunset.
- nocturnal period: one hour after sunset until one hour before sunrise.

I then determined the daily activity pattern of target species in their occurrences on the railway line following a classification method used by Gómez *et al.* (2005); Monterroso *et al.* (2014), and Houngbégnon *et al.* (2020), which is based on the proportion of captured events from the above mentioned three time periods. A species was classified as:

1) strongly diurnal: 90% or more of capture events recorded at diurnal period.
2) strongly nocturnal: 90% or more of capture events recorded at nocturnal period.
3) mostly diurnal: 70 – 89% of capture events recorded at diurnal period.
4) mostly nocturnal: 70 – 89% of capture events recorded at nocturnal period.
5) cathemeral: 30 – 69% of capture events recorded at diurnal and/or nocturnal period.

4.3.3. Seasonal activity overlap

To determine the extent of seasonal activity of overlap for each target species utilising the railway line with passing trains, I used the kernel density analysis developed by Ridout & Linkie, (2009). This is a non-parametric technique for estimating the probability density function of a random variable, which is time of day that the target species and trains were captured in our case. The degree of temporal overlap in seasonal activity between a target species and train was measured using the coefficient of overlapping (Δ), which ranges from 0 (no overlap) to 1 (complete overlap) (Ridout & Linkie, 2009). The coefficient of overlap is the area under the curve that is formed by taking the minimum of two density functions at each point in time.

For this study, I used Δ_1 and Δ_4 depending on the size of the two samples that are compared as recommended by Meridith & Ridout, (2014). Δ_1 was used when the sample sizes of capture events between a target species and trains is less than 75 and Δ_4 was used when the sample sizes of capture events from both target species and trains is more than 75. For this analysis, the activity of overlap on the railway by a target species and trains between seasons was defined as high if the $\Delta > 0.75$, moderate if $0.5 > \Delta \geq 0.75$, and low if $\Delta \leq 0.5$ (Houngbégnon *et al.*, 2020). Additionally, I calculated the mean and 95% confidence interval of activity overlap estimates from 1 000 bootstrap samples (Meridith & Ridout, 2014, Figure 6).

4.3.4. Factors affecting the activity of target species

I used the Generalized Linear Models (GLMs) to explore how the activity of target species (i.e., capture events) were affected by the distance to the railway, season, and habitat. I used negative binominal regressions as my data are counts of capture events were over-dispersed. I used the frequency with which the target species was captured as response variable and the distance from railway (meters), seasons, and habitat types as explanatory variables. Additionally, I accounted for varying camera trapping effort by incorporating the number of days each camera was functioning as an offset. For each target species, I constructed seven models including the main effects of distance the railway line, season and habitat variables and combination of these main effects.

To determine the most parsimonious model, I used model selection. Akaike Information Criterion adjusted for small sample sizes (AICc), with lowest AICc score indicating the best-performing model. However, models with the AICc score difference (ΔAICc) of less than 2 were regarded as having equal support (Burnham & Anderson, 2002). To validate the best-fitting model between competing models, I computed the Likelihood Ratio Test (LRT) to assess whether adding one predictor variable (main effect) significantly improves the model. I performed the statistical analysis in R program version 4.0.5 (R Core Team, 2021) using the 'lubridate' (Grolemund & Wickham, 2011), 'tidyverse' (Wickham *et al.*, 2019) 'overlap' (Ridout & Linkie, 2009), 'MuMIn' (Barton, 2020), 'AICcmodavg' (Mazerolle, 2020), 'visreg' (Breheny & Burchett, 2017), 'sjPlot' (Lüdecke, 2021) packages.

4.4. RESULTS

I recorded a total of 16 912 photographs of the six target species on and alongside the railway line from 262 days of camera trapping. Of these, 7 356 photos were classified as independent capture events (Table 4). Impala was the most frequently captured species with 4 463 capture events, followed by African elephant (*n* = 1 462), giraffe (*n* = 541), spotted hyaena (*n* = 462), African buffalo (*n* = 355) and lion (*n* = 73). I registered a total of 3 387 trains during the period of this study (12.93 trains per day, range: 5 – 23 trains/day).

Table 4: Number of capture events of target mammal species at different distances (m) from the railway (RR) and the total proportion of capture events for each target species (%) during the study period.

SPECIES	DISTANCE (m)					TOTAL	%
	0 (RR)	50	100	250	500		
African buffalo	15	125	113	55	47	**355**	**5**
African elephant	131	435	443	230	223	**1462**	**20**
Giraffe	56	124	132	109	120	**541**	**7**
Impala	264	908	1204	931	1156	**4463**	**61**
Lion	7	12	18	12	24	**73**	**1**
Spotted hyaena	42	124	126	74	96	**462**	**6**
TOTAL	**515**	**1728**	**2036**	**1411**	**1666**	**7356**	**100**

Table 5: Classification of daily activity patterns of target mammal species on the railway based on the proportion of capture events (%) at different activity periods according to Gómez *et al.* (2005); Monterroso *et al.* (2014), and Houngbégnon *et al.* (2020).

Species	*N*	Diurnal (%)	Nocturnal (%)	Crepuscular (%)	Classification
African buffalo	15	20	60	20	Cathemeral
African elephant	131	44.3	34.4	21.3	Cathemeral

Giraffe	56	82	2	16	Mostly diurnal
Impala	264	75	4	21	Mostly diurnal
Lion	7	29	71	0	Mostly nocturnal
Spotted hyaena	42	7	67	26	Cathemeral

4.4.1. African buffalo (*Syncerus caffer*)

The African buffalo exhibited a cathemeral pattern in their occurrences on the railway line, 60% of captured events occurred at nighttime and 20% during daytime period (Table 5). The activity of overlap by buffalo with trains on the railway line differed between seasons. I found a high degree of overlap during the dry season (Δ_1 = 0.77, CI = 0.28 – 0.80) and a moderate overlap during the wet season (Δ_1 = 0.55, CI = 0.28 – 0.71) in the diel activity of African buffalo with train on the railway line (Figure 7).

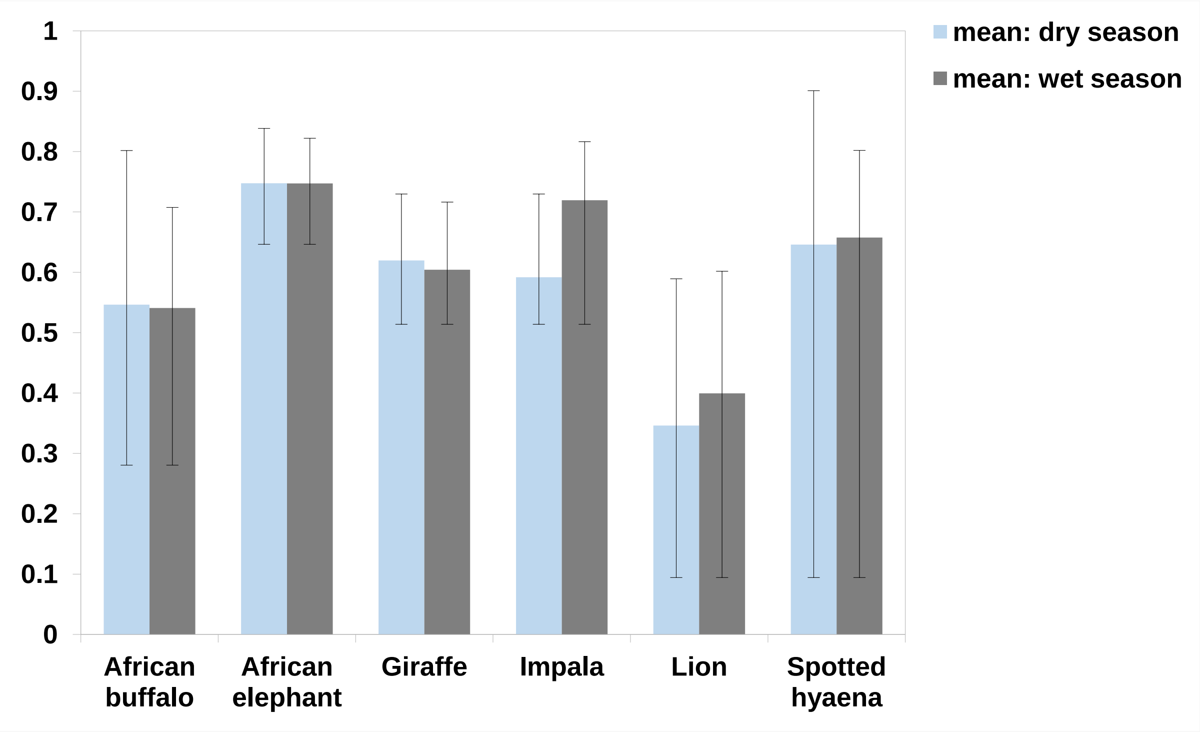


Figure 6: Mean and 95% bootstrap Confidence Intervals (CI) estimates in the seasonal activity overlap between target species and trains on the railway line.

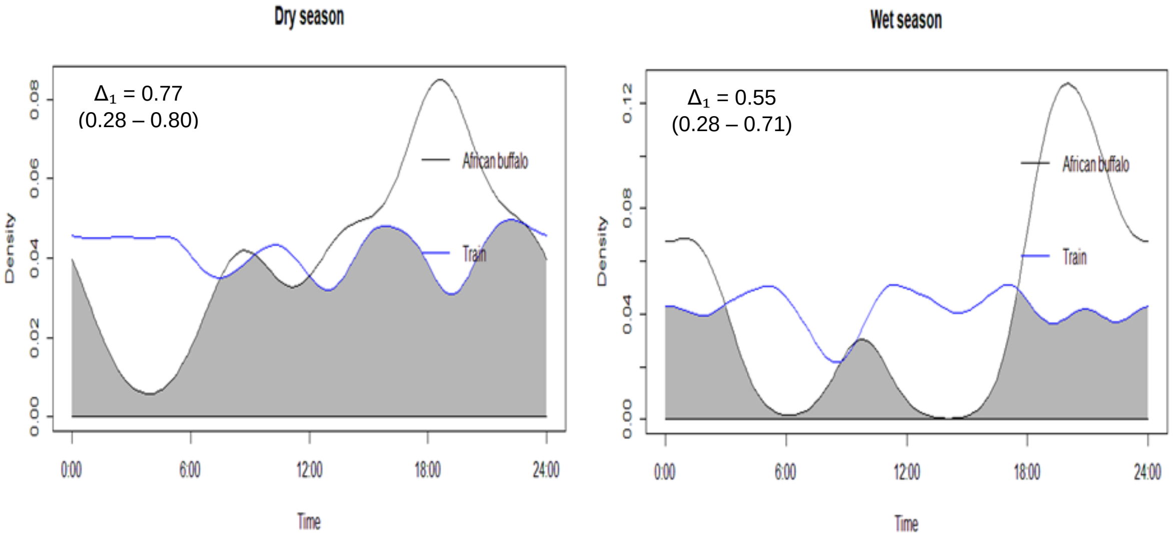


Figure 7: Estimates of temporal activity overlap (Δ) between African buffalo (black line) and train (blue line) in the dry season (left) and wet season (right). Grey shaded area is the coefficient of overlapping.

I found similar support that the distance to the railway line and surrounding habitat (AICc = 832.93, wAICc = 0.41) and the combination of distance, habitat, and season (AICc = 833.06, wAICc = 0.13) affect the activity of buffalo (Table 6). However, adding season to the distance and habitat model did not significantly improve the model (LRT: $p > 0.05$), and thus, distance and habitat model was selected as the best fit model in explaining the activity of buffalo around the railway.

Table 6: Ranked (low – high) GLMs examining the effects of distance, habitat, and season on African buffalo activity in proximity to the railway line. Models showing values for Akaike Information Criterion corrected for small sample sizes (AICc), differences between models and the top-ranked model (ΔAICc), Akaike weight (wAICc), Log-likelihood (LL), and the number of parameters (K).

	AICc	**ΔAICc**	**wAICc**	**LL**	**K**
Distance + Habitat	832.93	0.0	0.41	-411.36	5
Distance + Habitat + Season	833.06	0.13	0.38	-410.39	6
Habitat	835.27	2.34	0.13	-413.57	4
Habitat + Season	836.31	3.38	0.08	-413.06	5
Distance	874.49	41.56	0.00	-434.20	3
Distance + Season	875.14	42.41	0.00	-433.51	4
Season	880.80	47.87	0.00	-437.37	3

African buffalo are significantly less active with increasing distance from the railway ($p = 0.030$), and significantly less active in open grassland ($p < 0.001$) and woodland ($p = 0.034$) compared to the mixed shrubland habitat bisected by the railway line (Table 7).

Table 7: GLM results of factors affecting the activity of African buffalo on the landscape bisected by the railway line.

	Estimate	Std. Error	z-value	Pr(>|z|)
(Intercept)	-3.052	0.165	-18.550	<0.001
DISTANCE	-0.002	0.001	-2.167	0.030
HABITAT open grassland	-2.032	0.317	-6.419	<0.001
HABITAT open woodland	-0.391	0.185	-2.116	0.034

4.4.2. African elephant (*Loxodonta africana*)

44.3% and 34.4% capture events were recorded during diurnal and nocturnal periods for elephant on the railway, indicating cathemeral behaviour in their daily occurrences on the railway line (Table 5). The extent of overlap in the diel activity of elephant with trains on the railway were similar between seasons, both the dry ($\Delta_1 = 0.75$, CI = 0.65 – 0.84) and wet season ($\Delta_4 = 0.70$, CI = 0.66 – 0.82) showing a moderate overlap (Figure 8)

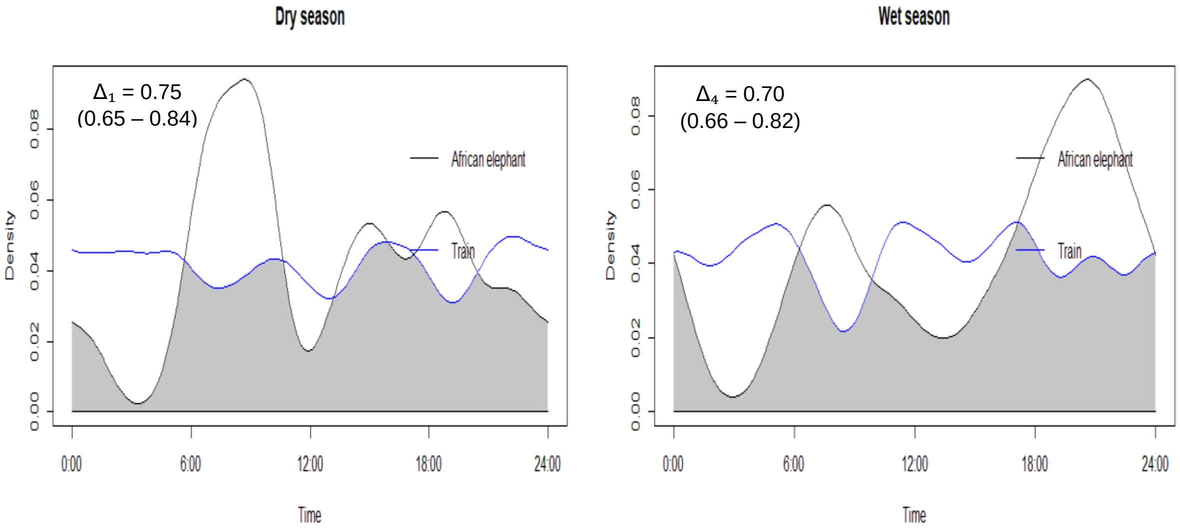


Figure 8: Estimates of temporal activity overlap (Δ) between African elephant (black line) and train (blue line) in the dry season (left) and wet season (right). Grey shaded area is the coefficient of overlapping.

A combination of distance to the railway line, habitat and season had the highest support in explaining the activity of elephant (AICc = 1 558.28, wAICc = 0.92) and the model was retained as there were no other competing models with support from the data (Table 8).

Table 8: Ranked (low – high) GLMs examining the effects of distance, habitat, and season on African elephant activity in proximity to the railway line. Models showing values for Akaike Information Criterion corrected for small sample sizes (AICc),

differences between models and the top-ranked model (ΔAICc), Akaike weight (wAICc), Log-likelihood (LL), and the number of parameters (K).

	AICc	ΔAICc	wAICc	LL	K
Distance + Habitat + Season	1558.28	0.0	0.92	-773.00	6
Distance + Habitat	1564.57	6.29	0.04	-777.18	5
Habitat + Season	1564.80	6.52	0.04	-777.30	5
Habitat	1572.36	14.08	0.00	-782.11	4
Distance + Season	1589.02	30.74	0.00	-790.45	4
Season	1595.56	37.28	0.00	-794.74	3
Distance	1595.96	37.68	0.00	-794.94	3

African elephants are significantly less active with increasing distance from the railway line ($p = 0.004$), while significantly more active in the wet season compared to the dry season around the railway line ($p = 0.003$) (Table 9). Additionally, elephants are significantly less active in open grassland ($p < 0.001$) and significantly more active in open woodland ($p = 0.017$) compared to mixed shrubland habitat bisected by the railway line.

Table 9: GLM results of factors affecting the activity of African elephant on the landscape bisected by the railway line.

	Estimate	Std. Error	Z-value	Pr(>|z|)
(Intercept)	-2.320	0.145	-15.972	<0.001
DISTANCE	-0.002	0.001	-2.919	0.004
SEASON wet	0.379	0.128	2.964	0.003
HABITAT open grassland	-0.744	0.182	-4.091	<0.001
HABITAT open woodland	0.348	0.146	2.389	0.017

4.4.3. Giraffe (*Giraffa camelopardalis*)

The activity pattern of giraffe in their occurrences on the railway line is mostly diurnal (82% of records occurring at daytime; Table 5). Giraffe showed a moderate degree of overlap with trains both in the dry ($\Delta_1 = 0.75$, CI = 0.51 – 0.73) and wet ($\Delta_1 = 0.59$, CI = 0.49 – 0.72) season in their activity on the railway line (Figure 9).

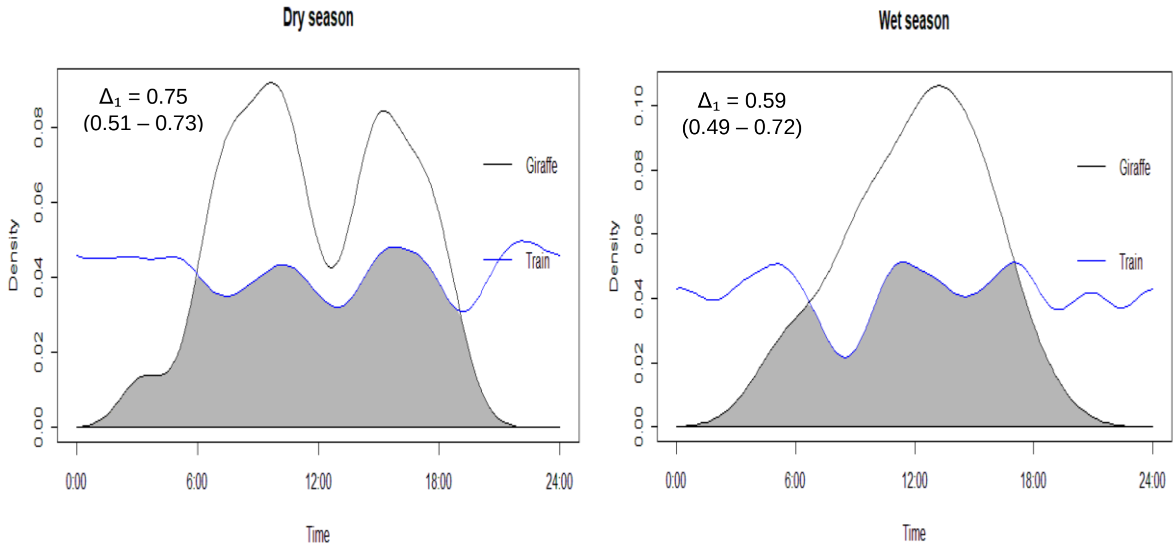


Figure 9: Estimates of temporal activity overlap (Δ) between giraffe (black line) and train (blue line) in the dry season (left) and wet season (right). Grey shaded area is the coefficient of overlapping.

For giraffe, I found similar support that the habitat and season (AICc = 973.41, wAICc = 0.61) and the distance, habitat, and season (AICc = 975.22, wAICc = 0.25) were two competing models explaining the factors affecting their activity around the railway line (Table 10). Including distance from the railway was not a significant improvement to the model (LRT: *p* > 0.05). Therefore, habitat and season was retained as a most parsimonious model in explaining the activity of giraffe around the railway line.

Table 10: Ranked (low – high) GLMs examining the effects of distance, habitat, and season on giraffe activity in proximity to the railway line. Models showing values for Akaike Information Criterion corrected for small sample sizes (AICc), differences between models and the top-ranked model (ΔAICc), Akaike weight (wAICc), Log-likelihood (LL), and the number of parameters (K).

	AICc	**ΔAICc**	**wAICc**	**LL**	**K**
Habitat + Season	973.41	0.0	0.61	-481.60	5
Distance + Habitat + Season	975.22	1.81	0.25	-481.47	6
Habitat	977.02	3.61	0.10	-484.45	4
Distance + Habitat	978.85	5.44	0.04	-484.33	5
Season	1064.89	91.48	0.00	-529.40	3
Distance	1065.81	92.40	0.00	-529.87	3
Distance + Season	1066.81	93.40	0.00	-529.34	4

Giraffe are significantly less active in the wet season compared to the dry season (*p* = 0.016), while significantly more active in open grassland (*p* < 0.001) and woodland (*p* < 0.001) compared to the mixed shrubland habitat bisected by the railway line (Table 11).

Table 11: GLM results of factors affecting the activity of giraffe on the landscape bisected by the railway line.

	Estimate	Std. Error	Z-value	Pr(>|z|)
(Intercept)	-4.956	0.234	-21.134	<0.001
SEASON wet	-0.405	0.168	-2.412	0.016
HABITAT open grassland	2.578	0.268	9.639	<0.001
HABITAT open woodland	2.045	0.252	8.126	<0.001

4.4.4. Impala (*Aepyceros melampus melampus*)

The daily activity patterns of impala on their occurrences on the railway line is mostly diurnal as indicated by 75% of capture events during daytime period (Table 5). Impala had a moderate overlap in their diel activity with trains on the railway line in the dry season (Δ_4 = 0.57, CI = 0.51 – 0.73) and wet season (Δ_4 = 0.70, CI = 0.49 – 0.82) (Figure 10).

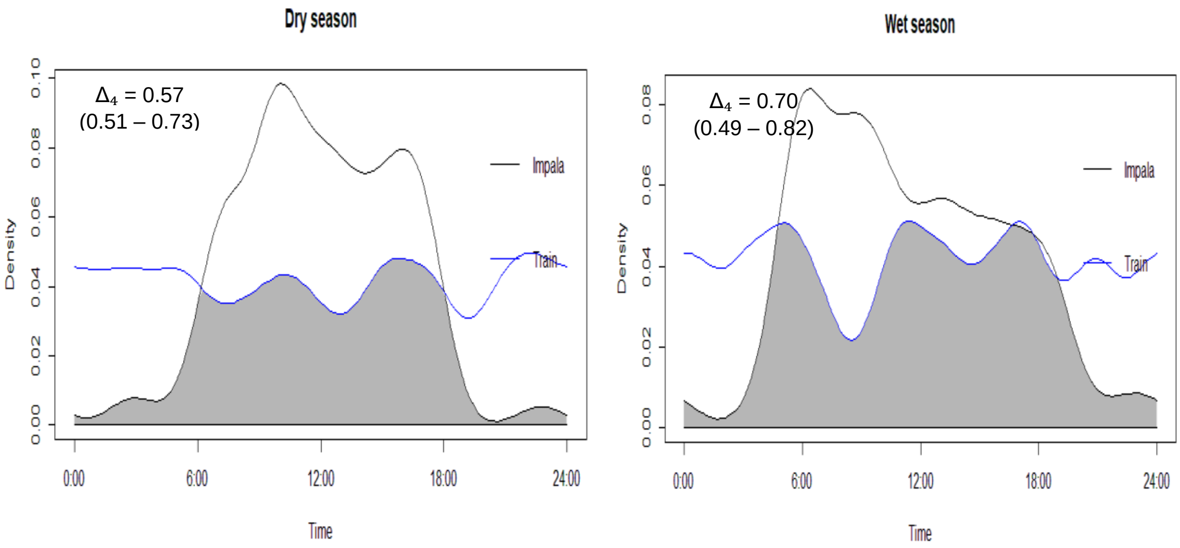


Figure 10: Estimates of temporal activity overlap (Δ) between impala (black line) and train (blue line) in the dry season (left) and wet season (right). Grey shaded area is the coefficient of overlapping.

The distance to the railway, habitat, and season (AICc = 2034.08, wAICc = 0.51), distance and habitat (AICc = 2035.75, wAICc = 0.22) as well as habitat and season (AICc = 2035, wAICc = 0.21) were three the competing models in explaining the factors affecting the activity of impala around the railway line (Table 12). Because the top-ranked model with the highest support (lowest AICc score) include all variables that are tested (full model), it was retained as the best-fit model, and this was supported by that the full model fits the data significantly better than the nested models (subset of variables) ($p < 0.05$).

Table 12: Ranked (low – high) GLMs examining the effects of distance, habitat, and season on impala activity in proximity to the railway line. Models showing values for

Akaike Information Criterion corrected for small sample sizes (AICc), differences between models and the top-ranked model (ΔAICc), Akaike weight (wAICc), Log-likelihood (LL), and the number of parameters (K).

	AICc	ΔAICc	wAICc	LL	K
Distance + Habitat + Season	2034.08	0.0	0.51	-1010.90	6
Distance + Habitat	2035.75	1.65	0.22	-1012.77	5
Habitat + Season	2035.89	1.81	0.21	-1012.85	5
Habitat	2038.33	4.25	0.06	-1015.10	4
Distance	2155.85	121.77	0.00	-1074.88	3
Distance + Season	2156.98	122.81	0.00	-1074.42	4
Season	2157.78	123.70	0.00	-1075.85	3

Impala are significantly more active with increasing distance from the railway (p = 0.035), while significantly less active in the wet season compared to the dry season (p = 0.027) (Table 13). Moreover, impala are significantly more active in open grasslands (p < 0.001) and woodland (p = 0.002) compared to the mixed shrubland habitat intersecting the railway line.

Table 13: GLM results of factors affecting the activity of impala on the landscape bisected by the railway line.

	Estimate	Std. Error	Z-value	Pr(>|z|)
(Intercept)	-2.311	0.170	-13.619	<0.001
DISTANCE	0.001	0.001	2.111	0.035
SEASON wet	-0.326	0.147	-2.218	0.027
HABITAT open grassland	2.281	0.197	11.600	<0.001
HABITAT open woodland	0.536	0.173	3.094	0.002

4.4.5. Lion (*Panthera leo*)

71% of capture events on the railway were recorded during nighttime periods for lions, indicating that the occurrences of lions on the railway line is mostly nocturnal (Table 5). The degree of overlap in the activity of lion with train activity was low in both the dry (Δ_1 = 0.48, CI = 0.09 – 0.59) and wet season (Δ_1 = 0.43, CI = 0.10 – 0.60) (Figure 11).

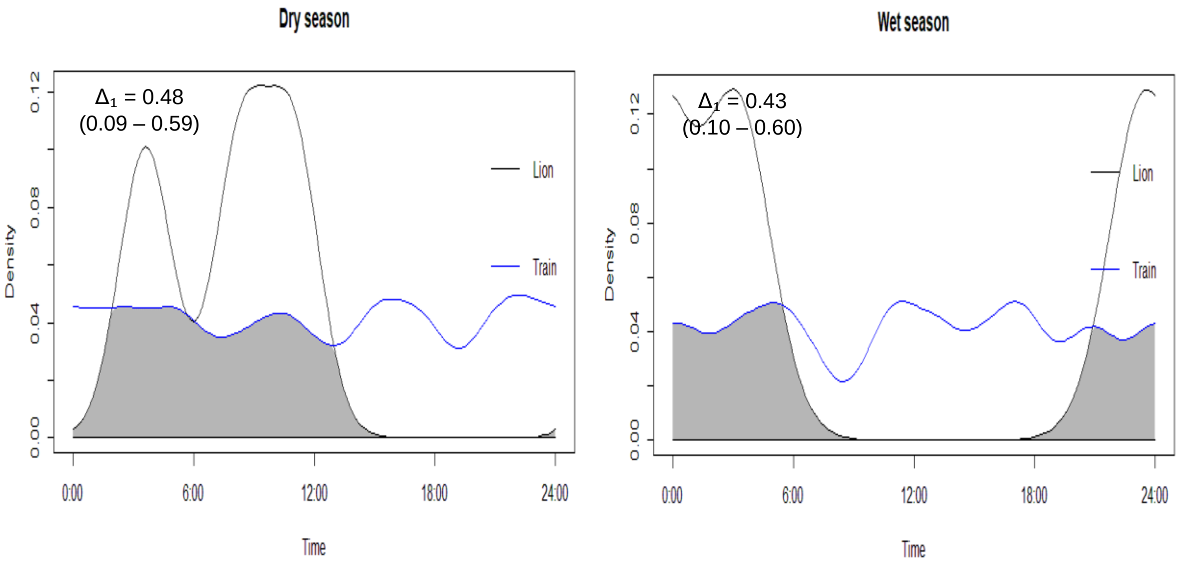


Figure 11: Estimates of temporal activity overlap (Δ) between lion (black line) and train (blue line) in the dry season (left) and wet season (right). Grey shaded area is the coefficient of overlapping.

I found similar support that habitat and season (AICc = 324.81, wAICc = 0.56) and distance, habitat, and season AICc = 325.73, wAICc = 0.35; Table 14) were competing models in explaining the factors affecting lion activity around the railway line. However, including distance from the railway to the habitat and season model did not significantly improve the model (LRT: $p < 0.05$). As a result, habitat and season model was selected as the best-fit model for explaining the activity of lions around the railway.

Table 14: Ranked (low – high) GLMs examining the effects of distance, habitat, and season on lion activity in proximity to the railway line. Models showing values for Akaike Information Criterion corrected for small sample sizes (AICc), differences between models and the top-ranked model (ΔAICc), Akaike weight (wAICc), Log-likelihood (LL), and the number of parameters (K).

	AICc	ΔAICc	wAICc	LL	K
Habitat + Season	324.81	0.0	0.56	-157.31	5
Distance + Habitat + Season	325.73	0.92	0.35	-156.72	6
Habitat	329.97	5.16	0.04	-160.92	4
Distance + Habitat	330.06	5.25	0.04	-159.93	5
Season	339.53	14.72	0.00	-166.73	3
Distance + Season	341.10	16.29	0.00	-166.49	4
Distance	346.91	22.10	0.00	-170.42	3

Lions are significantly less active in the wet season compared to the dry season (p = 0.006), while significantly more active in open grassland (p = 0.001) compared to the mixed shrubland habitat bisected by the railway line (Table 15). Although the activity of lion around the railway line decreased in open woodland compared to the mixed shrubland habitat, the association between their activity and open woodland habitat was not significant (*p* = 0.606).

Table 15: GLM results of factors affecting the activity of lion on the landscape bisected by the railway line.

	Estimate	**Std. Error**	**Z-value**	**Pr(>|z|)**
(Intercept)	5.362	0.355	-15.115	<0.001
SEASON wet	-1.033	0.373	-2.767	0.006
HABITAT open grassland	1.510	0.438	3.450	0.001
HABITAT open woodland	-0.236	0.457	-0.516	0.606

4.4.6. Spotted hyaena (*Crocuta Crocuta*)

Spotted hyaena exhibited a cathemeral behavior in their occurrences on the railway line, 7% and 67% of capture events occurred during diurnal and nocturnal periods (Table 5). Hyaena had moderate degree of activity overlap with trains during the dry season (Δ_1 = 0.66, CI = 0.09 – 0.90) and wet season (Δ_1 = 0.60, CI = 0.10 – 0.80) (Figure 12).

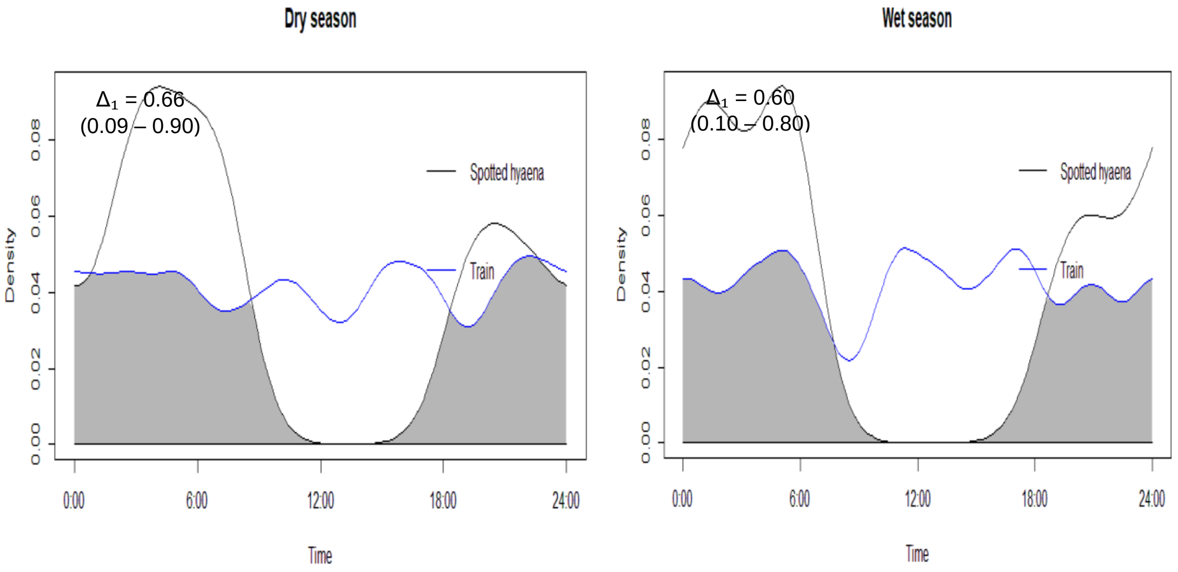


Figure 12: Estimates of temporal activity overlap (Δ) between spotted hyaena (black line) and train (blue line) in the dry season (left) and wet season (right). Grey shaded area is the coefficient of overlapping.

I found similar support that habitat model (AICc = 942.66, wAICc = 0.42), habitat and season model (AICc = 943.65, wAICc = 0.25), as well as distance and habitat model (AICc = 944.03, wAICc = 0.21) affects the activity of spotted hyaena around the railway line (Table 16). However, including season (LRT: *p* > 0.05) or distance (LRT: *p* > 0.05) to the habitat model does not significantly improves the model. Therefore, the habitat model was retained as the best-performing model to explain spotted hyaena activity on the landscape bisected by the railway line.

Table 16: Ranked (low – high) GLMs examining the effects of distance, habitat, and season on spotted hyaena activity in proximity to the railway line. Models showing values for Akaike Information Criterion corrected for small sample sizes (AICc), differences between models and the top-ranked model (ΔAICc), Akaike weight (wAICc), Log-likelihood (LL), and the number of parameters (K).

	AICc	**ΔAICc**	**wAICc**	**LL**	**K**
Habitat	942.66	0.0	0.42	-467.26	4
Habitat + Season	943.65	0.99	0.25	-466.72	5
Distance + Habitat	944.03	1.37	0.21	-466.92	5
Distance + Habitat + Season	945.17	2.51	0.12	-466.45	6
Season	983.96	41.30	0.00	-488.94	3
Distance	984.14	41.48	0.00	-489.03	3
Distance + Season	985.88	43.22	0.00	-488.88	4

Spotted hyaena are significantly more active in open grassland (*p* < 0.001) and woodland (*p* < 0.001) compared to the mixed shrubland habitat intersected by the railway line (Table 17).

Table 17: GLM results of factors affecting the activity of spotted hyaena on the landscape bisected by the railway line.

	Estimate	**Std. Error**	**Z-value**	**Pr(>|z|)**
(Intercept)	-4.648	0.199	-23.392	<0.001
HABITAT open grassland	1.535	0.264	5.806	<0.001
HABITAT open woodland	1.532	0.236	6.481	<0.001

4.5. DISCUSSION

4.5.1. Daily activity patterns

Herbivores had differing daily activity patterns on occurrences on the railway line. African buffalo and elephant exhibited a cathemeral pattern. Meanwhile, giraffe and impala activity on the railway line was mostly diurnal. The body size of the animal can be closely associated with its activity pattern as animals with large body sizes tend to be active throughout the day due to their metabolism requirement (Van Schaik & Griffiths, 1996; Ramesh *et al.*, 2015; Cid *et al.*, 2020). This possibly explains the cathemeral activity of buffalo and elephant on the railway as they probably need to spend more time to find large quantities of food to meet their energy requirement (Du Toit & Yetman, 2005; Ramesh *et al.*, 2015). Prior studies documented that prey species can temporally adjust their activity patterns as a behavioural strategy to avoid predators (Fenn & Macdonald, 1995; Valeix *et al.*, 2009; Ross *et al.*, 2013; Tambling *et al.*, 2015). For example, African buffalo and kudu (*Tragelaphus strepsiceros*) were more nocturnal in the absence of predators but became diurnal after the reintroduction of nocturnal spotted hyaena and lions (Tambling *et al.*, 2015). It may also be case that giraffe and impala have adapted the predominantly diurnal pattern within my study area as an antipredator behaviour since they make up a diet for of large predator guild (Hayward & Kerley, 2005; Hayward, 2006; Thaker *et al.*, 2011; Belton *et al.*, 2016) that are assumed to be active mostly at night (Clauss *et al.*, 2021; Searle *et al.*, 2021).

From the carnivorous guild, lion activity on the railway line was mostly nocturnal, while, spotted hyaena exhibited a cathemeral pattern on the railway line. This is consistent with the current literature for lion but not for spotted hyaena (Clauss *et al.*, 2021; Searle *et al.*, 2021) The possible explanation is that spotted hyaena are less likely dependant on the camouflage of darkness to successful hunt their prey, unlike lions which stalk and ambush their prey, they instead sprint through the herd to separate prey and locate the weakened individual (Augustsson, 2016). Another possible explanation for spotted hyaena cathemerality behaviour on the railway line may be due to their opportunistic scavenging (Hayward, 2006; Belton *et al.*, 2016). Spotted hyaena may adapt a strategy of acquiring food easily by searching, at any time of the day, for corpses arising from rail-kills as trains traversing the reserve operates throughout the day. Although the result for spotted hyaena were contradictory with the studies by Clauss *et al.*, (2021) and Searle *et al.*, (2021), most of the daily activity occurred at night (67%) than during the daylight (7%). Hayward & Hayward, (2007) and Augustsson, (2016) put forward that spotted hyaena are sensitive to high temperatures and will limits their activity during the hottest hours of the day, which probably explain why they are far less active in the day light than at night on the railway line.

The primary objective of this study was to determine the daytime in which focal species are likely to be active on the railway line over the day period as to help advance our knowledge of when train collision for these species mostly likely to occur over a 24-hour cycle. So, while I attempt to suggest that the physical adaptation, life-history strategies, and predation-prey interaction are possible factors contributing to the daily rhythms of focal species on the railway line, it is important to point out that many other factors can influence their daily activity patterns, including human disturbances (Carter *et al.*, 2015; Gaynor *et al.*, 2018), environmental conditions (Bennie *et al.*, 2014), and competition for resources (Hayward & Slotow, 2009). To further detail the complexity of the subject, the daily activity pattern of wildlife may differ between seasons and within the same species (Ikeda *et al.*, 2016). Importantly, the daily activity patterns for a species showed in the study does not reflect the species daily activity pattern throughout the landscape but only on the railway line.

4.5.2. Seasonal activity overlap

Based on the idea that the dispersal behaviour of animals is influenced by the seasonal variation in resource availability (Ogutu *et al.*, 2008), animals are considered to move over wider distances to search for food and drinking water in the dry season than the wet season (Ogutu *et al.*, 2008; Owen-Smith & Ogutu, 2012). Consequently, this is likely to result in increased probabilities of wildlife-train interaction on the railway line, leading to a high temporal overlap of activity. This study showed varied results relative to my hypothesis that the activity of mammal species on the railway will highly overlap with those of trains in the dry season when compared to the wet season.

In agreement with my hypothesis, the activity of African buffalo indicated a high overlap with trains in the dry season and moderate overlap in the wet season with greatest peaks of overlap with trains from 07:00 – 24:00 during the dry season, and from 7:00 – 12:00 and again 18:00 – 03:00 in the wet season (Figure 7). The high overlap between African buffalo and train activity during the dry season obviously suggests that buffalo may have increased risks of collisions in the dry season as they appear not to avoid train activity. However, there is not enough mortality data to support this, except for one carcass recorded in the dry season (see Appendix F). Four of my focal species showed moderate activity overlap with trains with no seasonal differences in activity overlap, suggesting that the presence of trains on the landscape has little influence on their seasonal activity on the railway line. This may particularly be true given that the railway line has been accessible for more than half a century and these species are therefore likely to be habituated to train movements without any perceived risk (Li *et al.*, 2010; Marino & Johnson, 2012; Barrueto *et al.*, 2014). Specifically, African elephant activity moderately overlapped with that of trains in the dry and wet season with multiple peaks of activity overlap throughout the day from both seasons (Figure 8). Giraffe and Impala activity indicated a moderate degree of overlap with that of trains and both showing predominantly peaks of overlap with trains between 06:00 and 18:00 during the dry and wet season (Figure 9 & 10). Similarly, spotted hyaena activity moderately overlapped with train activity in both seasons, with greatest peaks in activity overlap from 18:00 – 10:00 in the dry season and 18:00 – 06:00 during the wet season (Figure 11).

Opposite to my expectations, lions had a low degree of activity overlap with trains between seasons, showing high peaks of activity overlap from 01:00 – 13:00 in the dry season and 20:00 – 06:00 in the wet season (Figure 12). The low seasonal activity overlap of lions with trains on the railway line supports the idea that lion temporal avoids the movement of trains on the landscape, probably perceived as a source of disturbance (noise or vibrations) or collision risk (Lucas *et al.*, 2017). The avoidance response to vehicle traffic by mammals have also been shown from several road ecology studies (Eldegard *et al.*, 2012; Northrup *et al.*, 2012; Evans *et al.*, 2019; Bojarska *et al.*, 2020). One could still argue why are lions frequently killed on the railway line when they temporal avoid the activity of trains. Perhaps, the most plausible explanation is that the avoidance behaviour to train traffic exhibited by lions is likely to differ between individuals depending on age, sex, and reproductive status (Oliveira, 2018), and this variation in the activity of focal species recorded on the railway line was not considered. Although the results indicate that lions appear to temporally avoid trains regardless of seasonal differences, making inference of this kind should be considered with great care given the lack of sample size of the species on the railway line (n = 7). Nevertheless, it is well documented that traffic avoidance by animals results to reduced crossing of linear infrastructure, and under high traffic volume and speed, can be a barrier that limits movement and access to important resources (Ford

& Fahrig, 2008; Rytwinski & Fahrig, 2012; Grilo *et al.*, 2015; Chen & Koprowski, 2016). Thus, further investigation is needed for clear understanding of temporal components between lion interaction with trains on the landscape.

4.5.3. Effects of distance

African buffalo and elephant were found to be more active in proximity to the railway line. Unexpectedly, this suggests that buffalo and elephant are positively affected by the distance from the railway line as their activity diminished with increasing distance from the railway. This is consistent with other literature, where Hien *et al.*, (2007) found a decrease in the population of elephant with increased distance from the road. Similarly, Van Vliet & Nasi, (2008) reported that African forest buffalo (*Syncerus caffer nanus*) appeared not to be affected with distance from the roads. It is more likely that buffalo and elephant are attracted close to the railway line to exploit forage found along the railway as it has been already established that herbivores forage on rail-side vegetation (Jaren *et al.*, 1991; Pollock *et al.*, 2017). The activity of impala significantly decreased with increasing distance, suggesting that they are negatively affected by the distance from the railway as I expected. In another study conducted at KNP, it was found that impala avoided close proximity (first 10 m) to paved roads (Mulero-Pázmány *et al.*, 2016). Road ecology studies suggest that the avoidance response by an animal at distance from the infrastructure is associated with presence of road surfaces (road avoidance) or traffic (road avoidance) (Rytwinski & Fahrig, 2012; Mulero-Pázmány *et al.*, 2016; Chen & Koprowski, 2016; Oliveira, 2018). Because of the high correlation between the effects of road and traffic intensity (Mulero-Pázmány *et al.*, 2016), studies indicate that it remains unclear to distinguish, as with this study, whether animal avoidance is due to traffic or road itself unless an animal is decides to cross the road (Rytwinski & Fahrig, 2012; Mulero-Pázmány *et al.*, 2016; Oliveira, 2018). Ford & Fahrig, (2008) suggested that the species response to road infrastructure is likely to differ between individuals due to many factors including previous experience and physiological conditions. Given that impala are known to live in large social groups (Apps, 2012), it is possible that some individuals within impala population that had witnessed collision from train limits their activity at distances deemed safer from the railway line, thereby resulting decreased activity in proximity to the railway.

It is put forward that species attracted or found closer to roads, irrespective of traffic, stands greater risk of collision unless they can escape from approaching vehicles, on the other hand, species that keeps a distance away from it suffer habitat loss as habitats closer to the infrastructure becomes unusable (Rytwinski & Fahrig, 2012). As already been established in this study, African buffalo and elephant seemed to be attracted to the railway line as their activity declined with increased distance, while impala appeared to be not attracted to the railway line as activity increased with increased distance. For appropriate management interventions, more work focused on the determinant factors attributing to the activity or movements of these species in proximity to the railway line is still needed as it was not within the scope of this study.

4.5.4. Effects of season

The movement patterns of large mammals, particularly herbivores, in savanna ecosystem is strongly influenced by the seasonal availability of resources such as water and food (Ogutu et *al.*, 2008; Owen-Smith & Ogutu, 2012). During the dry season when these resources become severe reduced on the landscape (Ogutu *et al.*, 2008; Davidson *et al.*, 2013; Owen-Smith, 2014), herbivores are likely to be forced to move over larger distances as to satisfy their forage and water intake (Venter *et al.*, 2015), thereby increasing the probability to be detected on and along the railway line. Kasiringua *et al.*, (2017) assert that ungulate drinks more frequently during the dry season than the wet season depending on their requirement. Thus, the significant increase in the activity of giraffe and impala around the railway line during the dry season was probably as the result of their seasonal movement associated with water needs. Although considered a highly mobile and water dependent species (Smuts, 1974; Skinner & chimimba, 2005; Smit *et al.*, 2020), African elephant activity around the railway line significantly increased in the wet season compared to the dry season. It has been found from other studies conducted elsewhere that elephants move shorter distances in the dry season than wet season due to limited resources (Wittemyer *et al.*, 2007; Birkett *et al.*, 2012; Buchholtz *et al.*, 2019). Birkett *et al.*, (2012) argued that elephants utilise smaller areas more intensively during the dry period to save energy which could have otherwise been wasted in their movement to seek out resources that satisfy their metabolism requirement. So, it is likely that elephants could have moved more frequently within my study area during wet season in response to increased forage availability on the landscape, resulting to increase activity on and along the railway line.

Carnivores are considered less water dependent than herbivores as many can acquire much of their water needs from the tissues of their prey when surface water is scare (Newmark *et al.*, 1996). It is therefore unlikely that water demands could have played a major role for the significant increase of lion activity around the railway line during the dry season. However, several studies indicate that waterholes are key features for lions in the dry season as they spend more time closer to them, not necessarily to drink water, but to ambush their prey arriving at waterholes to drink (Valeix *et al.*, 2009; Davidson *et al.*, 2013; Kittle *et al.*, 2016), suggesting that food acquisition is a major factor for lions in the dry season. There is therefore a possibility that herbivore distribution will influence their movement on the landscape. In fact, it has been reported that lions track the seasonal movements of their prey (Kariaga *et al.*, 1999; Schuette *et al.*, 2013; M'soka *et al.*, 2016). When this is a case, lions are likely to be detected more frequently during the dry season than the wet season, thereby resulting to increased lion activity on and along the railway line in the dry season.

5.5.5. Effect of habitat

Habitat is fundamental for the long-term survival by a species as it provides access to crucial resources, including food, water, and cover (Krausman, 1999; Chabwela *et al.*, 2017). The choice of habitat and spatial distribution of herbivores in the landscape is largely influenced by resource availability and predation (Riginos & Grace, 2008;

Burkepile *et al.*, 2013; Mariotti *et al.*, 2020). Consequently, herbivores are often forced to trade-off between resource acquisition and predation risk (Burkepile *et al.*, 2013; Bennitt *et al.*, 2015). The activity of buffalo around the railway decreased significantly in both open grassland and woodland compared to mixed shrubland. Similarly, elephant activity significant decreased in open grassland but increased in open woodland when compared to the mixed shrubland. The high concentrations of buffalo activity in dense vegetation cover (mixed shrubland) support the notion that their need to access resources may be more important than the presence of large predators in the landscape. Riginos & Grace, (2008) reported that elephants prefer areas with greater availability of trees, which explains the decline in their activity in open grassland and increased activity in open woodland. It is argued that larger herbivores need to optimise forage intake whereas smaller herbivores optimise forage quality (Anderson *et al.*, 2016). As the results, buffalo and elephants might have preferred these habitat types due to their increased metabolism requirement with little regard for predator encounters. In fact, several studies suggest that larger herbivores are less vulnerable to predation than smaller herbivores (Riginos & Grace, 2008; Valeix *et al.*, 2008; Dusseldorp, 2010). This may be due to their aggressive or fight response when attacked by predators (Dusseldorp, 2010), and there are even incidents of lions been killed (Hayward & Kerley, 2005). Additionally, the body size has a major effect on thermal regulation with large mammals heating and cooling at lower rates than smaller mammals (Valeix *et al.*, 2008). Thus, habitats with dense tree cover may be preferred by elephant and buffalo for shade to prevent overheating during the hottest hours of the day. A positive relationship was found between the activity of both giraffe and impala in open grassland and woodland habitat types as their activity around the railway line increased significantly when compared with mixed shrubland. This support the idea that predation is likely to play a major factor in habitat preference of these species rather access to suitable forage resources. This is consistent with a study from Kenya which found that giraffe, despite being strict browsers, spend greater time in areas with fewer tree cover to minimize the risk of predation (Riginos & Grace, 2008). Therefore, it is likely that the high concentration of giraffe and impala activity in open grassland and woodland is an anti-predator strategy due to low tree cover of these habitats that allows for greater visibility (Riginos & Grace, 2008; Burkepile *et al.*, 2013).

Among carnivores, the activity of lions around the railway line are positively associated with open grassland than the mixed shrubland. Their activity decreased in open woodland than mixed shrubland, but this was not significant. On the other hand, spotted hyaena activity around the railway line are positively associated with both open grassland and woodland than the mixed shrubland habitat type. It has been shown that the vegetation cover is as crucial for carnivores as it is for herbivores because it affects hunting success of their prey (Funston *et al.*, 2001; Davidson *et al.*, 2012; Burkepile *et al.*, 2013; Cozzi, 2013). For instance, Funston *et al.* (2001) found that increasing dense cover had a significant effect on the hunting success of impala by male lions, with greatest success rate in tall grass and dense shrub. This may be true for predators, such as lions, that need cover to stalk and bush their prey (Davidson *et* *al.*, 2012; Augustsson, 2016). On the contrary, lion and spotted hyaena activity were less pronounced in the mixed shrubland, suggesting that vegetation concealment for increased hunting success of their prey is less likely explain their habitat preferences around the railway line. The possible explanation for increased activity in open grassland by lions and both open grassland and woodland by spotted hyaena could be related to the spatial distribution of their preferred prey. If habitat of dense vegetation cover is avoided by herbivores to reduce predation risk, it is likely to results to low densities of prey on that habitat (Cozzi *et al.*, 2013), and ultimately, affects the spatial distribution of predators as well. For instance, Lion densities were closer to zero in mopane woodland probably as the results low densities in that habitat (Cozzi *et al.*, 2013). So, it is possible that higher concentration of lion and spotted hyaena in open habitat types was probably as a results of habitat preferences of their prey species.

4.6. CONCLUSION

The activity of six medium-large mammal species (≥ 10 kg) were monitored on and in proximity to the railway line using wildlife camera traps. Based on the proportion of capture events when the species is active on the railway relative to the time of sunrise and sunset, I discovered that the activity of African buffalo, African elephant and spotted hyaena on the railway is cathemeral. Whereas giraffe and impala activity are mostly diurnal, and lion was the only focal species indicating predominantly nocturnal activity on the railway line. From these results, it becomes clear the risk of train collisions for these species are likely to be more pronounced at certain time of the day connected with their daily activity patterns of occurrence on the railway line. Therefore, mitigation measures to reduce the risks of collision should be temporal, focused on the time of the day in which a species is likely to be active on the railway line over a 24-hour cycle. One possible way to minimise the probability of train collision for impala and giraffe would be to stop or reduce the number of trains running during the daytime period because it is the time in which they are most active on the railway line. However, this mitigation strategy will not necessarily be effective to reduce the probability of train collisions for buffalo, elephant, spotted hyaena and lions as they exhibit a different daily activity pattern on their occurrences on the railway line. Therefore, management intervention will need to be species specific bearing in mind a species that is considered a priority for conservation and with greatest numbers of train collisions on the landscape.

The study found varied results on the extend of seasonal overlap between the activity of focal species on the railway and that of train activity. African buffalo activity highly overlapped with train activity in the dry season but moderately overlapped in the wet season. This supported my hypothesis that the activity of overlap will vary between seasons, with high overlap in the dry season as they are likely to cover longer distances seeking food and water resources and resulting to increased chances of interaction with trains on the railway. Resource acquisition for African buffalo in the dry season is probably of greater importance than the risk of collision with trains on the railway. There was no evidence found on seasonal variation in the activity of overlap for African elephant, impala, giraffe and spotted hyaena with that of train activity as they all showed a moderate overlap in both seasons. The presence of train has minor effects on their seasonal activity on the railway probably due to habituation of train movements on the landscape (Li *et al.*, 2010; Marino & Johnson, 2012; Barrueto *et al.*, 2014). The activity of overlap for lion and trains was completely opposite from what was expected as the study found low activity of overlap between lions and trains on the railway in both the dry and wet season. The low overlap in activity implies that lions minimise or avoids encounter train activity on the landscape, and this could be due perceived collision risk, noise, or vibration caused by passing trains (Lucas *et al.*, 2017). However, concluding that lion population avoid train movements on the landscape would be wrong given the limited number of capture events obtained for lion on the railway line during the study period (Table 4). This therefore justifies for further investigation as the avoidance behaviour by lions to passing trains could potentially restricts their movements and access to critical resources on the landscape (Ford & Fahrig, 2008; Rytwinski & Fahrig, 2012; Grilo *et al.*, 2015; Chen & Koprowski, 2016).

A strong correlation in the activity of African buffalo, African elephant, and impala relative to the distance from the railway line was found. This was not the case for other focal species as the distance from the railway was not an important factor influencing their activity around the railway. The activity of buffalo and elephant declined with increasing distance from the railway line, rejecting my assumption that their activity would be negatively by the distance from the railway. However, this assumption was supported from the activity of impala around the railway line as they decreased with increasing distance from the railway line. Animals that exhibit attraction closer to transport infrastructure have increased risk of collision if they cannot escape oncoming traffic while those that keeps a distance away from it can suffer habitat loss (Rytwinski & Fahrig, 2012). Since it was not within the scope of this study to determine the possible factors that attracts buffalo and elephant populations closer to the railway, further investigation is deemed necessary to aid in mitigation measures that will reduce their risks of collision on the railway line. Similarly, research is needed to understand what contributes to the avoidance behaviour of impala population at distances from the railway line.

There was close association between seasons and the activity of African elephant, giraffe, impala, and lion around the railway, which is in line with my expectations that season will influence their activity. For African buffalo and spotted hyaena, seasonal variation was not an important variable affecting their activity around the railway line. African elephant is more likely to be active in the wet season than the dry season, while giraffe and impala and lion are less likely to be active in the wet season compared to the dry season around the railway line. The seasonal differences in the activity of these species support the idea that measures aimed at minimising their risk of collision with trains should be based on seasonal periods in which they are more likely to be active around the railway line. Again, management interventions will largely depend on the species considered because measures focused on reducing the probability of train collision for giraffe, impala and lion in the dry season cannot work for African elephants as their activity around the railway line are more pronounced in the wet season.

As hypothesised, habitat was the major factor influencing the activity of all my focal species around the railway line because the study found a strong correlation between their activity and rail-side habitat types. However, the activity of focal species around the railway line varied greatly between habitat types. Specifically, African buffalo activity decreased in open grassland and woodland than in mixed shrubland. Activity of African elephant decreased in open grassland but increased in open woodland compared to mixed shrubland. Giraffe and impala activity increased in open grassland and woodland than in mixed shrubland. Lion activity increased in open grassland in than mixed shrubland and although they decreased in open woodland than in mixed shrubland, this was not significant. Spotted hyaena activity increased in both open grassland and woodland compared to mixed shrubland. Based on these results, it is evidently clear that mitigation measures to reduce train collisions be spatial with more attention given on habitat sections bisecting the railway line which have high concentrations of activity of focal species.

CHAPTER 5: MORTALITIES OF WILDLIFE ON THE RAILWAY LINE.

5.1. INTRODUCTION

Railways are considered essential linear corridors for connecting people with important environmental and economic benefits when compared to roads (Borda-de-Água *et al.*, 2017; Blumenfeld *et al.*, 2019). Despite the economic and environmental benefits, wildlife mortalities on the railways are a major conservation concern which can contribute to the significant population declines. For example, moose population in Alaska declined by 35% between 1989–1990 of which more than 60% of deaths were due to train collisions (Popp & Boyle, 2017). WTC is the most obvious source of mortality on the railway line (Santos *et al.*, 2017) affecting several species of mammals (e.g., Clair *et al.*, 2020; Nezval & Bíl, 2020), birds (e.g., Godinho *et al.*, 2017; Garcia de la Morena *et al.*, 2017), reptiles (e.g., Kumar & Kumar, 2020), and amphibians (e.g., Budzik & Budzik, 2014). Mortalities of wildlife on the railway line can also occur as the result of entrapment with rail-associated structures, electrocution, or collision with overhead wires (Santos *et al.*, 2017). Rail mortalities not only pose a threat to wildlife management but can also result in substantial financial implications due to delayed train operations and compensations related to train repairs and wild animal losses (Jaren *et al.*, 1991; Roy & Sukumar, 2017). This demonstrates that the occurrences of wildlife mortalities on the railway is a challenge for both conservation and railway authorities, one that requires much needed attention as all species from different taxa can be affected by railways intersecting wildlife protected areas.

The risk of wildlife-train collision may be influenced by several factors associated with traffic characteristics, such as train intensity and speed (Visintin *et al.*, 2018; Jasińska *et al.*, 2019); landscape characteristics, such as rail-side vegetation, topography, and adjacent water source to the railway (Kušta *et al.*, 2014; Clair et al., 2020); environmental conditions, such as temperature and seasonal variation (Gundersen *et al.*, 1998; Krauze-Gryz *et al.*, 2017) and wildlife-related factors, such as population parameters and species response towards approaching trains (Rea *et al.*, 2010; Roy & Sukumar, 2017). Determining the specific factors affecting wildlife mortalities on the railway to assist decision-makers in making well-informed decisions, based on reliable data for implementing possible mitigation strategies, aimed at reducing wildlife fatalities on the railway line.

In this study, I examine the mortalities of wildlife from four different taxonomic groups (mammals, birds, reptiles, and amphibians) on the railway bisecting the landscape of BNR to determine the (1) seasonal patterns of wildlife mortalities on the railway line, (2) daily activity patterns of wildlife on rail mortalities, and (3) effect of surrounding habitat on rail mortalities. Firstly, I hypothesised that there will differences in rail mortalities between seasons, with more mortalities during dry season than the wet season because the dry season is generally the period of limited food and water resources (Ogutu *et al.*, 2008; Owen-Smith & Ogutu, 2012) and animals are likely to move over large distance, increasing their chances to cross the railway line and struck by trains. Secondly, I hypothesised there will be differences in the daily activity patterns of wildlife killed on the railway line, with more mortalities of nocturnal species than diurnal species because nocturnal species are likely to be blinded by the train lights and remain still rather than escaping from oncoming trains (Budzik & Budzik, 2014; Cserkesz & Farkas, 2015). Lastly, I hypothesised that rail mortalities of wildlife will be influenced by the surrounding rail-side habitat because the differences in habitat structure in proximity to the railway is likely to affect the ability for wildlife to notice and escape approaching train (Carvalho *et al.*, 2017).

5.2. METHODOLOGY

To assess wildlife mortalities on the railway line, I carried out foot surveys to record all carcasses found on and along the railway line across the four taxonomic groups (Adopted from Heske, 2015; Godinho *et al.*, 2017). The foot surveys are an ideal method for this study as they increase the probability of rail-kill detection (Guinard *et al.*, 2012), especially given access limitations to the railway line as the results of topographic features in the study area. I conducted 5 km foot survey in each of the three broad habitat types bisecting the railway line (as outlined in chapter 4), for a total for a 15 km of the 31.3 km (Figure 13). Prior to the actual data collection, I performed a 3-day trial on the railway line to determine the length of railway that can be walked, and the time it takes walking without causing any fatigue during process of rail-kill data collection. From these survey trials, it was determined that a 5 km walk along the railway over 1 hour and 52 minutes on average (excluding the stoppage time for passing trains) was reasonably adequate.

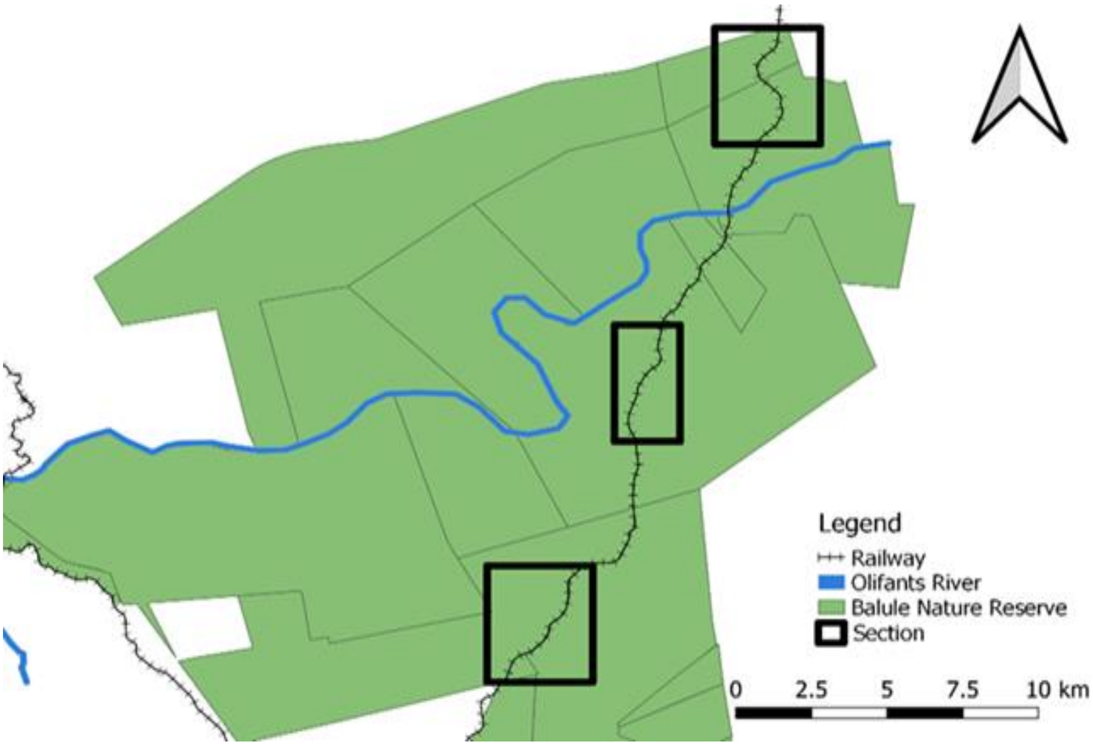


Figure 13: Surveyed railway sections to record wildlife mortalities in the study area.

When I observed a carcass of a mammal, bird, reptile, or amphibian species on the railway, and along the railway edges, I identified it to species level whenever possible. Carcasses that could not be identified to species level were classified as ‘unknown’ and photographic evidence and samples were collected and taken to the research facilities for assistance with identification by other fellow researchers. At each observed rail-kill, I recorded the date, time, images, and GPS location on a data sheet to prevent double counting of rail-kills during continuous days of survey (Appendix E).

For seasonal comparison of rail-kills, I conducted foot surveys after every second day for 15 days at each 5 km section during the dry and wet season. Therefore, a total of 90 days was spent to assessing wildlife mortalities on the railway line (Table 18).

Table 18: Sampling period for monitoring rail mortalities according to the seasonal rainfall experienced in the study area classified by Lagendijk *et al.*, (2015).

SEASON	RANGE	SAMPLING PERIOD	SAMPLING DAYS
Dry	May - October	mid-May - mid-September	45
Wet	November - April	November - March	45

To determine effects of surrounding habitat on rail-kills, I recorded each encountered carcass along the surveyed sections into one of three habitat types (as outlined in chapter 4). Since it was not possible to determine the exact time of the day when rail-kill incident occurred, the observed rail-kills for identifiable species were classified according to their dominant activity period as either diurnal or nocturnal by reference to existing literature (Skinner & chimimba, 2005; Hockey *et al.*, 2005; Alexander & Marais, 2007; Carruthers & Du Preez, 2011). For rail-kills that could not be identified to species level, their activity patterns were classified as ‘unknown’. During the study period, other rail mortalities that were occasional reported by the train operators to the reserve management were recorded on the database but could not be supplemented due to bias toward large mammals. Reported wildlife mortalities on the railway line during the period of this study are found in Appendix A.

5.3. DATA ANALYSIS

To assess the differences in the overall rail mortalities between seasons, I used the Mann Whitney U test to compare rail-kill frequency between the dry and wet season as the frequency of recorded rail-kills between seasons followed a non-normal distribution that was tested using a Kolmogorov-Smirnov Test of Normality (K-S test: $D = 0.266$; $p < 0.05$). To determine whether there is a difference in activity patterns on rail mortalities, I performed a chi-square goodness of fit test by comparing the number of observed deaths on the railway line from diurnal species and nocturnal species.

To evaluate the effect of habitats bisecting the railway line on the occurrences of rail mortalities, I used the Jacob’s Index which is based on habitat preference independent to the relative abundance of habitat available to the animals (Jacobs, 1974). The Jacobs’ Index was calculated using the formula: $D = (r - p) / (r + p - 2rp)$ where, r is the proportion of the total number of recorded rail-kills at each habitat type, p is the proportion of habitat type surveyed on the railway line and D is the Jacob’s index score which produces a value ranging from +1 (maximum preference – high rail-kill occurrences) to -1 (maximum avoidance – low rail-kill occurrences) and 0 (preference proportional to availability – moderate rail-kill occurrences). To determine whether the relationship in the frequency of recorded rail-kills and habitat types exists, I computed the Kruskal–Wallis test. The statistical analyses of rail mortality data were performed using Microsoft excel 365 (Microsoft Inc., Redmont, USA).

5.4. RESULTS

I recorded a total of 99 rail-kills from a total of 450 km surveyed over a 90-day period. Of these rail-kills, 29 death individuals were mammals (29.29%) with 13 identified species, 26 individuals were birds (26.26%) with 10 identified species, 26 individuals were reptiles (26.26%) from 11 identified species and 18 individuals were amphibians (18.18%) from 4 identified species (Table 19). Impala (*Aepyceros melampus melampus; n* = 7) carcasses were most frequently recorded for mammals. The Lalic-breasted Roller (*Coracias caudatus*; *n* = 5) was the dominant rail-kill species for birds. Turner's Tubercled Gecko (*Chondrodactylus turneri; n* = 7) was the most killed reptile species on the railway line. For amphibians, the Eastern Olive Toad (*Sclerophrys garmani*; *n* = 8) incurred most rail mortalities. The rate of rail-kill was 0.44 per km with mammals comprising highest proportion (0.064 km^{-1}), followed by birds (0.058 km^{-1}), reptiles (0.058 km^{-1}), and amphibians (0.040 km^{-1}).

Table 19: Recorded number of rail mortalities from four taxonomic groups.

Taxonomic group	**Common name**	**Scientific name**	**Recorded rail-kill**	**Rail-kill rate (km^{-1})**
Mammals	Impala	*Aepyceros melampus melampus*	7	0,016
	Tree squirrel	*Paraxerus capapi*	3	0,007
	Woodland mouse	*Grammomys dolichurus*	2	0,004
	Scrub hare	*Lepus saxatilis*	1	0,002
	Slender mongoose	*Galerella sanguinea*	1	0,002
	Spotted hyaena	*Crocuta crocuta*	1	0,002
	African wild dog	*Lycaon pictus*	1	0,002
	Vervet monkey	*Cercopithecus pygerythrus*	1	0,002
	Namaqua rock mouse	*Micaelamys namaquensis*	1	0,002
	Porcupine	*Hystrix africaeaustralis*	1	0,002
	Greater cane rat	*Thryonomys swinderianus*	1	0,002
	Waterbuck	*Kobus ellipsiprymnus*	1	0,002
	African buffalo	*Syncerus caffer*	1	0,002
	Unidentified mammal	Unknown	7	0,016
		Total	**29**	**0,064**
Birds	Lalic-breasted Roller	*Coracias caudatus*	5	0,011
	Red-billed Hornbill	*Tockus erythrorhynchus*	4	0,009
	Southern Yellow-billed Hornbill	*Tockus leucomelas*	3	0,007
	African Wood-Owl	*Strix woodfordii*	3	0,007
	White-backed Vulture	*Gyps africanus*	2	0,004
	Cape Glossy Starling	*Lamprotornis nitens*	2	0,004
	Crested Francolin	*Dendroperdix sephaena*	1	0,002
	Black-chested Snake Eagle	*Circaetus pectoralis*	1	0,002
	Spotted Eagle-Owl	*Bubo africanus*	1	0,002
	Laughing Dove	*Streptopelia senegalensis*	1	0,002

	Unidentified bird	Unknown	3	0,007
		Total	**26**	**0,058**
Reptiles	Turner's Tubercled Gecko	*Chondrodactylus turneri*	7	0,016
	Leopard Tortoise	*Stigmochelys pardalis*	4	0,009
	Yellow-throated Plated Lizard	*Gerrhosaurus flavigularis*	3	0,007
	Southern African python	*Python natalensis*	2	0,004
	Lowveld Flat Gecko	*Afroedura langi*	2	0,004
	Rock Monitor	*Varanus albigularis*	2	0,004
	Western Stripe-bellied Sand Snake	*Psammophis subtaeniatus*	2	0,004
	Marsh Terrapin	*Pelomedusa subrufa*	1	0,002
	Rainbow Skink	*Trachylepis margaritifer*	1	0,002
	Common Tiger Snake	*Telescopus semiannulatus*	1	0,002
	Flap-neck Chameleon	*Chamaeleo dilepis*	1	0,002
		Total	**26**	**0,058**
Amphibians	Eastern Olive Toad	*Sclerophrys garmani*	8	0,018
	Southern Foam-nest Frog	*Chiromantis xerampelina*	4	0,009
	Broad-banded Grass Frog	*Ptychadena mossambica*	3	0,007
	Plain Grass Frog	*Ptychadena anchietae*	3	0,007
		Total	**18**	**0,040**
Total rail-kill			**99**	**0,440**

5.4.1. Seasonal patterns of wildlife rail mortality

Overall, there is no significant difference in the frequency of wildlife mortalities on the railway line between seasons ($U = 286.5$, $n = 49$, $p = 0.421$). In total, 43 rail mortalities were observed during the dry season and 56 during the wet season (Appendix F). There were more mammal mortalities on the railway during the dry season than the wet season, however this difference was not significant ($p > 0.05$; Table 20). For birds, most deaths were recorded during the wet season than the dry season, but the difference was not significant ($p > 0.05$). Similarly, reptiles were recorded more frequently during the wet season compared to the dry season, but reptile mortalities did not significantly differ between seasons ($p > 0.05$). All amphibian mortalities were recorded during the wet season.

Table 20: Seasonal differences in the rail mortality of each taxon.

Taxonomic group	**number of rail-kills**		**difference**	
	dry season	**wet season**	***U*-test**	***p* value**
Mammals	22	7	35	0.582
Birds	11	15	23	0.342
Reptiles	10	16	20	0.317
Amphibians	0	18	-	-

5.4.2. Daily activity patterns of wildlife on rail mortality

Of the rail-kills identified to species level, there were disproportionately more diurnal species than nocturnal species (Appendix F). Overall, the rail mortalities of diurnal species (*n* = 48) did not differ significantly from nocturnal species (*n* = 41) ($x^2 = 0.55$, *df* = 1, *p* = 0.458). However, there were significantly more mortalities of diurnal species than nocturnal species on the railway line during the dry season ($p < 0.05$) (Table 21). In the wet season, there was no significant difference in rail mortalities between diurnal species and nocturnal species ($p > 0.05$).

Table 21: Differences in rail mortality of diurnal and nocturnal species in the dry and wet season.

Season	**number of rail-kills**		**difference**		
	Diurnal	**Nocturnal**	***x²***	***df***	***p value***
Dry	24	9	6.82	1	0.009
Wet	24	32	1.14	1	0.285

5.4.3. Effect of rail-side habitat on rail mortality

Most encountered deaths on the railway line occurred in a mixed shrubland section (*n* = 47), followed by the open grassland (*n* = 31) and open woodland (*n* = 21; Appendix F). The occurrences of rail mortalities for each habitat type were proportionally close to the habitat available (Figure 14) and this is further supported by no significant association in the frequency of rail mortalities and rail-side habitat type (*H* = 0.84, *df* = 2, *p* = 0.657)

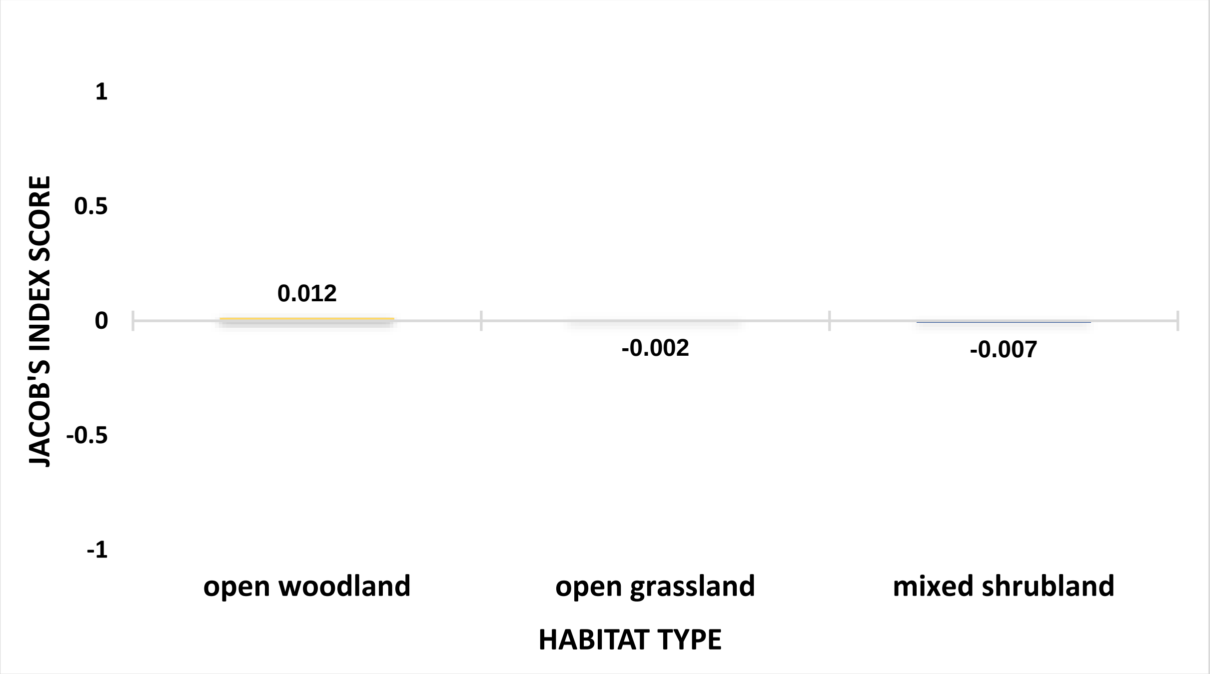


Figure 14: Jacob's Index scores showing rail-mortalities from different habitat types.

5.5. DISCUSSSION

5.5.1. Seasonal patterns of wildlife rail mortality

The seasonal patterns of wildlife mortalities on the railway are associated with their behavioural cycles as many studies show that rail mortalities increase during the period of migration or dispersal (Gundersen *et al.*, 1998; Budzik & Budzik, 2014; Krauze-Gryz *et al.*, 2017). Dry season is general the period of food and water scarcity for wildlife (Ogutu *et al.*, 2008; Owen-Smith & Ogutu, 2012). Consequently, animals are likely to disperse over larger distances to seek these resources increasing the risk of collision with trains. Unexpectedly, mortalities were registered more often in the wet season than the dry season, but rail mortality did not significant differ between seasons. This lack of significant variation in the seasonal patterns of rail mortality may be due to random chance of recorded rail-kills on a given survey day between seasons as dead animals killed on the railways during and before the survey day were recorded (Coelho *et al.*, 2008). A second explanation could be the limited number of recorded rail-kills between seasons (Conard & Gipson, 2006), suggesting that sampling of rail mortality should be performed for longer periods for assessment of seasonal patterns. The high proportion of recorded rail-kills in wet season than the wet season was probably due to the increase of surface water and food availability across the landscape since animals are no longer confined in areas where there is forage and water supply during this period (Lala *et al.*, 2021).

The rail mortalities of mammals were encountered more frequent in the dry season. Meanwhile, bird and reptile mortalities on the railway line were recorded more often in the wet season. However, seasonal patterns of rail mortality for each taxon did not significant differ suggesting that other important factors rather than the effects of seasonal changes influence their temporal pattern of rail-kill in the study area. Resource shortages in the dry season is likely to explain the peak of recorded mammal mortality on the railway line because of their increased movement activity to seek out for forage and water during this period (Njovu *et al.*, 2019). A study in the Southern Kalahari, South Africa, reported that the increase in bird mortalities on roads in the summer, which corresponds to the wet season in the study area, was likely due to increased food supply (Bullock *et al.*, 2011). They argued that adult moths, butterflies, and reproductive termites are only active in the summer season (wet), a source of food for insectivorous birds (Bullock *et al.*, 2011). The results of this study partially support this because nearly all identified bird species killed on the railway line include insects on their diet, except for White-backed Vulture and Laughing Dove (*Streptopelia senegalensis*) (Hockey *et al.*, 2005) and were registered more often in the wet season than the dry season. Insect mortalities on the railway line due to collision with trains is known (Pop *et al.*, 2020) and the clear attraction of insectivorous bird species closer to the railway line has also been found (Wiącek *et al.*, 2015). The vulnerability of reptiles during the wet season on the railway line could be related to their seasonal movement for breeding as this season coincide with their breeding period (Cuyckens, *et al.*, 2016; Akrim *et al.*, 2019). This could also be the case for a peak in bird mortalities on the railway line during the wet season (Bullock *et al.*, 2011; Akrim *et al.*, 2019).

The seasonal variation for amphibian mortalities on the railway line could not be tested because they were they were recorded only in the wet season (Table 20). This support the notion that amphibians are likely remain inactive during the dry season in the study area (Budzik & Budzik, 2014; Mestre *et al.*, 2019). Amphibians are considered as the group of terrestrial vertebrates most sensitive to water availability (Hirschfeld & Röde, 2011) and rains are critical determinants for their movement (Mestre *et al.*, 2019). It is therefore unsurprising that the rainfall events, which predominantly occur during the wet season (M'marete, 2003), initiated their movement and making them vulnerable to the railway line. A study in Costa Rica reported a mass mortality of amphibians (93.5%) because of their seasonally high aggregation in temporary ponds and ditch drainages next to the road (Arévalo *et al.*, 2017). Similarly, it is possible that amphibians are attracted to temporal pools along the railway line during the wet season and making them vulnerable to train collision.

5.5.2. Daily activity patterns of wildlife on rail mortality

Rail mortalities of diurnal species were greater than those of nocturnal species, but this difference was not significant. These results disagree with my expectations that rail-kills of nocturnal species will be higher compared to rail-kills of diurnal species as they are likely to be blinded by train headlight and freeze instead of moving away from rail track. The activity patterns of wildlife mortalities on the railway line are positively associated with train intensity, with more wildlife-train collisions likely to occur during the times of the day of high train traffic (Kušta *et al.*, 2014; Krauze-Gryz *et al.*, 2017). Based on the number of circulating trains between daytime (06:00 – 18:00) and nighttime (18 – 06:00) in the study (Adopted from Roy & Sukumar, 2017), it is unlikely that that train traffic attributed to the increase of rail mortalities for diurnal species because trains passed more frequently during nighttime (= 1 726; 51%) than daytime hours (= 1661; 49%). The close association between wildlife rail mortalities and their daily activity patterns in the dry season, with significantly more significant more mortalities of diurnal species than nocturnal species. However, this was not the case during the wet season. Again, it is not likely that train volume is related to increased mortalities of diurnal species in the dry season as passing trains were recorded more often in the nighttime (= 891; 52%) than daytime (= 823; 48%). The possible reasons behind the increase of rail mortalities by diurnal species and their association with dry season remains unclear and justify further research.

5.5.3. Effect of rail-side habitat on rail mortality

Surrounding rail-side habitat did not influence the occurrences of rail mortalities as hypothesised (Figure 14). However, rail mortalities recorded more frequently in a mixed shrubland than open grassland and woodland habitat type. A similar pattern of high roadkill mortality on habitats with denser vegetation cover have been shown (Lala *et al.*, 2021). While the increased shrub cover is likely to provide greater protection and security for animals before crossing the railway (Clevenger *et al.*, 2003), the time for wildlife to detect approaching train and escape from the railway tract may be reduced due to poor visibility (Carvalho *et al.*, 2017). The results of this study support this because the rail mortality of medium-large mammal species which have greater chances of noticing the trains from a distance, occurred at mixed shrubland section (Appendix F).

5.6. CONCLUSION

The study assessed mortalities of wildlife on the railway line traversing BNR and a total of 99 deaths were recorded from four different taxonomic groups. Rail mortalities of mammals were encountered more often than those of birds, reptiles, and amphibians. Although this difference in rail-kill patterns between taxa may be associated with the local patterns in vertebrate diversity (Lala *et al.*, 2021), comparison of this kind should be cautiously interpreted considering the persistence and detectability of carcasses among the different taxonomic groups. For instance, carcasses from taxon with predominantly smaller body sizes, such as amphibians, are likely to persist for shorter periods either due to scavenging by other animals or weather conditions (Santos *et al.*, 2011; Teixeira *et al.*, 2013) and because to their small body size, they are more likely to be unnoticed on the railway during the surveys (Teixeira *et al.*, 2013; Santos *et al.*, 2016). Moreover, amphibians are likely to be inactive at certain times of the year in response to climatic conditions (Budzik & Budzik, 2014; Mestre *et al.*, 2019), and this is also common for most reptile species (Kioko *et al.*, 2015). Therefore, their brief period of activity reduces the probability of being encountered on the railway line due to shorted sampling period compared to other taxa.

It should be noted that the rail mortalities presented are considered an underestimate in both the number of individuals and species killed on the railway line just like other existing studies on railways (e.g., Godinho *et al.*, 2017; Hamr *et al.*, 2019) and roads (e.g., Kiros *et al.*, 2016; Healey *et al*., 2020). Animals might be struck by the trains and eventually die a distance away from the railway and carcasses might be consumed by scavengers. In fact, carcass persistence was evidently a major factor that influenced the number of recorded rail-kills during the study period as marks of blood between the rails were observed on several occasions, White-backed Vultures aggregating around the buffalo carcass just few hours it was killed by the train, and spotted hyaena walking directly on the railway, presumably searching for carcasses (*pers. obs*). Additionally, the applied procedures in the assessment of rail mortalities on the railway line, such as time intervals and walking speed, might have also influenced the probability of detecting carcasses during the surveys (Bager and Da Rosa, 2011). To try and correct for underestimation of rail mortality, a standardized survey method that consider carcass persistence and detection among different vertebrate groups should be developed. For instance, surveys of monitoring rail mortality could be one day or even shorter intervals for high quality data, but this will obviously depend on time and financial resource available (Santos *et al.*, 2011). Carcass removal rates can also be estimated before or in conjunction with monitoring surveys (Coelho *et al.*, 2008).

Despite these limitations, the study still serves as evidence that several smaller species from different vertebrate groups are killed by on the railway and mortality of wildlife a result of train collision can be a threat to other species of conservation concern that were not documented before this study, such as the White-backed Vulture (IUCN, 2021; see Appendix F). This highlights the need for continual monitoring of rail mortality in the landscape across all taxonomic groups. Based on the body damage of encountered carcasses, it was evidently clear that nearly all recorded deaths were overrun by trains which suggest that WTC is a major source of mortality in the study area. However, this does not rule out the possibility that rail entrapment or collision with overhead wires could be another source of rail mortality. For example, the Marsh Terrapin (*Pelomedusa subrufa*) carcass was found between the rail but with no sign being hit by the train and might have died of hunger and desiccation. This reflects the need for correct identification of the source of mortality for every individual killed to be taken into considerations during monitoring of wildlife mortality on the railway.

The study results reject my hypothesis that rail mortality of wildlife differs between seasons. This could be due to random chance effect of recorded rail-kills and the limited number of recorded rail-kills between seasons as the result of the survey method applied (sampling period and intervals). Moreover, the seasonal variation did not explain the rail-kill temporal patterns of mammals, birds, and reptiles as rail mortalities for each taxon group did not significantly vary between seasons. However, there was seasonal difference in the temporal patterns of amphibian rail-kill, with all amphibian mortality on the railway line occurring in the wet season. Small crossing structures, such as tunnels or drainage pipes, can be used to facilitate safe passage of amphibians on the railway line to reduce their mortality in the wet season. These crossing structures could be combined with fencing on both sides at shorter distances (± 50 m) to guide amphibians to the underpass (Healey *et al.*, 2020). There was no relationship found between the daily activity patterns of wildlife and mortality on the railway line as rail-kills of diurnal and nocturnal species did no significant differ. However, this association was found in the dry season with significantly more diurnal species killed on the railway line than nocturnal species. Although it was beyond the scope of this study to determine the effects of train speed and volume on rail mortality of wildlife, reducing train traffic and speed during the daytime hours in the dry season can be a mitigating strategy to minimise rail mortality of diurnal species as been shown from other studies that rail mortality of wildlife increases with train intensity (e.g., Kušta *et al.*, 2014) and speed (e.g., Clair *et al.*, 2020). The study also found no evidence that rail-side habitat influences the mortality of wildlife on the landscape.

CHAPTER 6: MANAGEMENT IMPLICATIONS

6.1. ACTIVITY PATTERNS

The activity patterns of the medium-large mammal species (≥ 10 kg) differed in both time (time of the day and seasons) and space (rail-side habitat) on and along the railway line. Buffalo and elephant, and spotted hyaena are active on the railway line throughout the day. Giraffe and impala are mostly active during the daytime period. Meanwhile lions are mostly active on the railway line at nighttime period. To reduce the risks of collision, management intervention should focus on the time of the day in which an animal is mostly active on the railway line. This could be mitigation measures like stopping or reducing the number of running trains during the daytime period to minimise train collision of animals that are mostly active on the railway line during this period, such as impala and giraffe.

Similarly, elephants are more active on and around the railway in the wet season than dry season. Meanwhile, giraffe, impala and lion are more active in the dry season than wet season. Again, measures to reduce the risk of train collision of these species should be focused on seasonal periods in which their activity around the railway line is most likely to occur. Because these species are mostly active on and around the railway line at differences times of the day and seasons, decisions for any management intervention must priorities a species that is of conservation concern and/or with higher number of train collisions.

African buffalo are more active around the railway line in mixed shrubland than any other habitat type. While african elephant are more active in open woodland and less active in open grassland than compared to mixed shrubland. Giraffe and impala activity around the railway are more concentrated in both grassland and woodland than in mixed shrubland. Most lion activity occur in open grassland than any other habitat type bisecting the railway. Spotted hyaena more active in open grassland and woodland than mixed shrubland. To reduce the risk of train collisions, more attention given on habitat sections bisected by the railway line which have high concentrations of activity these focal species.

Lions appeared to minimise or avoid encounters of train activity on the landscape as the study found a low overlap in their activity with that of trains. Lions are likely to be avoiding trains to avoid collisions or because of the noise or vibrations caused by trains. This avoidance behaviour by lions to passing trains can limit their movements and access to critical resources on the landscape. But to due limited number of capture events obtained for lion on the railway line during the study (*n* = 7), it would be wrong to conclude that lions are avoiding train activity. Therefore, further investigation is needed to confirm whether lions are truly sensitive to train movements and determine what mitigation measures could be done.

African buffalo and elephant tend to be attracted closer to the railway line as their activity declined with increasing distance from the railway line. As such, they have higher risk of collisions with trains. On the other hand, impala seemed to keep a distance from the railway line as I found that their activity increased with increasing distance from the railway line. Although they do not stand greater risk of collision with train, like buffalo and elephants, but they are likely prone habitat loss. It remains unclear whether elephants or buffalo are attracted to the railway due to available forage found along the railway and whether impala keep a distance away from the railway due train traffic or the railway itself. Because this was beyond the scope of this study, future research is necessary to determine what causes attraction of buffalo and elephant to the railway to help find mitigation measure aimed at reducing their risks to collision with trains. Similarly, more investigation is need for impala population to determine what contributes to their avoidance behaviour at distances from the railway line.

6.2. RAIL MORTALITIES

The study serves as proof that other small mammals and wildlife groups (amphibians, reptiles, and birds) are killed by train on the railway line. Even so, species of conservation concern from other groups that were not never documented before are liked by trains. Therefore, monitoring of rail mortalities on the landscape should continue and must include all groups of wildlife.

Rail mortality assessment was heavily influenced by carcass persistence. So, a standardized method should be developed for future assessment of rail mortality which corrects for carcass persistence from different wildlife groups to minimise underestimation of rail-kill mortality.

Amphibian mortality on the railway line occurred only in the wet season. Small crossing structures, such as tunnels or drainage pipes, can be used to facilitate safe passage of amphibians on the railway line to reduce their mortality in the wet season. These crossing structures could be combined with fencing on both sides at shorter distances (± 50 m) to guide amphibians to the underpass.

Animals that are active during the daytime period are killed more often that those that are active at night. Although it was beyond the scope of this study to determine the effects of train speed and volume on rail mortality of wildlife, reducing train traffic and speed during the daytime hours in the dry season can be a mitigating strategy to minimise rail mortality of animals active during the daytime period.

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APPENDICES

Appendix A: Number of wildlife mortalities and through collision with trains in BNR between 1993 and 2019 (Elliot *et al.*, 2019) and the conservation status of each species reportedly killed on the railway (IUCN, 2021). Number of WTC that were reported during the period of this study (May 2020 – April 2021) shown in brackets.

Common name	Latin name	Collisions	Status
African civet	*Civettictis civetta*	1 (0)	Least Concern
African buffalo	*Syncerus caffer*	98 (1)	Near Threatened
African elephant	*Loxodonta africana*	32 (3)	Endangered

African wild dog	*Lycaon pictus*	1 (3)	Endangered
Black rhinoceros	*Diceros bicornis*	1 (0)	Critically Endangered
Blue wildebeest	*Connochaetes taurinus*	4 (0)	Least Concern
Bush pig	*Potamochoerus larvatus*	0 (1)	Least Concern
Cheetah	*Acinonyx jubatus*	2 (0)	Vulnerable
Giraffe	*Giraffa camelopardalis*	57 (2)	Vulnerable
Hippopotamus	*Hippopotamus amphibius*	14 (0)	Vulnerable
Impala	*Aepyceros melampus melampus*	86 (11)	Least Concern
Black-backed Jackal	*Canis mesomelas*	3 (0)	Least Concern
Klipspringer	*Oreotragus oreotragus*	7 (0)	Least Concern
Kudu	*Tragelaphus strepsiceros*	48 (0)	Least Concern
Leopard	*Panthera pardus*	3 (0)	Vulnerable
Lion	*Panthera leo*	96 (1)	Vulnerable
Porcupine	*Hystrix africaeaustralis*	3 (0)	Least Concern
Spotted hyaena	*Crocuta crocuta*	26 (0)	Least Concern
Warthog	*Phacochoerus africanus*	13 (0)	Least Concern
Waterbuck	*Kobus ellipsiprymnus*	3 (0)	Least Concern
White rhinoceros	*Ceratotherium simum*	1 (0)	Near Threatened
Plains zebra	*Equus quagga*	3 (0)	Near Threatened

Appendix B: Data sheet used for the deployment of camera traps during the period of this study.

DATA SHEET: CAMERA TRAP DEPLOYMENT								
CAM ID	**SITE NO**	**DISTANCE (m)**	**START DATE**	**START TIME**	**GPS COORDINATES**	**HABITAT TYPE**	**CHECK-UP DATE**	**COMMENT**

Appendix C: Data sheet used when revisiting deployed camera traps during the period of this study.

DATA SHEET: CAMERA TRAP CHECK-UP								
CAM ID	**SITE NO**	**DISTANCE (m)**	**DATE**	**END TIME**	**GPS COORDINATES**	**NO. OF PHOTOS**	**HABITAT TYPE**	**COMMENT**

Appendix D: Number of recorded photos from camera trapping for each mammal species at distances from the railway line (RR) during the period of this study. Focal medium-large mammal species (≥ 10 kg) that were monitored around the railway line are highlighted in bold.

Common name	Latin name	Distance (m)					TOTAL
		0 (RR)	50	100	250	500	
Aardvark	*Orycteropus afer*	0	2	3	2	0	7
African buffalo	***Syncerus caffer***	**36**	**303**	**388**	**148**	**163**	**1038**
African civet	*Civettictis civetta*	0	20	71	26	22	139
African elephant	***Loxodonta africana***	**197**	**645**	**655**	**353**	**397**	**2247**
African wildcat	*Felis silvestris cafra*	0	11	18	9	22	60
Banded mongoose	*Mungos mungo*	0	2	14	9	7	32
Black rhinoceros	*Diceros bicornis*	0	10	17	11	25	63
Black-backed jackal	*Canis mesomelas*	0	2	10	3	4	19
Blue wildebeest	*Connochaetes taurinus*	2	7	14	7	53	83
Bushbuck	*Tragelaphus scriptus*	0	11	16	15	9	51
Caracal	*Caracal caracal*	0	0	1	0	1	2
Chacma baboon	*Papio hamadryas ursinus*	83	199	191	136	131	740
Common duiker	*Sylvicapra grimmia*	1	300	367	465	302	1435
Giraffe	***Giraffa camelopadrdalis***	**71**	**164**	**164**	**160**	**174**	**733**
Hippopotamus	*Hippopotamus amphibius*	0	8	2	1	0	11
Honey badger	*Mellivora capensis*	0	2	1	3	0	6
Impala	***Aepyceros melampus melampus***	**475**	**2587**	**3350**	**2718**	**3161**	**12291**
Kudu	*Tragelaphus strepsiceros*	37	144	173	239	142	735
Large-spotted genet	*Genetta tigrina*	0	13	24	17	17	71
Leopard	*Panthera pardus*	0	14	12	11	26	63
Lesser bushbaby	*Galago moholi*	0	0	0	1	0	1
Lion	***Panthera leo***	**7**	**16**	**37**	**15**	**26**	**101**
Nyala	*Tragelaphus angasii*	0	4	4	10	2	20
Plains zebra	*Equus quagga*	86	154	159	171	218	788
Porcupine	*Hystrix africaeaustralis*	0	3	6	3	8	20
Scrub hare	*Lepus saxatilis*	0	65	37	133	101	336
Sharpe's grysbok	*Raphicerus sharpei*	0	41	55	41	70	207
Slender mongoose	*Galerella sanguinea*	0	2	0	2	2	6
Small-spotted genet	*Genetta genetta*	0	0	5	9	6	20
Spotted hyaena	***Crocuta crocuta***	**50**	**139**	**133**	**78**	**102**	**502**
Steenbok	*Raphicerus campestris*	0	182	232	164	160	738
Tree squirrel	*Paraxerus cepapi*	0	14	8	4	4	30
Vervet monkey	*Cercopithecus pygerythrus*	0	7	2	2	0	11
Warthog	*Phacochoerus africanus*	0	10	16	24	19	71
Waterbuck	*Kubus ellipsiprymnus*	8	16	16	86	59	185
White rhinoceros	*Ceratotherium simum*	8	51	70	42	53	224
Wild dog	*Lycaon pictus*	0	1	1	2	3	7
	TOTAL	**1063**	**5149**	**6272**	**5120**	**5489**	**23093**

Appendix E: Data sheet used to record encountered rail-kill on and along the railway line during the study period.

DATA SHEET: RAIL-KILL									
DATE:				**START TIME:**	**STARTING POINT GPS COORDINATES:**				
OBSERVER:				**END TIME:**	**ENDING POINT GPS COORDINATES:**				
#	**SPECIES**	**TIME**	**PHOTO ID**	**HABITAT TYPE**	**GPS COORDINATES**	**RAIL-KILL POSITION**	**RAIL-KILL SEX**	**RAIL-KILL AGE**	**COMMENT**

Appendix F: Summary of the number of recorded species killed on the railway line during the study period. Recorded rail-kill species classified according to dominant Daily Activity Pattern (N = Nocturnal, D = Diurnal, U = Unknown; Skinner & chimimba, 2005, Hockey *et al.*, 2005, Alexander & Marais, 2007, Carruthers & Du Preez, 2011); Seasons (Dry = Dry season; Wet = Wet season), rail-side Habitat Type (OW = Open Woodland, OG = Open Grassland, MS = Mixed Shrubland) and Conservation Status (LC = Least Concern, EN = Endangered, NT = Near Threatened, CR = Critically Endangered; IUCN 2021).

CLASS	ORDER	FAMILY	LATIN NAME	COMMON NAME	ACTIVITY	DRY	WET	OW	OG	MS	STATUS
Mammalia	Lagomorpha	Leporidae	*Lepus saxatilis*	Scrub hare	N	-	1	1	-	-	LC
	Carnivora	Herpestidae	*Galerella sanguinea*	Slender mongoose	D	1	-	-	1	-	LC
	Carnivora	Hyaenidae	*Crocuta crocuta*	Spotted hyaena	N	1	-	-	-	1	LC
	Carnivora	Canidae	*Lycaon pictus*	African wild dog	D	1	-	-	-	1	EN
	Primates	Cercopithecidae	*Cercopithecus pygerythrus*	Vervet monkey	D	-	1	-	-	1	LC
	Rodentia	Muridae	*Micaelamys namaquensis*	Namaqua rock mouse	N	1	-	-	-	1	LC
	Rodentia	Hystricidae	*Hystrix africaeaustralis*	Porcupine	N	1	-	-	1	-	LC
	Rodentia	Sciuridae	*Paraxerus capapi*	Tree squirrel	D	3	-	2	-	1	LC
	Rodentia	Thryonomyidae	*Thryonomys swinderianus*	Greater cane rat	N	-	1	-	-	1	LC
	Rodentia	Muridae	*Grammomys dolichurus*	Woodland mouse	N	-	2	1	1	-	LC
	Ruminantia	Bovidae	*Aepyceros melampus melampus*	Impala	D	5	2	-	6	1	LC
	Ruminantia	Bovidae	*Kobus ellipsiprymnus*	Waterbuck	N	1	-	-	-	1	LC
	Ruminantia	Bovidae	*Syncerus caffer*	African buffalo	N	1	-	-	-	1	NT
	Unknown	Unknown	Unknown	Unknown	U	7	-	-	2	5	-
Aves	Bucerotiformes	Bucerotidae	*Tockus erythrorhynchus*	Red-billed Hornbill	D	-	4	-	-	4	LC
	Bucerotiformes	Bucerotidae	*Tockus leucomelas*	Southern Yellow-billed Hornbill	D	2	1	-	1	2	LC
	Columbiformes	Columbidae	*Streptopelia senegalensis*	Laughing Dove	D	-	1	-	1	-	LC
	Coraciiformes	Coraciidae	*Coracias caudatus*	Lalic-breasted Roller	D	2	3	1	3	1	LC
	Falconiformes	Accipitridae	*Circaetus pectoralis*	Black-chested Snake Eagle	D	-	1	-	-	1	LC
	Falconiformes	Accipitridae	*Gyps africanus*	White-backed Vulture	D	-	2	-	1	1	CR

	Galliformes	Phasianidae	*Dendroperdix sephaena*	Crested Francolin	D	1	-	-	-	1	LC
	Passeriformes	Sturnidae	*Lamprotornis nitens*	Cape Glossy Starling	D	1	1	-	1	1	LC
	Strigiformes	Strigidae	*Bubo africanus*	Spotted Eagle-owl	N	-	1	-	1	-	LC
	Strigiformes	Strigidae	*Strix woodfordii*	African Wood-Owl	N	2	1	-	1	2	LC
	Unknown	Unknown	Unknown	Unknown	U	3	-	2	-	1	-
Reptilia	Testudines	Testudinidae	*Stigmochelys pardalis*	Leopard Tortoise	D	3	1	-	1	3	LC
	Testudines	Pelomedusidae	*Pelomedusa subrufa*	Marsh Terrapin	D	-	1	1	-	-	LC
	Squamata	Scincidae	*Trachylepis margaritifer*	Rainbow Skink	D	1	-	-	-	1	LC
	Squamata	Pythonidae	*Python natalensis*	Southern African Python	D	2	-	-	-	2	LC
	Squamata	Gekkonidae	*Chondrodactylus turneri*	Turner's Tubercled Gecko	N	2	5	4	1	2	LC
	Squamata	Gerrhosauridae	*Gerrhosaurus flavigularis*	Yellow-throated Plated Lizard	D	2	1	-	-	3	LC
	Squamata	Colubridae	*Telescopus semiannulatus*	Common Tiger Snake	N	-	1	1	-	-	LC
	Squamata	Chamaeleonidae	*Chamaeleo dilepis*	Flap-neck Chameleon	D	-	1	-	1	-	LC
	Squamata	Gekkonidae	*Afroedura langi*	Lowveld Flat Gecko	N	-	2	1	1	-	LC
	Squamata	Varanidae	*Varanus albigularis*	Rock Monitor	D	-	2	1	1	-	LC
	Squamata	Colubridae	*Psammophis subtaeniatus*	Western Stripe-bellied Sand Snake	D	-	2	1	-	1	LC
Amphibia	Anura	Bufonidae	*Sclerophrys garmani*	Eastern Olive Toad	N	-	8	-	5	3	LC
	Anura	Ptychadenidae	*Ptychadena mossambica*	Broad-banded Grass Frog	N	-	3	-	-	3	LC
	Anura	Ptychadenidae	*Ptychadena anchietae*	Plain Grass Frog	N	-	3	2	-	1	LC
	Anura	Rhacophoridae	*Chiromantis xerampelina*	Southern Foam-nest Frog	N	-	4	3	1	-	LC
					TOTAL	**43**	**56**	**21**	**31**	**47**	

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