Factors influencing the spatial patterns of vertebrate roadkill in South Africa: The Greater Mapungubwe Transfrontier Conservation Area as a case study

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ABSTRACT

Few studies have investigated the factors that influence roadkill occurrence in developing countries. In 2013, we monitored a 100-km section of the road (comprising the R572 and R521 regional highways and the D2662) that pass through the Greater Mapungubwe Transfrontier Conservation Area in South Africa, to assess the possible factors influencing roadkill. Over a period of 120 days, and across the three ecological seasons, we recorded 981 roadkills (rate = 0.08 roadkill/km/day) from four vertebrate taxonomic groups. We generated predictive models of roadkill from one combined data set that considered eight variables identified from the literature as potential correlates of roadkill. The model that included the distance of the fence from the road, habitat type adjacent to the road, and the presence of a hill in the road (i.e., elevation) or a bank on the side of the road best explained roadkill occurrence. More roadkill was predicted to occur in both open and dense mopane and dense mixed bushveld habitats, on a hill, when there was a bank on the side of the road, and as the distance between the road verge and a fence decreased. Our model provides some insight into the significant predictors of roadkill occurrence and is therefore a valuable tool in identifying sites of high-potential roadkill frequency and formulating mitigation measures for reducing road mortalities.

KEYWORDS

biodiversity, fence type, predictive model, road ecology, wildlife–vehicle collision

1. INTRODUCTION

Despite widespread recognition of roads being a threat to biodiversity, road density continues to increase worldwide (Laurance, Sayer, & Cassman, 2014). In developing countries, huge budgets are devoted to the construction and upgrading of roads with little or no allocation to mitigation measures to protect biodiversity (Van der Ree, Jaeger, Grift, & Clevenger, 2011). Furthermore, the number of vehicle collisions with large mammals is increasing in developed countries and is estimated to be several million individuals each year (Malo, Suarez, & Diez, 2004).

Roads and traffic are destructive to animal populations in many ways: by fragmenting habitats, genetic isolation of populations, and changes in land use (Hels & Buchwald, 2001), and through mortality from wildlife–vehicle collisions (WVC; i.e., roadkill; Clevenger, Chruszcz, & Gunson, 2003), which has an immediate impact. Understanding the factors influencing the likelihood of roadkill occurrence allows the implementation of strategies to minimise WVCs, ultimately improving human safety and reducing roadkill occurrence (van der Ree et al., 2011).

The factors influencing roadkill occurrence can be classified into two broad categories: ecological and physical. Ecological or environmental factors are any abiotic or biotic factors that influence living organisms, which may include ambient temperature and amount of sunlight, whilst physical factors are nonliving factors that affect organisms and their survival (Allaby, 2010). Many studies around the world have investigated the possible ecological and physical factors influencing roadkill occurrence such as season (Garriga, Franch, Santos, Montori, & Llorente, 2017; Snow, Andelt, & Gould, 2011), landscape (Cuyckens, MochI, Vallejos, Perovic, & Biganzoli, 2016; Husby, 2016; Snow et al., 2011; Son et al., 2016), roadside fencing (Braz & França, 2016; Son et al., 2016), traffic volumes and vehicle speed (Husby, 2016; Snow et al., 2011) and road surface (Braz & França, 2016). Only a few of these studies have been conducted in Africa (Bullock, Malan, & Pretorius, 2011; Dean & Milton, 2003; Drews, 1995; Haverschmidt, 1955; Van der Hoeven, Boer, & Prins, 2009; Kioko, Kiffner, Jenkins, & Collinson, 2015; Mkanda & Chansa, 2010; Siegfried, 1965), and few roadkill studies have assessed ecological and physical factors simultaneously (Burgin & Brainwood, 2008; Ha & Shilling, 2018). In addition, most studies are limited to only a few specific variables (Braz & França, 2016; Van Langevelde, Dooremalan, & Jaarsma, 2009), providing only roadkill counts (Balakrishnan & Afework, 2008; Barthelmess & Brooks, 2010) or are taxon-specific (Balakrishnan & Afework, 2008; Snow et al., 2011). Understanding the spatial patterns of roadkill requires detailed assessment of the ecological and physical factors, which may affect the spatial patterns of vertebrate roadkill.

We assessed the ecological and physical factors that potentially can contribute to the likelihood of roadkill occurrence, using the Greater Mapungubwe Transfrontier Conservation Area (GMTFCA) in South Africa as a study site. This site was selected for several reasons: (a) as a conservation area it is home to a wide diversity of vertebrates (Branch, 1998; Hockey et al., 2005; Skinner & Chimimba, 2005), one of which is globally threatened (e.g., African wild dog; *Lycaon pictus*), whilst the cheetah (*Acinonyx jubatus*) and leopard (*Panthera pardus*) are listed on the IUCN Red List as Vulnerable (Child, Roxburgh, Do Linh San, Raimondo, & Davies-Mostert, 2017); (b) numerous roads (~600 km) intersect the site, of which ~two-thirds are low-volume traffic/farm roads (Peace Parks Foundation, 2010); and (c) it is expected that recent coal mining and tourism developments will result in elevated traffic volumes. Combined, these factors make it an ideal location for assessing the potential factors influencing roadkill occurrence in South Africa.

2. MATERIALS AND METHODS

2.1. Study area

Our study site was within the GMTFCA, northern Limpopo, South Africa, and comprised an area of approximately 4,900 km^2 (Collinson, Parker, Bernard, Reilly, & Davies-Mostert, 2014; Figure 1) within latitude 22°14′S; 22°19″S and longitude 29°17′E; 29°18′E. The area falls within the subtropical region of South Africa (Cowling, Richardson, & Pierce, 2004) and experiences three ecological seasons: hot/dry (September–January), hot/wet (February–May) and cold/dry (June–August) (Viljoen et al., 2008). The region is characterised by hot summers (average temperatures range between 17°C and 27°C), and mild (4–20°C) winters with occasional frost (Nel & Nel, 2009). The mean annual temperature is 22.5°C with extreme maximum and minimum temperatures of 43.5°C and −3.8°C, respectively (Nel & Nel, 2009). The mean annual rainfall is 278 mm, but can be as low as 154 mm during dry years and as high as 451 mm during wetter years (Nel & Nel, 2009). The rainy season falls from November to March (summer), when the province receives 90% of its total annual rainfall (M'Marete, 2003).

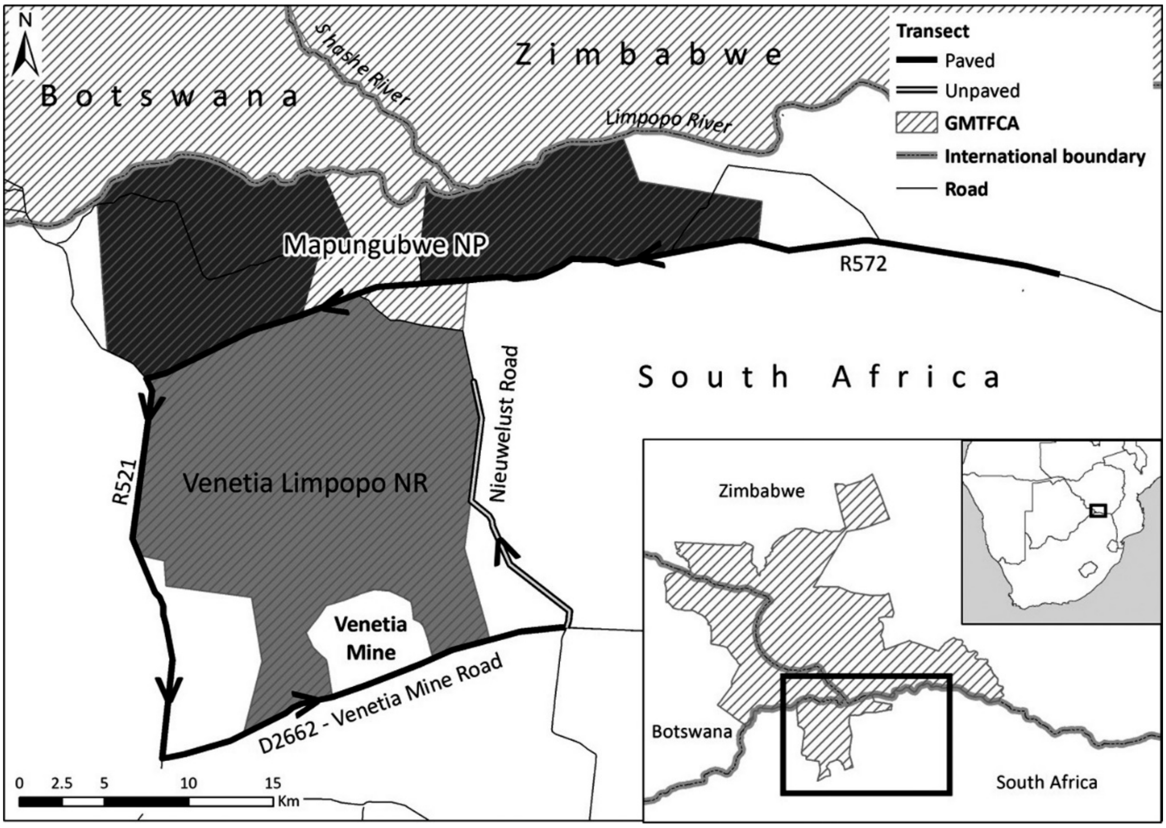

Figure 1. A map of the Greater Mapungubwe Transfrontier Conservation Area (GMTFCA), northern Limpopo Province (South Africa), showing the roads sampled during our study. The 100 km road section is in bold, showing the R572 regional highway (57.1 km), the R521 regional highway (23.7 km), and the D2662 Venetia Mine Road (19.2 km) (Collinson et al., 2014)

The Limpopo Province is situated in a dry savannah subregion within the savannah biome, which is the largest biome in South Africa (Mucina & Rutherford, 2006). It is characterised by a grassy ground layer, with intermediate stages of growth and scattered trees and bushes, and is known locally as bushveld (Mucina & Rutherford, 2006). The study area falls within the Mopane Bioregion, the smallest bioregion in the savannah biome, consisting of two vegetation units: Musina Mopane bushveld and Limpopo Ridge bushveld (Mucina & Rutherford, 2006). Sixteen of the 18 vegetation types that occur in the region are dominated by these two vegetation types, with short (~1.5 m) mopane (*Colophospermum mopane)* woodland being most common (O'Connor, 1992). It is classified as Mopane Veld and found on sandy, loamy to rocky soils derived mainly from gneiss (Acocks, 1988).

Current competing land uses include nature conservation, heritage site conservation, game ranching, livestock ranching, tourism (~60% collectively), agriculture (~20%) and infrastructure related to diamond and coal mining (~20%) (Braack, 2009; Hermann, 2013).

Traffic volumes are very low (range: 101–452 vehicles/day; Mikros Traffic Monitoring, 2011) in comparison with other studies (mean = 2,347 vehicles/day on a regional road in Spain, D'Amico, Román, de los Reyes, & Revilla, 2015; mean = 451–13,968 vehicles/day on rural roads in New York State, USA, Langen, Ogden, & Schwarting, 2009).

The GMTFCA harbours high species richness of reptiles (~120 species; Branch, 1998), birds (≥429 species; Hockey et al., 2005) and mammals (~100 species; Skinner & Chimimba, 2005), but amphibian species richness is considered low (~12 species; Carruthers & du Preez, 2011).

2.2. Road section sampling

We selected one 100 km road section to monitor roadkill occurrence (comprising the R572 and R521 regional highways and the D2662; Figure 1) and were selected as they formed a circuit that buffered a national park, mine and private land. Several roads (paved and unpaved) traverse the area and elevated traffic volumes are anticipated as a result of expected increases in local mining and tourism activities (Collinson, Parker, Bernard, Reilly, & Davies-Mostert, 2015). Both road types (i.e., paved and unpaved) are single-lane roads with an average width of 6 m (range = 4–8 m). A maximum speed of 60 km/hr is permitted on the unpaved roads and 120 km/hr on the paved roads. Mean traffic volume was 149 vehicles per day for the paved roads (range = 74–228 vehicles, *c* = 37.6) and 11 vehicles per day for the unpaved roads (range = 7–16 vehicles, *SD* = 3.92; Mikros Traffic Monitoring, 2011). The roads are bordered on either side by fences. Cattle fences—erected for domestic livestock—are ~1.2 m high and vary between three and six strands (19% of the study area; Bothma & du Toit, 2009). Game fences—erected to enclose wild game—are 2.4 m high and are either nonelectrified, comprising 19 wire strands (50% of the study area), or constructed with 23 strands of high strain steel wire, with four live wire strands providing an output voltage of ~7,000 volts (29% of the study area). The remaining 2% of fencing consists of a cattle/electric combined fence comprising a cattle fence nearest the road verge with an electric fence ~20 m further away.

A single observer, who was also the driver, drove the vehicle at speeds of between 40 and 50 km/hr, using the protocol for roadkill detection as outlined by Collinson et al. (2014). The road was sampled in each of the three ecological seasons and driven daily for 40 consecutive days, commencing 1.5 hr after sunrise (Collinson et al., 2014). We only counted roadkill carcasses that were detected on the road and excluded carcasses on road verges to avoid potential detection bias (Guinard, Prodon, & Barbraud, 2015). Furthermore, to overcome inconsistencies in roadkill data collection, we followed a standardised protocol to minimise detection bias and make data more comparable (Collinson et al., 2014; Guinard et al., 2015). A photograph, to verify species identification, and geographic coordinates (using a Garmin eTrex 10 GPS) were noted for each carcass.

2.3. Variables assessed

We recorded 22 characteristics associated with the site of each roadkill to evaluate their potential influence on the incidence of roadkill (Table A1). Based on the literature, our knowledge of the study area and some initial data exploration, we identified and settled on eight variables as possible a priori factors influencing roadkill from the initial list of 22. The final variables were as follows: proximity to water (categorical with two factors), roadside habitat type (categorical with seven levels), grass height (continuous, 0–100 mm), fence distance to verge (continuous, five fence distance categories between 0 and 25 m), presence/absence of a hill (categorical with two levels), presence/absence of a roadside bank (categorical with two levels), proximity to a junction in the road (categorical with two levels) and taxon (categorical with four levels) (Table A1). We hypothesised that more roadkill was likely to occur when the road was close to a water source (Mkanda & Chansa, 2010), situated in dense roadside habitat (Mkanda & Chansa, 2010) and where grass height was highest (Seo, Thorne, Choi, Kwon, & Park, 2015). In addition, we hypothesised that more roadkill was likely to occur the further the fence was from the road verge (Eloff & Van Niekerk, 2005) or on a hill (Slater, 2002), although less likely to occur when there were banks (i.e elevated slopes) on the sides of the road (Malo et al., 2004).

To assess whether roadkill sites were associated with a particular variable(s), we also characterised a series of non-roadkill (control) sites generated along the road sections using a random number generator (Microsoft Office Excel, 2010). Based on the average roadkill rate detected during preliminary surveys conducted in March 2011 (Collinson et al., 2014), we generated 10 random points for each day of sampling, providing 1,200 “control” points in total. We generated each point from a number range (1–1000) that corresponded to an actual distance along the survey route, and each position was separated by 100 m and linked/paired with actual roadkill sites: the number one represented 0.0 km and the number 1,000 represented 100 km along the selected road section. If an actual roadkill was detected within 100 m of the randomly generated point, we drove another 100 m to record the next control point. This was to ensure that the random points (n = 286) did not reflect actual roadkill sites on the day the roadkill occurred. At each random point, we recorded the same eight variables that were recorded for each roadkill.

2.4. Variable characterisation

To standardise the collection of both ecological and physical data, we recorded the predominant habitat category within a 10 m radius of where the roadkill was detected, adopting the method used by Conard and Gipson (2006) to assess vegetation type, which was assumed to remain constant during the study (i.e., vegetation types were unlikely to change over a 120-day period). However, grass height was quantified separately for each record (see below). We used Mucina and Rutherford's (2006) classification of Mopane Veld, to identify seven vegetation communities along the road transect: grassland, mixed bushveld, mopane, riparian, Salvadora (*Salvadora angustiflora*), Vachellia (*Vachellia* spp.) and “other.” These were further categorised, by subjective visual estimation, as dense, when the distance between trees (canopy cover) was less than 2 m (on average), and open, when the distance was greater (O'Connor, 1992). Riparian areas were defined as areas within 50 m of a stream, running either perpendicular or parallel to the roadway (Conard & Gipson, 2006). Category “other” was used when the vegetation could not definitely be classed as one of the seven categories: for example, when the area was dominated by rocks or bare soil. To assess the availability of each vegetation/habitat type, the extent was recorded during the hot/wet season of 2012 by slowly driving the route (~20 km/hr) and recording the distance (km) of each habitat on both sides of the road, based on odometer readings.

We measured grass height using a one-metre L-shaped chequered ruler, divided into 10 cm lengths, to take grass height measurements at the road edge, one metre from the verge, and two metres from the verge, on both sides of the road. From this, we calculated the sample mean and standard error of grass heights on each side.

We visually estimated the distance of a fence from the verge (m) in one of six proximate categories (0–5, 6–10, 11–15, 16–20, 21–25 and > 25 m) to allow distinction between different groups. We recorded the distance for both sides of the road at each roadkill detection. We recorded additional road features, including the proximity to a water course, banks adjacent to the road, road shape (straight or curved), hills and proximity to a road junction.

2.5. Data analysis

We generated predictive models of roadkill from one combined data set (Braz & França, 2016; Bueno, Sousa, & Freitas, 2015). Most published literature for predictive roadkill modelling target specific taxonomic groups (amphibians, Coelho, Teixeira, Colombo, Coelho, & Kindel, 2012; reptiles, Mackinnon, Moore, & Brooks, 2005, Langen et al., 2009; birds, Clevenger et al., 2003, Gomes, Grilo, Silva, & Mira, 2009; mammals, Clevenger et al., 2003, de Freitas, Oliveira, Ciocheti, Vieira, & Silva Matos, 2015). Few models generalise across taxonomic groups, and, as mitigation tools, may be less informative for mitigation strategies (Burgin & Brainwood, 2008; Farmer & Brooks, 2012). Despite body size being the key driver for assessing home ranges for terrestrial species (Jackson & Fahrig, 2015), we elected to use landscape structure as our scale of measurement since body size was not considered to be a reliable indicator for predicting roadkill occurrence across taxonomic groups (Jackson & Fahrig, 2015). For example, many flying species are likely to have a wider home range than terrestrial species of the same body mass (Jackson & Fahrig, 2015).

We constructed a global candidate model, which included all eight of our a priori predictor variables, to examine their influence on our response variable (roadkill presence or absence). We did not include interactions as we could not justify their ecological relevance a priori, and we wished to keep the resulting candidate models as simple as possible (Burnham & Anderson, 1998). Grass height, proximity to a water course, presence/absence of a bank, hill or junction, vegetation type, fence distance were all included as fixed effects, whilst taxon was included as a random effect. Prior to model selection, we tested for colinearity between variables by calculating the variation inflation factor (Table A2; VIF; Zuur, Ieno, & Elphick, 2010). We selected a value of 5 as the threshold for colinearity (Montgomery & Peck, 1992), whereby we excluded variables with a VIF greater than this value from the analysis (Zuur et al., 2010). All of our predictor variables had VIF values < 5. We used the glmer function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2014) followed by a dredge function from the MuMIn package (Barton, 2009) of R 3.0.2 (R Development Core Team, 2014) for our model selection and Akaike's information criterion (AIC) and Akaike weights $AIC_c wi$ to assess the appropriateness of the models (Table 1; Table A2; Burnham & Anderson, 1998; Burnham, Anderson, & Huyvaert, 2011).

Table 1. Model selection table showing the candidate models using all eight of our a priori predictor variables, to examine their influence on our response variable (roadkill presence or absence)

Model	Model combination	Intercept	*df*	loglik	AICc	Delta AIC	Weight
1	• Presence of a bank (yes) • Fence distance from roadside verge • Presence of a hill (yes) • Presence of a junction (yes) • Vegetation type	0.1	14	−1,301.9	2,632.0	0.00	0.34
2	• Presence of a bank (yes) • Fence distance from roadside verge • Grass height • Presence of a hill (yes) • Presence of a junction (yes) • Vegetation type	0.02	15	−1,301.6	2,633.4	1.39	0.17
3	• Presence of a bank (yes) • Fence distance from roadside verge • Presence of a hill (yes) • Vegetation type	0.09	13	−1,303.7	2,633.6	1.61	0.15
4	• Presence of a bank (yes) • Fence distance from roadside verge • Presence of a hill (yes) • Presence of a junction (yes) • Vegetation type • Proximity to a water course	0.1	15	1,301.9	2,634.0	2.02	0.12
5	• Presence of a bank (yes) • Fence distance from roadside verge • Grass height • Presence of a hill (yes) • Vegetation type	0.009	14	−1,303.5	2,635.1	3.11	0.07
6	• Presence of a bank (yes) • Fence distance from roadside verge • Grass height • Presence of a hill (yes) • Presence of a junction (yes) • Vegetation type • Proximity to a water course	0.02	16	−1,301.6	2,635.4	3.42	0.06
7	• Presence of a bank (yes) • Fence distance from roadside verge • Presence of a hill (yes) • Vegetation type • Proximity to a water course	0.09	14	−1,303.7	2,635.6	3.63	0.05

Model	Model combination	Intercept	*df*	loglik	AICc	Delta AIC	Weight
8	• Presence of a bank (yes) • Fence distance from roadside verge • Grass height • Presence of a hill (yes) • Vegetation type • Proximity to a water course	0.01	15	−1,303.4	2,637.1	5.13	0.03
9	• Fence distance from roadside verge • Presence of a hill (yes) • Presence of a junction (yes) • Vegetation type	0.25	13	−1,311.1	2,648.5	16.47	0.00
10	• Fence distance from roadside verge • Presence of a hill (yes) • Vegetation type	0.24	12	−1,312.8	2,649.9	17.85	0.00

Our model selection process indicated that the top seven models (which included all the original fixed and random variables) all had substantial support (Table 1; Table A3). We then used the lme4 package in R to run a conditional generalised linear mixed model with a logit link function to assess the effects of the predictor variables on roadkill presence.

3. RESULTS

We monitored a total of 12,000 km over 522 hr, with a daily average of 180 min (range: 132–278 min). We recorded a total of 991 roadkill, 10 of which we could not identify (Supporting Information); the remaining 981 represented four vertebrate taxonomic groups (amphibians, reptiles, birds and mammals; rate = 0.08 roadkill/km/day) which we used in our modelling. A total of 159 species were recorded; birds formed the majority (n = 80; 0.035 roadkill/km/day), followed by mammals (n = 44; 0.024 roadkill/km/day) and reptiles (n = 32; 0.019 roadkill/km/day) and amphibians (n = 3; 0.01 roadkill/km/day). (A complete list of roadkill species can be found in Collinson et al., 2015.).

3.1. Factors influencing roadkill

After running the conditional logistic regression, the random effect of taxon had a variance and a standard deviation approaching zero, suggesting that there was insufficient group-level variation to warrant adding taxon as an additional group-level random effect to the overall model to explain the observed variation in the data.

The likelihood of roadkill decreased as the distance of the fence from the road increased (Table 2). Habitat type adjacent to the road appeared to influence roadkill, with the likelihood of roadkill being significantly higher in dense and open mopane, and dense mixed bushveld habitats. The likelihood of roadkill was also significantly higher when there was a hill in the road or a bank on the side of the road.

Table 2. The coefficients of the fixed effect variables most likely to influence roadkill incidences in the Greater Mapungubwe Transfrontier Conservation Area, Limpopo Province, South Africa, in 2012/13

Coefficient	Estimate	*SE*	*z* value	*p*-Value
Intercept	0.02	0.28	0.07	0.95
Vegetation type				
Dense mopane	0.76	0.22	3.43	<0.001
Open mopane	0.49	0.22	2.27	<0.05
Other vegetation type	−0.45	0.61	−0.74	0.46
Open grassland	−1.22	1.12	−1.06	0.23
Riparian	−0.12	0.41	−0.29	0.76
Salvadora	−0.69	0.48	−1.42	0.16
Dense mixed bushveld	0.62	0.24	2.55	<0.05
Open mixed bushveld	0.41	0.22	1.81	0.07
Grass height	0.15	0.19	0.8	0.42
Proximity to a water course	−0.04	0.34	−0.1	0.91
Road characteristic				
Presence of a bank (yes)	0.99	0.24	4.11	<0.001
Presence of a hill (yes)	1.92	0.35	5.46	<0.001
Presence of a junction (yes)	0.63	0.33	1.9	0.05
Fence distance from roadside verge	−0.1	0.02	−4.34	<0.001

4. DISCUSSION

4.1. Summary of key findings

4.1.1. Road section sampling per taxonomic group

Our roadkill rate for each taxonomic group was high for mammals (0.024 roadkill/km/day) and birds (0.035 roadkill/km/day) over the 12,000 km (road section = 100 km over 40 days during three seasons) in comparison with other studies (0.002 mammals and birds respectively roadkill/km/day in North America, Clevenger et al., 2003; 0.05 mammal roadkill/km/day and 0.014 bird roadkill/km/day in South Africa, Bullock et al., 2011). Data for reptiles were more difficult to compare due to the paucity of studies on this group.

From the total roadkill rate for the four taxonomic groups, we estimate that ~ 2,920 animals are killed each year on this section of road (n = roadkill rate × 365 days × 100 km), and highlights the potential negative effects of roads in the GMTFCA, particularly given the low traffic volumes recorded on this road section.

4.1.2. Best-fit models—factors of roadkill

As mitigation tools, predictive models of roadkill are becoming more common in the published literature (Coelho et al., 2012; Langen et al., 2009; Malo et al., 2004); however, few models generalise across multiple taxa and are thus less useful for management scenarios that target multiple species. We found that a model with four of the eight variables (habitat type, fence distance to the roadside verge and presence/absence of a hill, or a bank on the side of the road) best explained roadkill occurrence out of all possible model combinations for the factors of roadkill.

4.2. Factors influencing roadkill

We hypothesised that roadkill occurrence would be influenced by grass height (Seo *et al*., 2015) and dense roadside habitat (Mkanda & Chansa, 2010). Only roadside habitat type appeared to influence roadkill occurrence with roadkill more likely to occur in both open and dense mopane and dense mixed bushveld habitats. This would suggest that whilst other studies found either dense roadside habitat (Mkanda & Chansa, 2010) or open roadside habitat (Clevenger et al., 2003) as being factors of roadkill occurrence, our model favours both dense and open, specifically mopane habitat. This is the dominant habitat type in the study area (Mucina & Rutherford, 2006) and therefore our model's predictions may simply be a statistical artefact because this habitat is the most prevalent. Nevertheless, our model does demonstrate that roadkill is spatially clustered, linked to specific vegetation types and adjacent land use (Clevenger et al., 2003; da Rosa & Bager, 2012).

We also hypothesised that more roadkill was likely to occur the further the fence is from the road verge (Eloff & Van Niekerk, 2005) since wider roadside verges often create micro-habitats resulting in many animals then wandering onto the road (Gubbi, Poornesha, & Madhusudan, 2012). This was in contrast to our model, which predicted fewer roadkill occurrences as the distance between the road verge and fence increased. Wider road verges may allow grazers and browsers to be less “spooked” by passing vehicles as well as provide a greater “safe” zone in which to feed (Eloff & van Niekerk, 2005).

Finally, we predicted that roadkill was more likely to occur on a hill (Slater, 2002), but less likely to occur when there were banks on the side of the road (Malo et al., 2004) although only one of these predictions were supported by our model. Seo *et al*., (2015) found similar predictors in Korea, with more roadkill occurring when there is a hill in the road, possibly because vehicles accelerate when coming down a hill, or because driver visibility is decreased on approaching the hill brow (Møller, Erritzøe, & Erritzøe, 2011; Seo *et al.,* 2015). Contrary to our expectation, it is difficult to determine why roadkill occurrence was more likely when a roadside bank was present, since previous studies (Malo et al., 2004) observed 50% fewer roadkill in Spain when the embankments on either side of the road were more than 2 m high, as did Seo *et al.* (2015) in Korea. Fewer raven (*Corvus* spp.) roadkills was also found in Canada (Clevenger et al., 2003) where there were embankments on either sides of a road, as they can fly over the road at a greater height than a vehicle and avoid being pulled into the vehicle's downdraught (Møller et al., 2011).

4.3. Recommendations

Our model provides some understanding of the variables that may influence vertebrate roadkill occurrence in the GMTFCA. These variables may vary in other parts of the country where the characteristics of each factor differ. Since our model demonstrated that roadkill is likely to increase when there is a hill in the road, roadside banks, dense and open mopane and dense mixed bushveld and the closer the fence is to the road, we propose the following recommendations to reduce roadkill in the GMTFCA:

4.3.1. Distance to roadside verge

Few studies have compared the effect of fence distance from the road on roadkill as well as the diversity of fence types in South Africa; our study provides an opportunity for future studies to examine the effectiveness of each fence type in reducing roadkill as well as its distance to the road verge. Despite fencing being a deterrent, many animals will dig under, push through, jump (Owen-Smith, 1985; Vosloo, Bastos, Sahle, Sangare, & Dwark, 2005) or climb over fences (Thompson, 1978) and consequently, collide with vehicles, particularly when there is a narrow road verge (Eloff & van Niekerk, 2005). Whilst we excluded fence type from our model, modifications to improve existing fencing, and thus prevent access to the road verge in the GMTFCA could include; combining fencing with finer mesh to stop smaller animals getting through (Waring, Griffis, & Vaughn, 1991), or a lip bent at right angles at the top of the fence (with a one metre extension) to prevent animals from climbing over (Waring et al., 1991) and ultimately preventing wildlife access to road verges. This has proved effective in Canada for preventing black bears (*Ursus americanus;* Lewis et al., 2011) and cougars (*Puma concolor*) from climbing over fences (Clevenger et al., 2003). One-way gates have also shown some success (Ludwig & Bremicker, 1983) in providing an escape route for those animals that manage to bypass a fence and then find themselves trapped next to the road, particularly on narrow road verges. Alternatively, mowing of narrow roadside verges to increase visibility for drivers, should an animal find itself on the road verge may also be effective in preventing a WVC (Goosem, 2004).

4.3.2. Presence of a roadside bank

Studies conducted by Clevenger et al., (2003), Malo et al., (2004), Møller et al., (2011) and Seo *et al*., (2015) all found fewer roadkill when there were banks on the sides of the road. Since this was in contrast to our study, and few other studies have used these factors in their models, we propose that future predictive models of roadkill incorporate these road characteristics to further determine their influence in roadkill occurrence.

4.3.3. Summary

Our predictive models may be less informative than other studies for specific taxonomic groups (particularly for species influenced by season and who are more active during wetter periods like amphibians), but they can be valuable management tools if we consider that roadkill probability shares common risk factors across multiple groups. Statistical analysis from recent literature (Garriga et al., 2017; Lin, 2016) may allow an improvement on model prediction aiding more efficient implementation of mitigation measures for specific taxonomic groups. Furthermore, given the limitations of the current literature regarding scales at which to sample multiple vertebrate taxa, we suggest that future surveys should be clear about these confines and limit measurements of landscape structure to within the range of scales for which management can be accomplished (Jackson & Fahrig, 2015). Using the variables from our models, we can begin to predict sections of our road in the study area where roadkill is most likely to occur. We recommend further investigation on our road section in the GMTFCA to determine the whereabouts and existence of potential roadkill “hot spots,” as well as species most at risk. This will enable the consideration of appropriate mitigation strategies, which includes an infrastructure that accommodates animal mobility, lessens the impacts of habitat fragmentation and roadside fencing as barriers (Kroll, 2015).

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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