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Using road patrol data to identify factors associated with carnivore roadkill counts

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Abstract.

As the global road network expands, roads pose an emerging threat to wildlife populations. One way in which roads can affect wildlife is wildlife-vehicle collisions, which can be a significant cause of mortality through roadkill. In order to successfully mitigate these problems, it is vital to understand the factors that can explain the distribution of roadkill. Collecting the data required to enable this can be expensive and time consuming, but there is significant potential in partnering with organisations that conduct existing road patrols to obtain the necessary data. We assessed the feasibility of using roadkill data collected daily between 2014 and 2017 by road patrol staff from a private road agency on a 410 km length of the N3 road in South Africa. We modelled the relationship between a set of environmental and anthropogenic variables on the number of roadkill carcasses, using serval (*Leptailurus serval*) as a model species. We recorded 5.24 serval roadkill carcasses/100 km/year. The number of carcasses was related to season, the amount of wetland, and the number of owls killed on the roads, but was not related to any of the anthropogenic variables we included. This suggests that roadkill patterns may differ greatly depending on the ecology of species of interest, but targeting mitigation measures where roads pass through wetlands may help to reduce serval roadkill. Partnering with road agencies for data collection offers powerful opportunities to identify factors related to roadkill distribution and reduce the threats posed by roads to wildlife.

1. Introduction.

Roads are integral to a country's continued development and prosperity, especially developing countries such as South Africa (Karani, 2008; Keshkamat, Looijen & Zuidgeest, 2009). However, traffic can also have a direct negative impact on both people and wildlife (Verster & Fourie, 2018), with many species at risk from wildlife-vehicle collisions (WVCs), often resulting in an animal's death, or 'roadkill'. For the last three decades the field of road ecology has highlighted the negative impacts that roads and their associated users have on biodiversity, and their potential to limit wildlife populations (Kioko et al., 2015; Laurance et al., 2015; Parchizadeh et al., in press).

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Infrastructure development impacts biodiversity and ecosystems through exposing ecological habitats to disturbance and fragmentation (Benítez-López, Alkemade & Verweij, 2010), land-use and land cover change, and limiting connectivity in the landscape (Perz et al., 2013; Liang et al., 2014). Effective mitigation efforts required to reduce such impacts often require a detailed understanding of the factors driving wildlife-vehicle-collisions (Gunson & Teixeira, 2015). In developed countries such as the USA and Europe there have been several studies that successfully quantified the factors affecting wildlife-vehicle-collisions (Gunson & Teixeira, 2015; Rytwinski et al., 2015). Stemming from these results mitigation measures have been applied to many roads to reduce wildlife-vehicle-collisions (Jackson & Griffin, 2000; Forman et al., 2003; Grilo, Bissonette & Santos-Reis, 2009), allowing safe passage for animals, promoting habitat connectivity, accessibility, and encouraging natural movements (Goosem, Izumi & Turton, 2001; Bager & Rosa, 2010).

However, in developing countries, efforts to reduce wildlife mortality around main roads are often hampered due to a lack of research, with other priorities usually dictated by the country's socio-economic situation (Collinson et al., 2015a). For example, the collection of roadkill data by dedicated research teams can be extremely costly due to the high sampling effort required (Abra et al., 2018). This often limits the number of roadkill studies, and to date only a handful of studies have focussed on roadkill in Africa (Collinson et al., 2015b), and yet these data are vital in order to implement effective mitigation strategies (Gunson & Teixeira, 2015). This is unfortunate because while Africa is incredibly rich in biodiversity (Mittermeier et al., 2011), it also has the fastest growing human population (and associated infrastructure) in the world (United Nations, 2015), which could have serious environmental impacts (Calvin et al., 2016).

One of the ways in which costly sampling strategies can be overcome is to adopt a citizen science approach, whereby scientific data are collected by members of the public (Conrad & Hilchey, 2011). For example, as a consequence of citizen science surveys used to monitor the status of birds in the United Kingdom, the UK government introduced targets to reverse population declines identified by the surveys (Gregory & van Strien, 2010; Greenwood, 2012). While citizen science can be a powerful tool to collect scientific data, biases in survey effort in such studies can hinder studies of variables such as roadkill rates. An alternative but underutilised source of data on roadkill rates, that has the potential to offer more consistent and measurable survey effort, is road patrols. Many highway agencies conduct regular patrols in order to resolve any issues that could affect road users, so partnerships between researchers and road patrol agencies offer significant potential for more effective data collection (Périquet et al., 2018).

In this study, we used data collected by road patrol staff of the N3 Toll Concession (N3TC) to explore the potential for partnering with road agencies to conduct roadkill studies. In 2011, a partnership was established between the Endangered Wildlife Trust (EWT) and the N3 Toll Concession (N3TC), an organisation that operates a 415 km of the N3 highway in South Africa, with the aim of managing the impact of roads on wildlife. N3TC patrol staff began collecting data on roadkill incidents, following training from the EWT. Exploratory analyses of the data collected suggested that serval (*Leptailurus serval*) appear to be particularly susceptible to roadkill on the N3 (Fig. 1).

DATE	23-04-2017
TIME	17:29
ROUTE MARKER	N3 24,6 S
PATROLLER	Williams
REMARK	wild Animal
TYPE	SERVAL

Figure 1. Photograph of serval carcass taken by N3TC road patrol staff. Image credit: N3TC.

The serval is a medium-sized carnivore weighing 8-12 kg (Skinner & Chimimba, 2005). It displays a preference for wetland habitats (Ramesh & Downs, 2015/2), the degradation and loss of which constitute the principal threat to serval populations (Thiel, 2011). Rodents make up a large proportion of serval diets, but they are also known to feed on other small prey such as birds, reptiles, and insects (Ramesh & Downs, 2015). The species is listed as Least Concern on the IUCN Red List of threatened species (Thiel, 2015), and Near Threatened on the South African Red List (Ramesh et al., 2016), although serval numbers have declined throughout their range (Ramesh & Downs, 2013). Home ranges can be between 8 and 38 km^2 (Geertsema, 1985; Ramesh, Kalle & Downs, 2015), and population densities can vary from approximately 6-100 individuals per 100 km^2 (Ramesh & Downs, 2013; Loock et al., 2018). Servals display largely crepuscular and nocturnal activity patterns (Thiel, 2011; Ramesh & Downs, 2013), but they can also be active during the day (Geertsema, 1985). Although roadkill is thought to present a serious threat to servals (Ramesh et al., 2016), there have been few attempts to quantify these threats or identify associated risk factors.

We set out to use data collected by N3TC road patrol staff as part of routine road patrols to identify which factors were related to serval roadkill counts on the N3. We modelled the relationship between a set of environmental and anthropogenic variables in order to determine which, if any, were related to serval roadkill counts, in order to inform the development of potential strategies to mitigate serval roadkill.

2. Materials & Methods.

2.1. Study site

The study focussed on a 410 km stretch of the N3 Toll Route (hereafter referred to as the N3), a major road linking Johannesburg and Durban in South Africa (Fig. 2). It is of strategic importance as it links the largest and third largest cities in the country, and it is a major route for transporting goods from South Africa's largest port. The N3 is classified as a national route, the highest category in the South African road network. Most segments of the national route network are maintained by the South African National Roads Agency (SANRAL), but some are maintained by provincial, local, or private road authorities. The N3 has been operated by N3TC since 1999 (N3 Toll Concession, 2018). Annual traffic volume for the section of the road studied was approximately 340,000 vehicles per km between 2014 and 2017, and the road is generally two lanes wide in each direction, with a speed limits of either 100 or 120 km/h. Passing through three of the eleven South African biomes (Savanna, Grassland and Indian Ocean Coastal Belt (Mucina & Rutherford, 2006)), the N3's diverse range of habitats also includes urban landscapes, communal land, and agricultural areas.

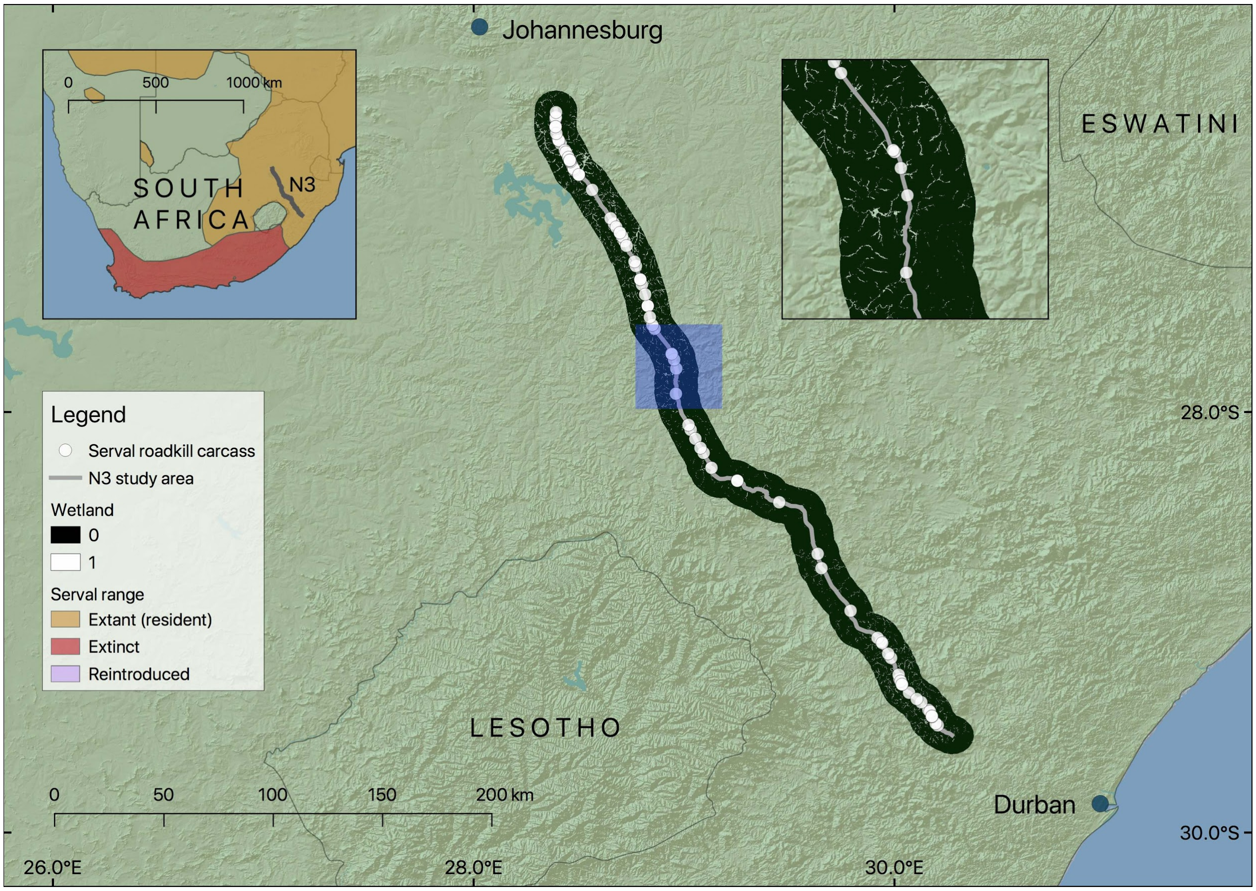

Figure 2. Map showing the location of the section of the N3 studied, serval roadkill carcass locations recorded from 2014 to 2018, wetland within 10 km of the road, and serval range in South Africa (adapted from Thiel (2015)). Inset map (location shown in blue) shows a closer view of serval roadkill carcass locations in relation to wetlands.

2.2. Data collection

N3TC road patrol staff collected field data as part of their routine patrols of a 410 km stretch of the N3 between Johannesburg and Durban (Fig. 2) every day between 01/01/2014 and 31/12/2017. The road patrol staff involved in the study undertook annual training with the Endangered Wildlife Trust (EWT) in wildlife identification and the collection of roadkill data. Patrols were driven four times a day (twice in each direction), with teams of two patrollers allocated to six shorter sections to ensure the entire road was covered effectively. Patrols were conducted at a speed of approximately 100 km/h.

Observers recorded the species of roadkill carcasses encountered, the date and time of the observation, and the carcass location using the nearest route marker, which were located at 200 m intervals along the road. Carcasses were removed from the road to avoid recounts (Collinson et al., 2014; Guinard, Prodon & Barbraud, 2015). For the current study we focussed on records of serval, owls (order Strigiformes), and guineafowl (family Numididae) roadkill, as these were among the most numerous. We classified roadkill observations collected between the 1st of October to the 31st of March as occurring during the wet season, and roadkill collected from the 1st of April to the 31st of September as occurring during the dry season (Cook, Reason & Hewitson, 2004).

In addition to roadkill data collected by the patrol teams, we also used existing data on habitat type (Geoterraimage, 2015). We also obtained data from N3TC on traffic volumes and speed limits, and the locations of infrastructure such as bridges and underpasses. We measured road width at 410 randomly-generated locations using Copernicus Sentinel satellite imagery (European Space Agency, 2017), measured in QGIS v3.0 (QGIS Development Team, 2018). Road shapefiles were obtained from OpenStreetMap (OpenStreetMap contributors, 2017).

2.3. Data analysis

We conducted all analyses in R v3.5.0 (R Development Core Team, 2018), and all code and data are publically available (Williams et al., 2018). We divided the N3 into 41 sampling units, each with a length of 10 km, corresponding to the home range size of serval (Geertsema, 1985; Bowland, 1990; Ramesh, Kalle & Downs, 2016). Within each sampling unit we summed the total number of serval carcasses, which we used as the response variable in our models. All other environmental and anthropogenic variables included in the models were used as potential predictors (Table 1).

We developed several hypotheses that could explain the number of serval roadkills (Table 1). First, we hypothesised that rodent abundance near the edges of roads could affect serval roadkill (Boyle, Litzgus & Lesbarrères, 2017). We used the number of owl roadkill as a proxy for rodent abundance since there is a well-established relationship between the abundance of owls and rodents (Ansara, 2008; Bullock, Malan & Pretorius, 2011). Secondly, we hypothesised guineafowl might be a food source for serval around road edges. We calculated the total number of owl and guineafowl roadkill carcasses per sampling unit from the roadkill survey data. Since serval prefer certain habitats, we also hypothesized that habitat type, in particular the amount of available wetland (Ramesh & Downs, 2015/2), would affect serval roadkill. We estimated habitat variables by first creating a buffer with a radius of 10 km around each sampling unit, and used land cover data (Geoterraimage, 2015) to calculate the most common habitat type, and the proportion of wetland within the buffer for each sampling unit. As carnivore home ranges are typically larger in seasons with lower rainfall (Macdonald & Loveridge, 2010), we hypothesised that serval roadkill counts would be higher during the dry season, as larger home ranges would be associated with increased contact with roads.

There is evidence that anthropogenic variables such as traffic volume and speed can also influence roadkill rates (Jaarsma, van Langevelde & Botma, 2006; Garriga et al., 2012). We thus also included several anthropogenic predictor variables (Table 1). To generate anthropogenic predictors we calculated the average speed limit, traffic volume, road width, and the total number of road infrastructure points for each sampling unit. We used the variance inflation factor (VIF) in package car (Fox & Weisberg, 2011) to check for colinearity among predictor variables, and excluded variables with a VIF > 3 (Zuur et al., 2009).

Table 1. Hypotheses about the relationships between serval roadkill counts and predictor variables included in the models.

Type	Variable name	Variable description	Direction of association	Rationale
Environmental	Owls	Count of owl carcasses	+	Areas with a greater abundance of serval prey will support greater densities of serval and owls
	Guineafowl	Count of guineafowl carcasses	+	Guineafowl may be preyed upon by serval, increasing serval density
	Wetland	Proportion of 10 km buffer composed of wetland	+	Serval would be more abundant in areas rich in their preferred habitat
	Season	Wet or dry season	More in dry	Serval may range over larger distances when water is scarce, making them more vulnerable to WVCs
Anthropogenic	Traffic	Average number of vehicles per km	-	More vehicles present more opportunities WVCs
	Speed	Average speed limit (km/h)	-	Faster cars will be more difficult to avoid
	Road width	Average width of road (m)	-	Wider roads take longer to cross
	Infrastructure	Total number of infrastructure points such as bridges and underpasses	-	Bridges and underpasses may provide more opportunities for serval to cross roads safely

We modelled the relationship between serval roadkill counts and predictor variables by fitting a generalised linear mixed-effect model using the lme4 package (Bates et al., 2015). Exploratory analyses showed that negative binomial or Poisson distributions were the most plausible for our dataset. The negative binomial distribution with log link outperformed other model structures based on the Akaike Information Criterion (AIC) and visual inspection of a serval roadkill count histogram comparing distributions (Figure S1), which was expected as the data were over-dispersed with an excess of zeros. This model structure was therefore used for the remaining analyses, following Valdivia et al. (2014).

We included each of the predictor variables listed in Table 1 as fixed terms in the model. To account for spatial autocorrelation we included sampling unit, nested within the most common habitat type, as random terms in the model, including an offset to account for the length of the sampling unit. We checked that there were no patterns in plots of fitted values against residuals to validate the model (Figure S2), and confirmed that there were no patterns evident in plots of predictor variables against residuals. We confirmed that spatial autocorrelation was not a problem in our models by performing Mantel tests (Mantel, 1967) (Figure S3) and by inspecting the sample variogoram for residuals (Figure S4). Overdispersion did not appear to be a problem for the final model ($\theta = 1.10$).

3. Results.

A total of 86 serval roadkill events were recorded at the study site between 01/01/2014 to 31/12/2017 (Fig. 3), which is equivalent to 5.24 carcasses/100 km/year. Our model showed support for effects of season, wetland, and owls on serval roadkill counts (Fig. 4, Output S5). The number of serval roadkill was greater in the dry season than the wet season, and in areas with more wetland, and with higher owl roadkill counts (Fig. 5). There was no support for effects of the number of guineafowl roadkill, vehicle speed limit, traffic volume, road width, or the amount of road infrastructure on serval roadkill (Fig. 4, Output S5).

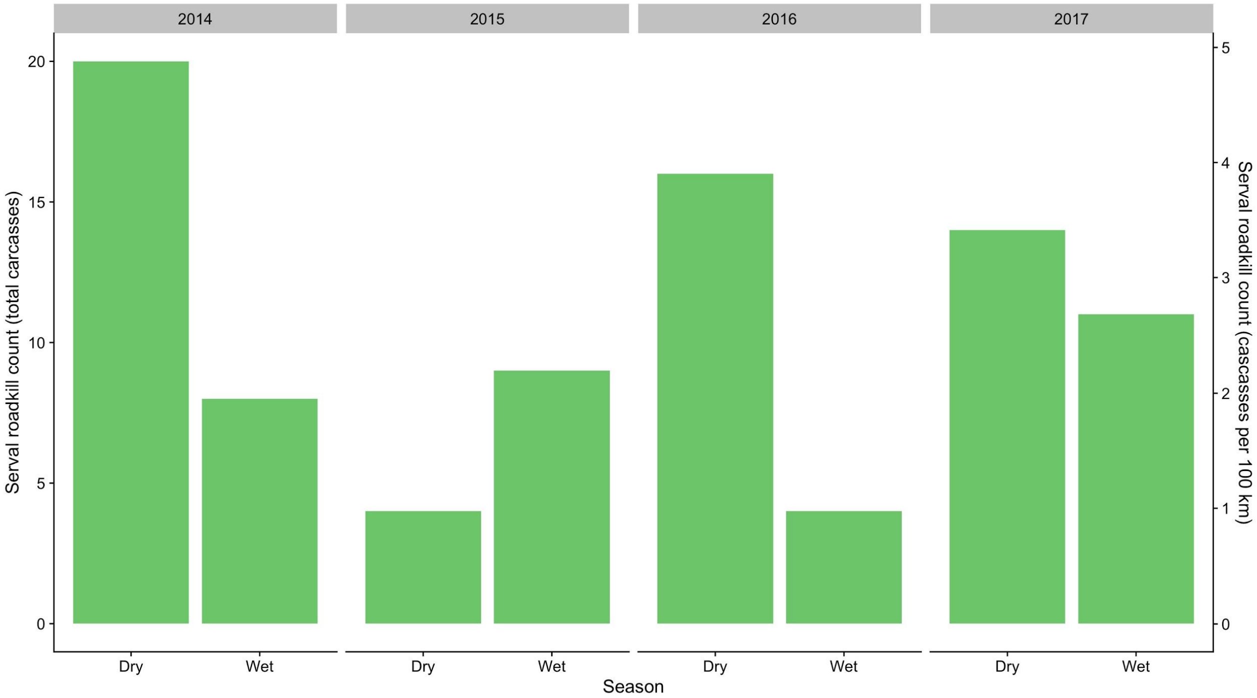

Figure 3. Total seasonal serval roadkill counts collected along a 410 km section of the N3 in South Africa between 2014 and 2017.

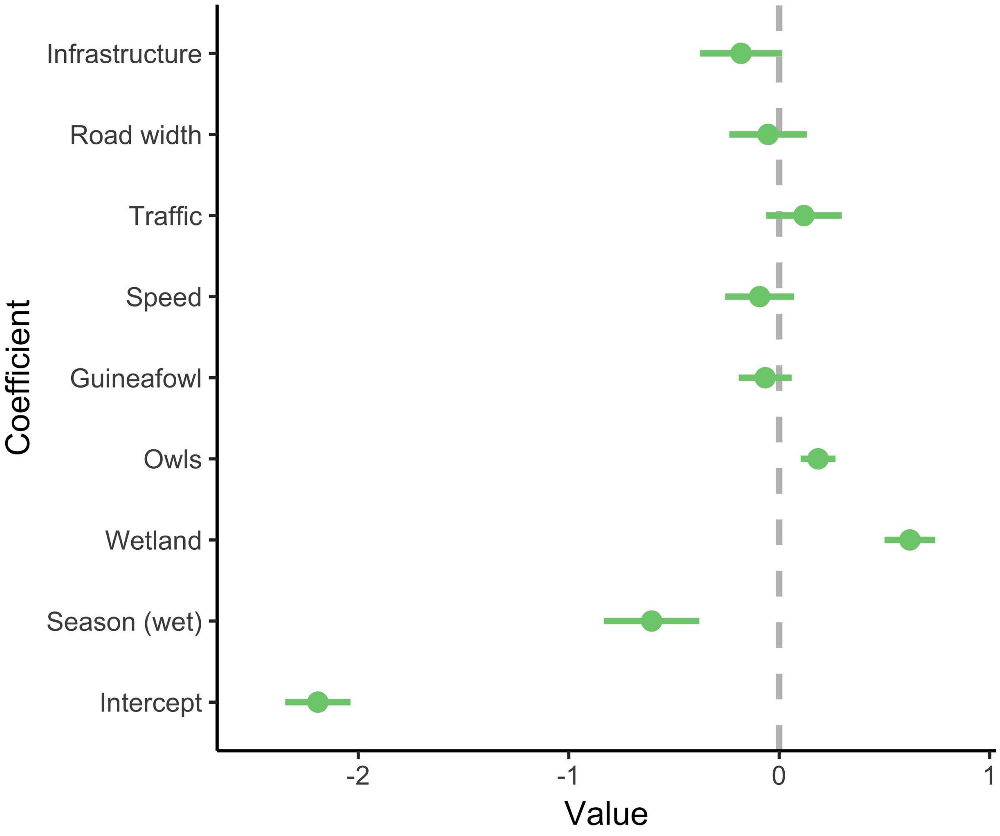

Figure 4. Coefficient estimates showing the effect of predictor variables on serval roadkill counts. Error bars represent 95% confidence intervals. We modelled roadkill counts using a generalized linear mixed effect model with a negative binomial distribution and log link. The full model summary is provided in Output S5.

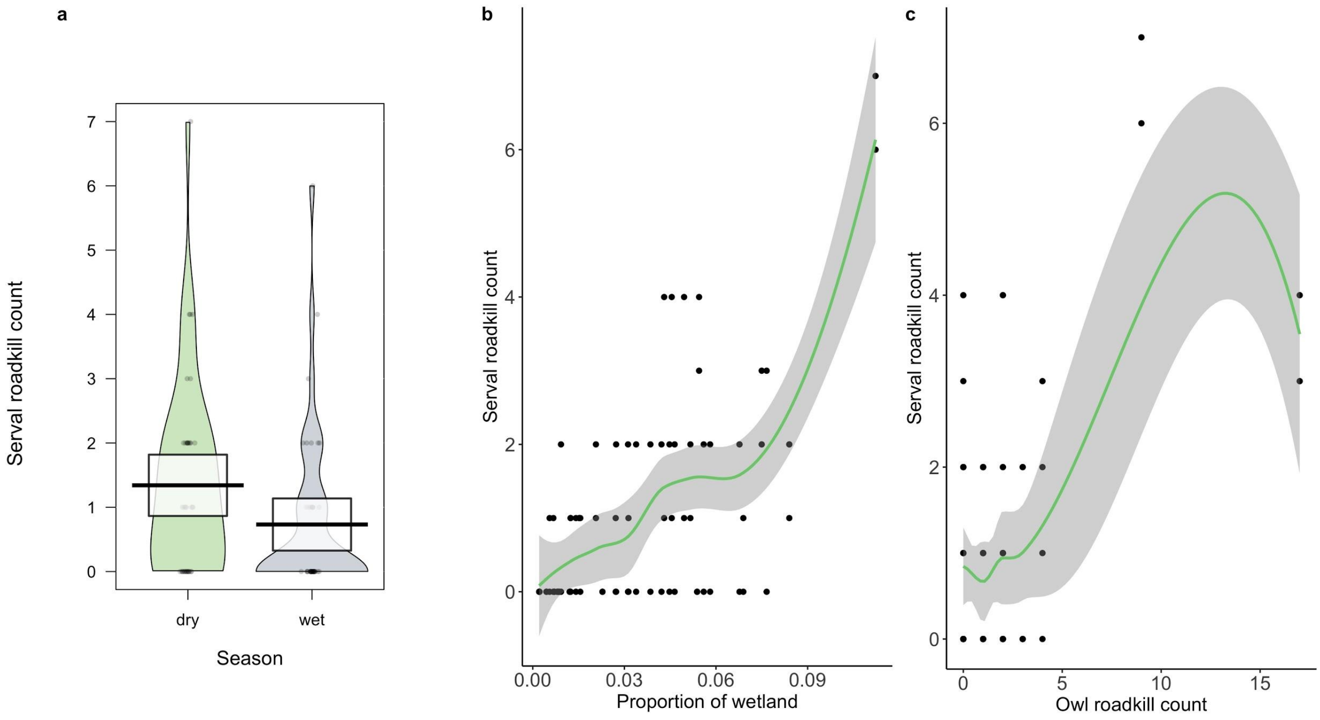

Figure 5. The relationship between serval roadkill counts in each 10km sampling unit and a) season, b) proportion of wetland; and c) owl roadkill counts on the N3 between 2014 and 2017. Boxes (Fig. 5a) and shaded areas (Fig. 5b and c) show 95% confidence intervals.

4. Discussion.

Our findings demonstrate that partnering with road patrol agencies can be a powerful strategy for collecting the necessary data to assess factors associated with roadkill rates, enabling targeting of mitigation strategies. Conducting twice-daily transects along both lanes of a 410 km stretch of a major highway solely to collect roadkill count data for research purposes would have been prohibitively costly, but by partnering with a road patrol agency we were able to gather the necessary data much more efficiently, and in a standardised manner (Collinson et al., 2014). We suggest that the development of partnerships between other road agencies and conservation or wildlife management organisations could also help to efficiently reduce roadkill rates, benefitting both drivers and biodiversity conservation and guide future mitigation measures (Abra et al., 2018).

We found support for the hypothesis that serval roadkill counts would be positively related to the amount of wetland, which suggests that servals are being killed on roads located in their preferred habitat (Ramesh & Downs, 2015/2), probably because they are more abundant in these areas (D'Amico et al., 2015). Similar findings were found with the raccoon dog (*Nyctereutes procyonoides viverrinus*) in Japan (Saeki & Macdonald, 2004), spotted turtles (*Clemmys guttata*) and Blanding's turtles (*Emydoidea blandingii*) turtle in North America (Beaudry, deMaynadier & Hunter, 2008), and owls in Portugal (Gomes et al., 2009). Our findings also support the hypothesis that there would be a positive association between roadkill counts of serval and owls. Areas with more owl roadkill may have a greater abundance of species that both owls and servals prey upon (Vernon, 1972; Ramesh & Downs, 2015), which supports a greater abundance of both owls and serval. Finally, we found support for the hypothesis that serval roadkill counts would be higher in the dry season than the wet season, as carnivores tend to have larger home ranges when water is scarce (Macdonald & Loveridge, 2010), which could put them at greater risk of WVCs.

We found no support for any of our other hypotheses, including that serval roadkill counts would be associated with guineafowl roadkill counts, or with anthropogenic variables such as traffic volume, speed limit, road width, or the amount of road infrastructure. This suggests that serval roadkill counts are influenced primarily by ecological drivers, and that this will vary between species with different ecological requirements. As a result roadkill mitigation strategies may need to be tailored to target species rather than relying on a more generalised approach.

We calculated an average of 5.24 serval carcasses/100 km/year (85 carcasses in total) on the N3, but there are few studies with which this can be compared. Serval were among the most common species recorded in a previous study on wildlife roadkill on the N3 (14.8% of 183 citizen scientist records, and 1.5% of 209 road patrol records between 2011 and 2014) (Périquet et al., 2018). Five of 17 collared serval were killed by snaring, hunting dogs, and WVCs in the Drakensberg Midlands, South Africa (Ramesh, Kalle & Downs, 2016), but the breakdown of these mortality sources is unclear. Serval roadkill has also been occasionally recorded elsewhere

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in Africa, with two serval carcasses recorded in a study on roadkill in Uganda (Cibot et al., 2015), but without data on survey effort this cannot be converted into a rate for comparison.

The rate of serval roadkill on the N3 is roughly in line with roadkill rates of other carnivores such as spotted hyaena (*Crocuta crocuta*), common genet (*Genetta genetta*), and black-backed jackal (*Canis mesomelas*) in the Tarangire–Manyara ecosystem, Tanzania (each at approximately 5 individuals/100km/year) (Kioko et al., 2015). Carnivore roadkill rates in Portugal were also similar (5-6 individuals/100 km/year) for species including Egyptian mongoose (*Herpestes ichneumon*), Eurasian badger (*Meles meles*), and common genet (Grilo, Bissonette & Santos-Reis, 2009). Carnivore roadkill rates can, however, vary greatly, for example from 1 to 20 individuals/100 km/year for Western polecats (*Mustela putorius*) and red fox (*Vulpes vulpes*) respectively (Grilo, Bissonette & Santos-Reis, 2009).

Without data on serval population sizes in the study area, or on other sources of mortality, it is difficult to determine the impacts that WVCs may have on the population dynamics of the serval population. Our findings nevertheless appear to support the suggestion by Ramesh et al. (2016) that WVCs could be a major source of mortality for the species, which is also true for other carnivores. Over 40% of Eurasian badgers in southwest England, for example, were thought to be killed each year in WVCs (Clarke, White & Harris, 1998). WVCs accounted for 35% of annual mortality of Florida panthers (*Puma concolor coryi*) in the USA (Taylor et al., 2002), 4-33% of annual mortality of jaguars (*Panthera onca*) in the Atlantic Forest, Brazil (Cullen et al., 2016), and 17% of annual mortality of Iberian lynx (*Felis pardina*) in southern Spain (Ferreras et al., 1992). Roadkill mitigation strategies could therefore contribute significantly conservation efforts for some species, so identifying factors that are associated with high roadkill rates is a useful first step. In this case study, one of the implications of our findings is that in order to reduce serval roadkill, mitigation efforts should be focussed in areas rich in wetland.

One measure that could help to reduce serval roadkill near wetlands is installing a combination of fencing and wildlife crossing structures (Clevenger, Chruszcz & Gunson, 2001). Wildlife under- and overpasses are used extensively in Europe and America (Danielson & Hubbard, 1998; Goosem et al., 2008; Bissonette & Rosa, 2012), and numerous studies have reported on the value of fencing in reducing wildlife road mortalities (Clevenger, Chruszcz & Gunson, 2001; Jaeger & Fahrig, 2004). This can be an effective solution (Seiler, 2005), but the tendency of serval to use wildlife crossing structures has not yet been assessed. These structures are widely used by many species (Clevenger, Chruszcz & Gunson, 2001), including carnivores (Grilo, Bissonette & Santos-Reis, 2008; Andis, Huijser & Broberg, 2017), so it is likely that they would be used by serval also, although we recommend testing this. We note, however, that care must be taken with this approach, as fencing can also reduce gene flow and fragment habitats (Flesch et al., 2010).

Another important factor to consider when planning the location of mitigation measures such as wildlife crossing structures and fencing is wildlife movement patterns. Movement patterns of many species are often associated with drainage lines, topography, and habitat, and through understanding the characteristics of target species, measures can be implemented at optimal sites (Clevenger, Chruszcz & Gunson, 2001; Rytwinski et al., 2016). Correct tunnel design and installation, as well as the presence of guiding fences are all factors to be considered when designing wildlife passages (Danielson & Hubbard, 1998).

In addition to the above, research suggests that using these measures alongside other methods such as implementing low speed zones, installing traffic-calming devices such as speed bumps (Glista, DeVault & DeWoody, 2009), or using species-specific warning-signage placed in strategic spots to alert road users to serval presence (Hardy, Lee & Al-Kaisy, 2006), may increase the effectiveness of the mitigation measures. Our data, however, suggests that anthropogenic variables such as traffic speed limits may not be an important predictor of serval roadkill rates on the N3, so these measures may be less effective in this situation. Removing roadside vegetation may also reduce the rate of serval and owl roadkill, as this could reduce the abundance of rodent prey species (Ruiz-Capillas, Mata & Malo, 2015), although this could impact the conservation of other species such as plants and small mammals. Keeping grass verges trimmed, rather than removing vegetation entirely, may also be effective, by manipulating the landscape of fear (Jacob & Brown, 2000) and causing wildlife to spend less time in verge habitats without altering their abundance. A further potential issue that could impact roadkill rates on the N3 is grain spilled on the road from agricultural vehicles (Ansara, 2008; Gangadharan et al., 2017). If this is a common occurrence the increased food availability could boost rodent abundance, drawing predators into the road and leading to increased WVCs (Gangadharan et al., 2017). We suggest that this would be a worthwhile area of future study.

Although useful, there were some caveats to this approach. For example, road patrol teams did not collect data that would have allowed us to model the number of missed detections (Shilling, Perkins & Collinson, 2015). Furthermore, recording data on which patrol teams conducted which patrols would have enabled us to control for inter-observer bias (Shilling, Perkins & Collinson, 2015). We were unable to record the age-sex class of carcasses, which would have been interesting to include in the models (Pallares et al., 2015). Additional data such as the density of servals and prey species at different sampling points along the length of the road would have been incredibly useful in determining the impact on local populations. Finally, the speed at which patrols were driven could bias roadkill detection towards larger species (Collinson et al., 2014), so this method would not be suitable to collect roadkill counts for all species. Further studies incorporating missed carcass detections, inter-observer bias, and population density of target species would be worthwhile. Despite these limitations, this study demonstrated that even the collection of very limited data such as the location, date, and species (or taxon) of roadkill carcasses can help to inform wildlife management policy while minimising additional workload burden on road patrol staff.

5. Conclusions.

Integrating roadkill data collection into existing road patrols can provide an efficient means of collecting data to allow identification of factors associated with carnivore roadkill. Our findings support the hypotheses that serval roadkill counts were higher in the wet season than the dry season, and they were also higher in areas with more wetland and in areas with higher owl roadkill counts. Anthropogenic factors such as traffic volume, speed limit, and the amount of road infrastructure did not influence serval roadkill counts. We suggest that efforts to mitigate serval roadkill, such as installing wildlife crossing structures in combination with fencing, should be targeted at wetlands, but this must be tailored to the ecological requirements of target species.

6. Acknowledgements.

We are extremely grateful to N3TC staff for collecting the field data and providing additional data on traffic volumes and speed limits.

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8. Supplementary Information.

All data and code used to perform the analyses underpinning this paper are publically available in Williams S., Collinson W., Patterson-Abrolat C., Marneweck DG., H. Swanepoel L. 2018. Serval roadkill dataset. Figshare. DOI [will be activated after article acceptance]: 10.6084/m9.figshare.6833378. Available from https://figshare.com/s/b982eebca51c8edc91d3.

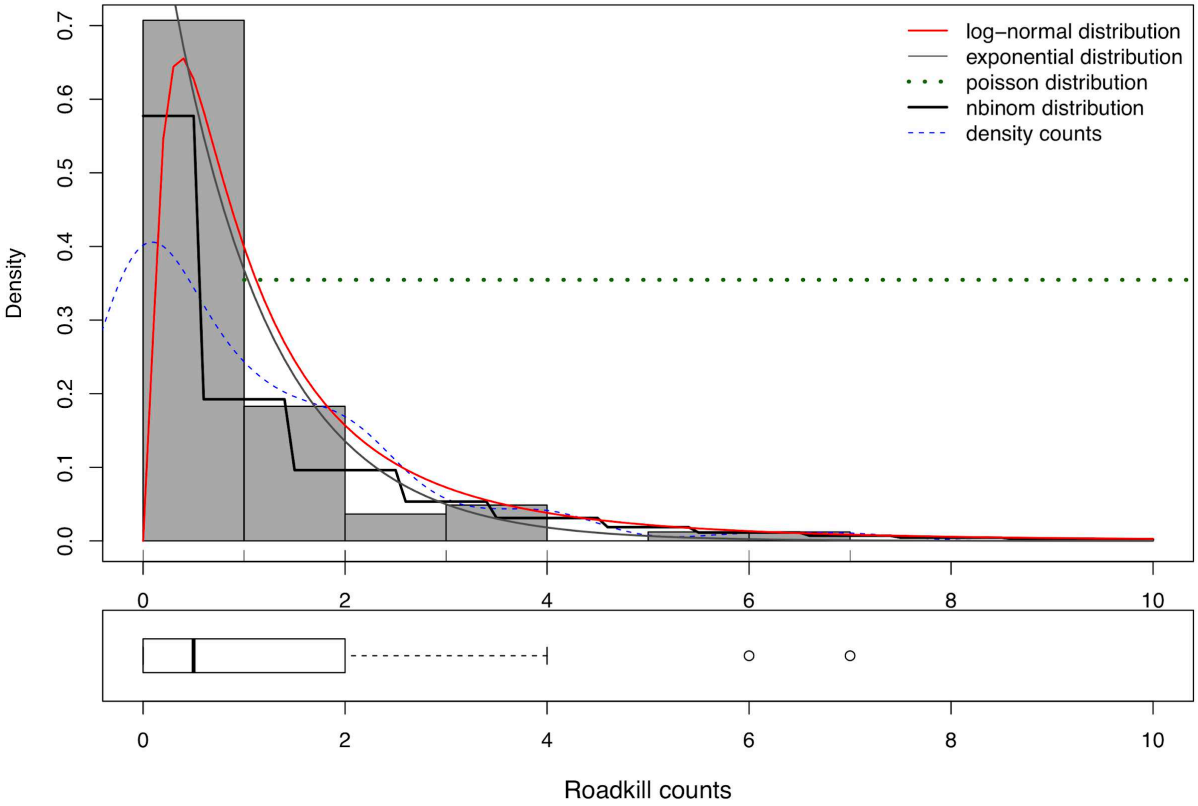

Figure S1. Histogram showing distribution of serval roadkill counts in relation to a range of distributions.

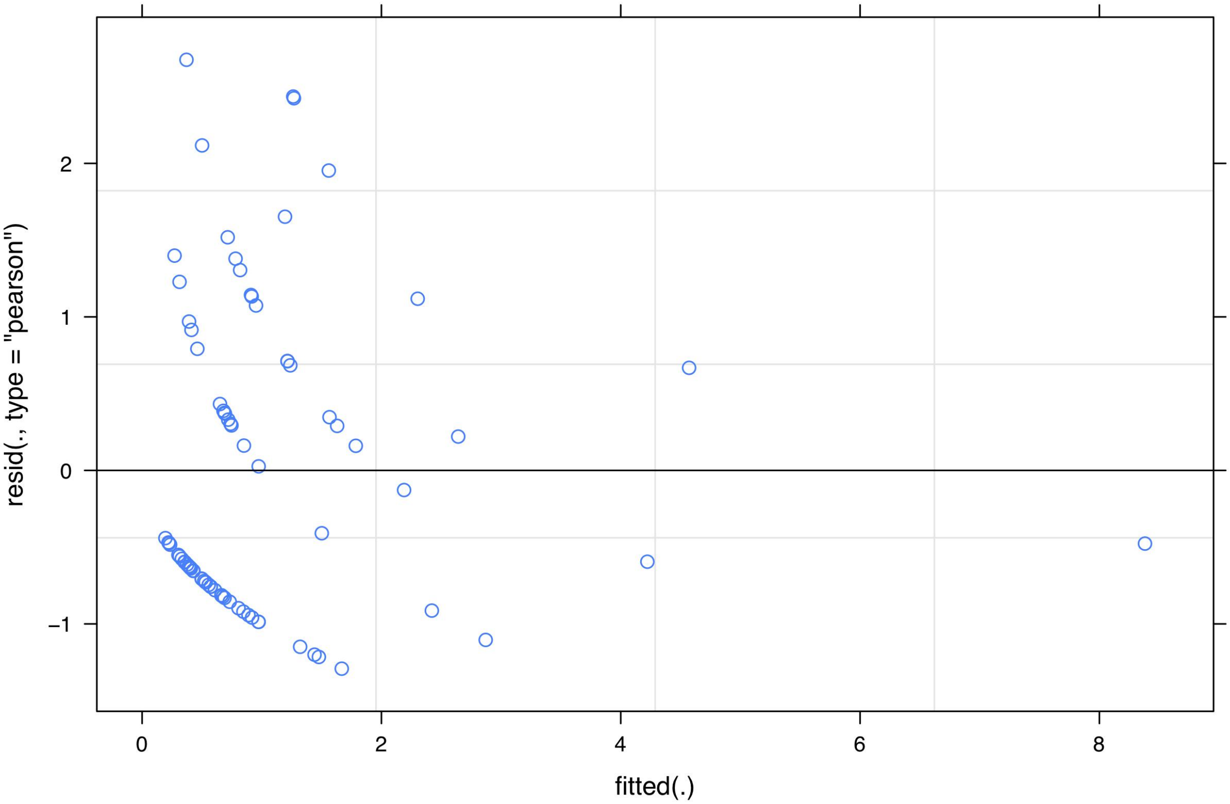

Figure S2. Scatter plot of fitted vs residual values for the full generalized linear mixed model with negative binomial distribution.

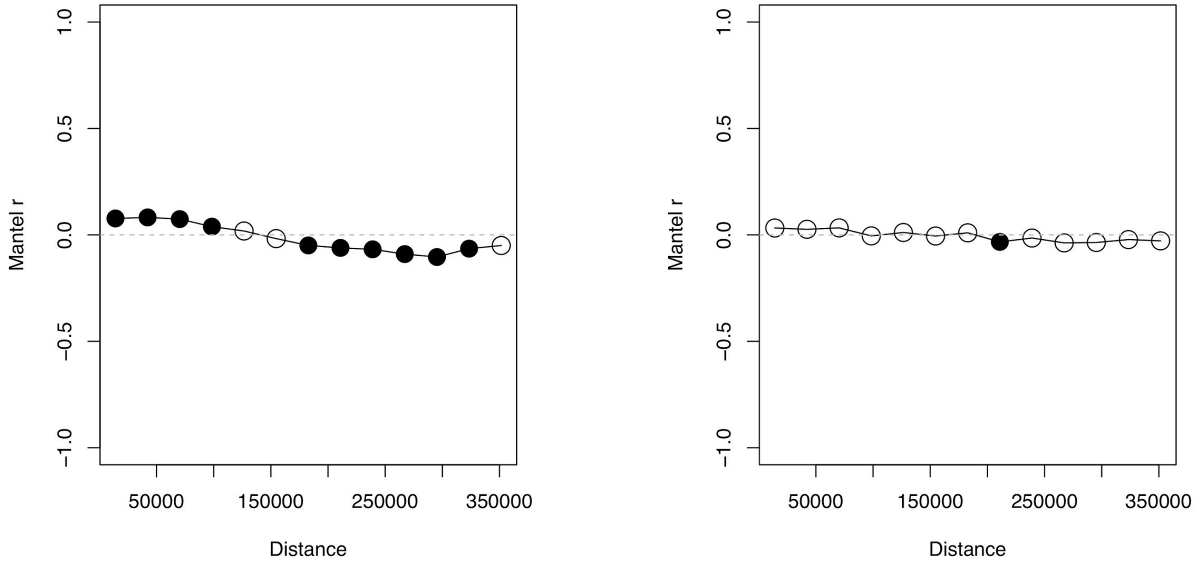

Figure S3. Mantel tests for the full generalized linear mixed model with negative binomial distribution.

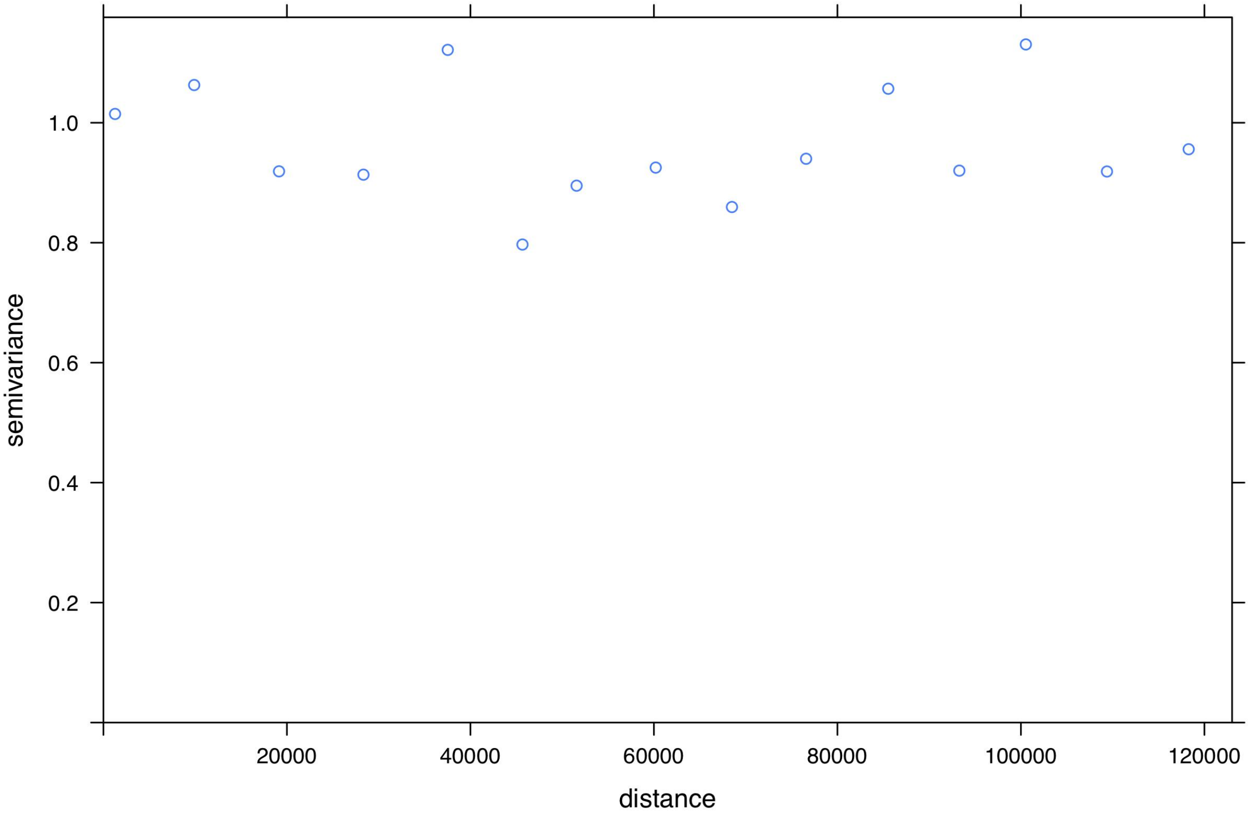

Figure S4. Variogram from for residuals for the full generalized linear mixed model with negative binomial distribution.

Output S5. Summary of full generalized linear mixed model with negative binomial distribution.

```
Generalized linear mixed model fit by maximum likelihood
(Laplace
  Approximation) [glmerMod]
 Family: Negative Binomial(25923.52)  ( log )
Formula:
roadkill ~ season + scale(wetland) + scale(owls) +
scale(guineafowl) +
    scale(speed) + scale(traffic) + scale(roadWidth) +
scale(infrastructure) +
    offset(log(LogArea)) + (1 | habitat/section)
   Data: RKdata2

     AIC      BIC   logLik deviance df.resid
   213.6    242.4    -94.8    189.6       70

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.2916 -0.7416 -0.4805  0.6802  2.6747

Random effects:
 Groups          Name        Variance  Std.Dev.
 section:habitat (Intercept) 2.435e-11 4.934e-06
 habitat         (Intercept) 4.208e-12 2.051e-06
Number of obs: 82, groups:  section:habitat, 41; habitat, 3

Fixed effects:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)           -2.19221    0.15516 -14.129  < 2e-16 ***
seasonwet             -0.60616    0.22678  -2.673  0.00752 **
scale(wetland)         0.62091    0.12052   5.152 2.58e-07 ***
```

```
scale(owls)              0.18479    0.08259   2.237  0.02527 *
scale(guineafowl)       -0.06648    0.12584  -0.528  0.59732
scale(speed)            -0.09286    0.16380  -0.567  0.57080
scale(traffic)           0.11736    0.17973   0.653  0.51378
scale(roadWidth)        -0.05302    0.18414  -0.288  0.77341
scale(infrastructure) -0.18124    0.19522  -0.928  0.35322
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) sesnwt scl(wt) scl(wl) scl(g) scl(s) scl(t)
scl(W)
seasonwet   -0.516
scal(wtlnd) -0.352  0.000
scale(owls) -0.120  0.000 -0.358
scal(gnfwl)  0.040  0.000 -0.162   0.146
scale(sped)  0.008 -0.001 -0.373  -0.073  -0.298
scal(trffc) -0.136  0.000  0.241   0.251   0.042 -0.079
scl(rdWdth)  0.110  0.001  0.011  -0.218   0.429 -0.306 -0.216
scl(nfrstr)  0.112  0.000 -0.384   0.060  -0.008  0.140 -0.645 -
0.202
```