

Assessing driver behaviour to reduce roadkill

Protecting the protected: reducing wildlife roadkill in protected areas

W.J. Collinson^{1*}, C. Marneweck², H.T. Davies-Mostert^{1,3}

¹ *Endangered Wildlife Trust, Private Bag X11, Modderfontein, 1609, Johannesburg, South Africa*

² *School of Biology and Environmental Sciences, University of Mpumalanga, Nelspruit, 1200, South Africa*

³ *Mammal Research Institute, University of Pretoria, Pretoria, 0028, South Africa*

* Corresponding author: Wendy Collinson, Endangered Wildlife Trust, Private Bag X11, Modderfontein, 1609 Johannesburg, South Africa, wendyc@ewt.org.za

Abstract

Social media discussions highlight public concern for wildlife-vehicle collisions (WVCs) inside protected areas. Using a quasi-experimental field trial, we investigated factors affecting the likelihood of WVCs within Pilanesberg National Park, South Africa, and assessed the comparative effectiveness of wildlife-warning signage (WWS) for altering driver behaviour. We laid a dummy snake crosswise on roads across four combinations of habitat and road shape and recorded 10 driver-related variables for 1454 vehicles that passed the dummy snake, including whether there was a collision. An interaction between speeding and driver occupation (staff/visitor) was the best indicator for WVC. When driving below the speed limit, visitors were almost three times more likely than staff to hit the dummy snake. Collision probabilities increased when speeding and became more similar between visitors and staff, although still significantly higher for visitors. We then investigated the effectiveness of roadside signage in modifying driver behaviour by erecting four variations of WWS, depicting a snake or a cheetah, and in photographic or silhouette form. We positioned the dummy snake 100 m or 1 km after the signage and recorded our 10 variables (n = 6400 vehicles). Sixty-one percent of drivers who passed a WWS changed their behaviour when they saw the dummy snake, compared to 37% with no sign present. Further, this behaviour change significantly reduced collisions, where 98% of drivers who changed their behaviour avoided a collision. Finally, an interaction between the animal depicted and distance before the dummy snake affected collisions. A WWS depicting a snake, and placed 100 m before the dummy snake, was most effective at reducing collisions. Our results suggest that drivers adapt their behaviour to signage that portrays smaller animals and awareness retention is low. Ultimately, to reduce WVCs within protected areas, we suggest steeper penalties for speeding and WWS placed in WVC hotpot areas.

Keywords

Mitigation, road, South Africa, visitors, wildlife-vehicle collision, wildlife-warning signage

Introduction

Roads, and their associated users, are the cause of many negative impacts on wildlife, such as landscape fragmentation (Trombulak & Frissell, 2000; D'Amico *et al.*, 2015), pollution (Rheindt, 2003; van der Ree *et al.*, 2011), and creating barriers for migration (Taylor & Goldingay, 2004; D'Amico *et al.*, 2015) and gene flow (Hels & Buchwald, 2001; Andrews & Gibbons., 2005; Anderson *et al.*, 2010). A further impact is wildlife-vehicle collisions (WVCs) (Forman, 2003; Coffin, 2007), resulting in an animal being injured or killed (roadkill).

Road networks are ever expanding and are an increasing threat within developing countries (Karani, 2008; Keshkamat *et al.*, 2009; Collinson *et al.*, 2015). However, much of the current literature is focussed on developed countries (Fahrig & Rytwinski, 2009; Caro *et al.*, 2014) and, even when focussed on developing countries, concentrated on roadkill occurring on national and regional roads (Coelho *et al.*, 2008; Garriga *et al.*, 2012). Although national parks and nature reserves are custodians of biodiversity, primarily intended to conserve animals, plants, and habitats, as well as biotic processes and functions, roadkill does occur and is of high concern. For example, in Spain, roadkill rates within protected areas are higher than outside due to the higher wildlife diversity and abundance in the former (Garriga *et al.*, 2012).

South Africa holds 23 national parks, protecting only 6.3% of the country's area but generating significant revenue through tourism (Statistics South Africa, 2015). However, with large numbers of visitors, WVCs commonly occur (Collinson *et al.*, 2017; unpublished data). Tourism is expected to grow significantly in South Africa by 2020 (Statistics South Africa, 2012), leading to more vehicles within protected areas and the potential for more WVCs. Further, recent social media reports have identified the overall public and ecological concern regarding WVCs within South Africa's protected areas (Supplementary material; Collinson *et al.*, unpublished data). It may be that as vehicle traffic increases, visitor speed may reduce due to congestion and ultimately reduce WVCs as observed on the Yellowhead Highway in Jasper National Park (Bertwistle, 1999). But we must first understand the drivers of WVCs within protected areas.

Common measures used to reduce the incidence of WVCs are static warning signs (Huijser *et al.*, 2009), traffic calming devices (e.g. speed bumps; Rytwinski *et al.*, 2016), wildlife fencing and eco-passages (e.g., overpasses, underpasses, and tunnels/culverts; Rytwinski *et al.*, 2016). Static warning signage has been found to be largely ineffective since drivers quickly habituate to it and fail to make adequate reductions in speed (Huisjer & McGowan, 2003; Huijser *et al.*, 2009; Huisjer *et al.*, 2015). Wildlife fencing and eco-passages are more successful (Jaeger & Fahrig, 2004), but they are costly and often impractical for implementation within protected areas where wildlife needs to roam naturally and not be impeded by a fence erected by the roadside (Smith, 2003). A public opinion survey to assess effectiveness of current warning signage in Australia showed modification in driving speed when signs were colourful and displayed images from different taxonomic groups (Bond & Jones, 2013). In Florida, USA, picture-based signs proved to be more effective than word-based signs in reducing speed and increasing vehicle braking (Grace *et al.*, 2015). Current South African road signage follows strict guidelines (Road Traffic Management Corporation, 1999) that limit images to a few domestic and wild mammalian species displayed in a mandatory red warning triangle. These signs are static and typically go unheeded (Huijser & McGowan, 2003).

In this study, we used a quasi-experimental field trial to investigate the factors affecting the likelihood of WVCs within a protected area, and to compare the potential effectiveness of photographic and silhouette images to alter driver behaviour and, ultimately, reduce WVCs.

Materials and Methods

We conducted this study in the 620 km² Pilanesberg National Park (PNP) between April and July 2017 on dry, sunny days (Fig. 1). PNP is the fourth largest state-run protected area park in South Africa, and the third most visited, receiving approximately 120,000 international and national visitors per year (Pilanesberg, 2018). The park is unique, as it exists within the transition zone between the dry Kalahari and wetter Lowveld vegetation, commonly referred to as "Bushveld" (Mucina & Rutherford, 2006). This transition zone has led to unique assemblages of mammals, birds, and vegetation. The large

Assessing driver behaviour to reduce roadkill

diversity of vertebrates includes 23 amphibian, 65 reptile, ~300 bird, and 61 mammal species (Pilanesberg, 2018). PNP's public road network is approximately 127 km long, of which 25.4% is paved. The speed limit for both paved and unpaved roads is 40 km/h. A 34-day pilot study revealed a roadkill rate of 0.11 animals/km/day and 0.001 animals/km/day on paved and unpaved roads, respectively (Collinson *et al.*, unpublished data). This was almost two times higher than roadkill rates on paved roads in the southern Kalahari (0.06 roadkill/km/day; Bullock *et al.*, 2011).

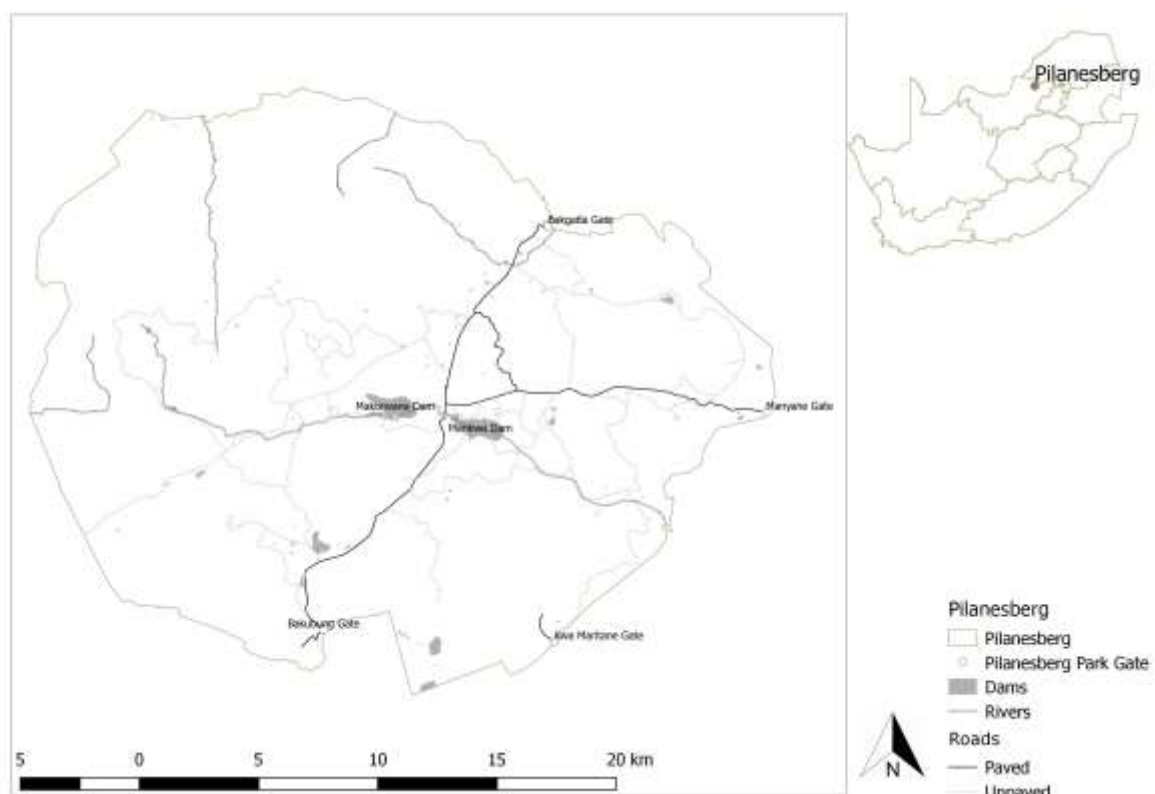


Figure 1. Pilanesberg National Park, showing the four sample locations on paved roads within the park.

To investigate the factors affecting WVCs, we laid a plastic, dummy snake in the approximate centre of a road 6 m wide (i.e. 3 m from the edge; Fig. 2) across four combinations of habitat (dense/open) and road shape (straight/curved). This placement allowed sufficient space for a vehicle coming from either direction to avoid the dummy snake but remain on the road. We chose a snake due to their natural basking behaviour, often on roads (Branch, 1998).



Figure 2. A photograph of the plastic, dummy snake approximately 3 m from the road's edge to assess driver behaviour in Pilanesberg National Park.

For all observations, an observer vehicle was positioned ~100 m from the dummy snake, on the side of the road always facing in the direction of the park gate. Due to this placement, vehicles entering the park would have the vehicle on their right, and vehicles exiting the park would have the vehicle on their left. The vehicle was visible to drivers but, as no one (staff or visitors) was aware of the study, and vehicles are frequently stationary in protected areas, we do not believe that this biased responses. For each vehicle passing the dummy snake ($n = 1454$), we recorded the following: (1) time period (am/pm) (2) driver head direction (forward/side facing), (3) driver gender (male/female), (4) number of people in the vehicle, (5) speed (speeding/not speeding), (6) direction of travel (entry/exit), (7) occupation (staff/visitor), (8) vehicle type (SUV/bakkie/truck/bus/game viewer), (9) change in behaviour in response to the dummy snake (slow down/stop/swerve/no response) and (10) whether the vehicle hit the snake. Prior to the trials, observer ability to determine whether a vehicle was speeding or not was tested against the actual speed of a control vehicle until 90% accuracy was achieved.

We then assessed the effectiveness of wildlife-warning signage of four variations depicting either a snake or a cheetah in either photograph or silhouette form (Fig. 3). We chose these animals based on a social media survey of members ($n = 235$) of the Endangered Wildlife Trust's Facebook page (EWT, 2018), who identified cheetahs as most likely to change driver behaviour and snakes as least likely (Supplementary Material), and as we were using a dummy snake in the experiment. We repeated the above collision experiment, using two wildlife-warning sides erected on both sides of the road (one facing in each direction), positioning the dummy snake either 100 m or 1 km after the warning sign and recording the same variables ($n = 10$) for a further 6400 vehicles.

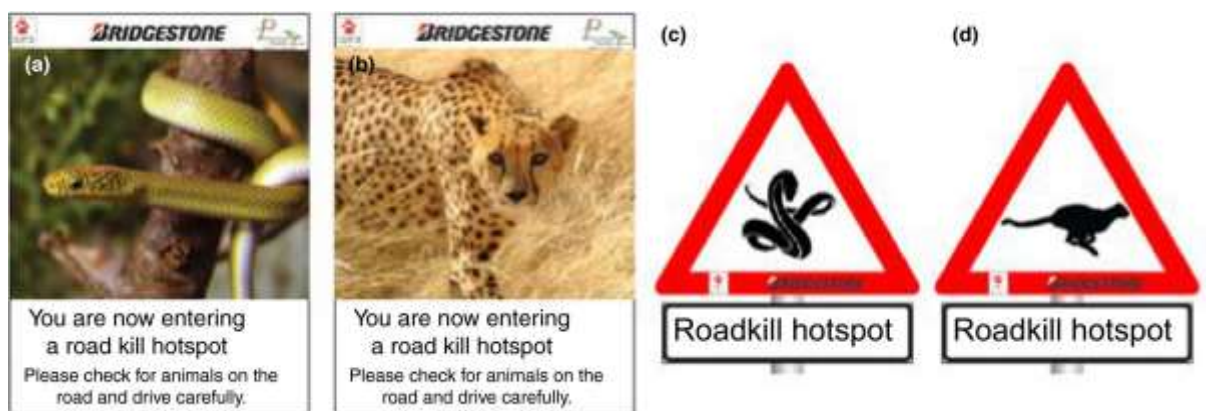


Figure 3. The four sign images used in the study, (a) snake photograph, (b), cheetah photograph, (c), snake silhouette and (d) cheetah silhouette.

Statistical analysis

To investigate factors affecting WVCs, we created 45 candidate generalised linear models with a binomial distribution. We set collision as the response ($\text{hit} = 1, \text{miss} = 0$), and the remaining variables, plus two-way interactions, as fixed effects predictors. We then used a two-proportions z-test to assess significance between proportions.

To explore the effect of wildlife-warning signage on driver behaviour, we ran a generalised linear model with a binomial distribution. We set change in behaviour in response to the dummy snake as the response (yes/no) and presence of a sign as a fixed effects predictor. We also set the direction of

travel (entry/exit), and its interaction with presence of a sign, to investigate if the sign location had an effect on the driver response. To explore the effect of changing driver behaviour on collisions, we ran another generalised linear model with a binomial distribution. We set collision (yes/no) as the response and change in behaviour as a fixed effects predictor.

To assess which behavioural response was most effective in reducing collisions when a driver changed their behaviour, we ran a generalised linear model with a binomial distribution. We set collision as the response variable (yes/no) and the behavioural response (slow/stop/swerve) as a fixed effects predictor. Finally, to investigate which sign reduced collisions most effectively, we created a further six candidate generalised linear models with a binomial distribution. We set collision as the response variable (yes/no), and animal depicted, distance, and image type, plus two-way interactions, as fixed effects predictors. We then used a two-proportions z-test to assess significance between proportions.

We assessed collinearity between independent explanatory variables prior to analysis using variance inflation factors (VIF) and Spearman rank correlation tests. Where high levels of correlation (Spearman's $\rho > 0.5$) were found between variables, one was discarded from analysis, ensuring that all variables had VIF values below 2 in the final statistical models. Vehicle type was correlated with occupation, thus we dropped vehicle type from all models. To identify the best model(s), we used model selection based on Akaike information criterion (AIC_c) and identified top models where $\Delta AIC_c \leq 2$, following Burnham and Anderson (2003). We performed all statistical analyses and created all figures in RStudio v 1.1.419 (Team, 2017) for Windows, using functions in the packages lme4 (Bates *et al.*, 2014) and MuMIn (Barton, 2017).

Results

An interaction between speeding and occupation was the best indicator of collision, explaining 98% of the variation (Table 1). When driving below the speed limit, visitors were three times more likely to hit the dummy snake than were staff, with a collision probability of 0.19 for visitors and 0.07 for staff ($\chi^2_{(1)} = 8.690$, $p = 0.003$; Fig. 4). When speeding, visitors and staff had similar collision probabilities (0.33

and 0.26, respectively; Fig. 4), but the probability of staff hitting the dummy snake was still significantly less ($\chi^2_{(1)} = 155.74$, $p < 0.001$; Fig. 4).

Table 1. The five top-ranking candidate models used to investigate factors affecting wildlife collisions. The top model is indicated in bold, where $\Delta AICc \leq 2$. For the full table showing all results of the 45 candidate models see supplementary material Table S1.

Rank	Model	df	LogLikelihood	AICc	delta AICc	weight
1	Occupation*Speed	4	-670.26	1348.54	0.00	0.98
2	Habitat*Occupation	6	-673.00	1358.05	9.52	0.01
3	Direction*Occupation	4	-675.20	1358.42	9.88	0.01
4	Occupation*Road	4	-676.20	1360.44	11.90	0.00
5	Head*Occupation	4	-676.99	1362.01	13.47	0.00

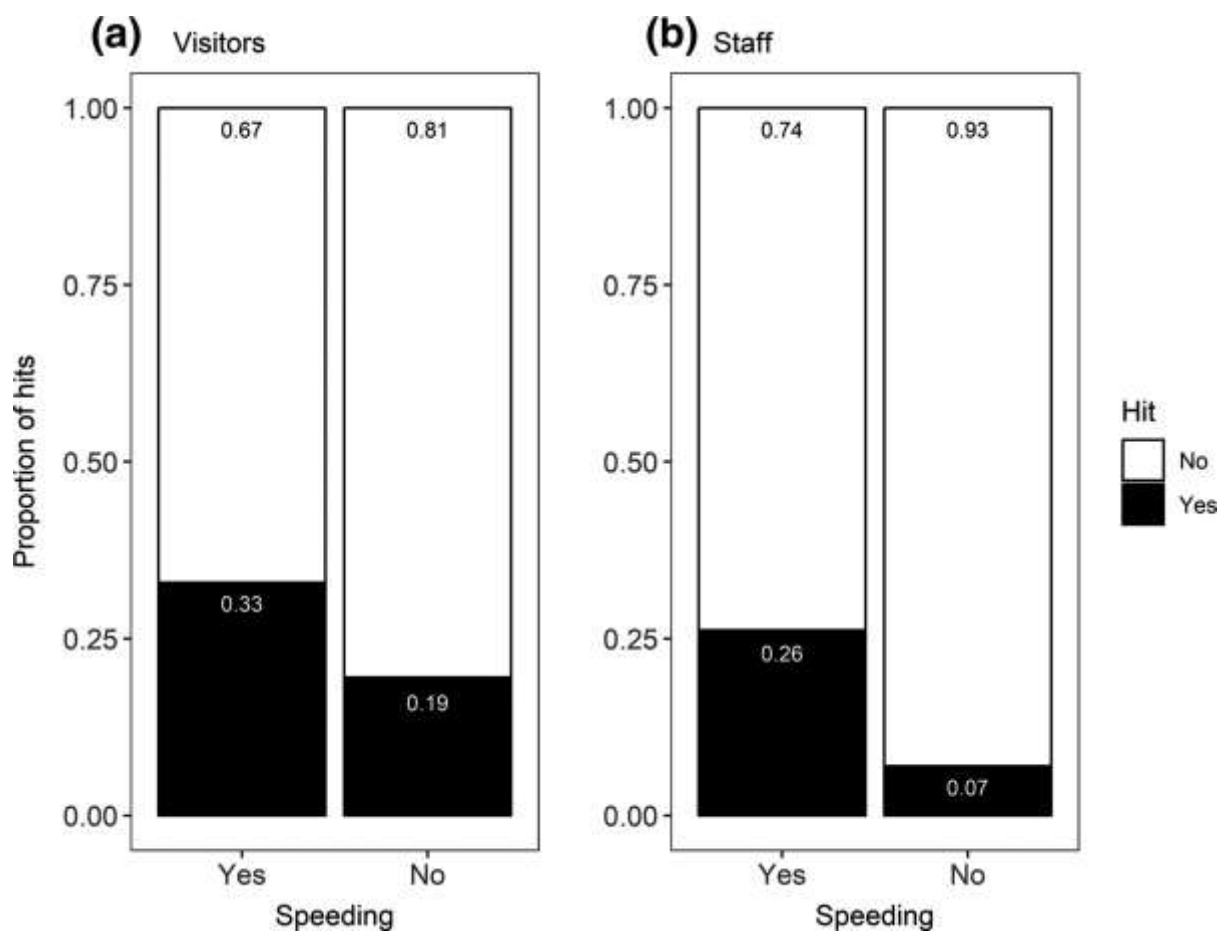


Figure 4. Proportion of wildlife collisions by (a) visitors, and (b) staff when speeding or not speeding.

The presence of a wildlife-warning sign ($Z = 16.153$, $p < 0.001$; Fig. 5a), plus the direction of travel ($Z = 9.237$, $p < 0.001$; Fig. 5b) affected driver behaviour in response to the dummy snake. There was no interaction between sign presence and direction of travel ($Z = -1.279$, $p = 0.201$). When no sign was present, 37% of drivers changed their behaviour in response to the dummy snake. Contrastingly, 61% of drivers who had passed a warning sign changed their behaviour when they saw the dummy snake. When exiting the park, 62% of drivers changed their behaviour in response to the dummy snake, compared to the 52% of drivers who changed their behaviour when entering the park. Further, changing behaviour in response to the dummy snake significantly reduced collisions ($Z = -29.190$, $p < 0.001$; Fig. 6a). Less than 2% of drivers who changed their behaviour hit the dummy snake, compared to the 36% of drivers who did not change their behaviour. When a driver responded by changing their behaviour, swerving was more effective in reducing hits than slowing down or stopping completely ($Z = 4.762$, $p < 0.001$; Fig. 6b).

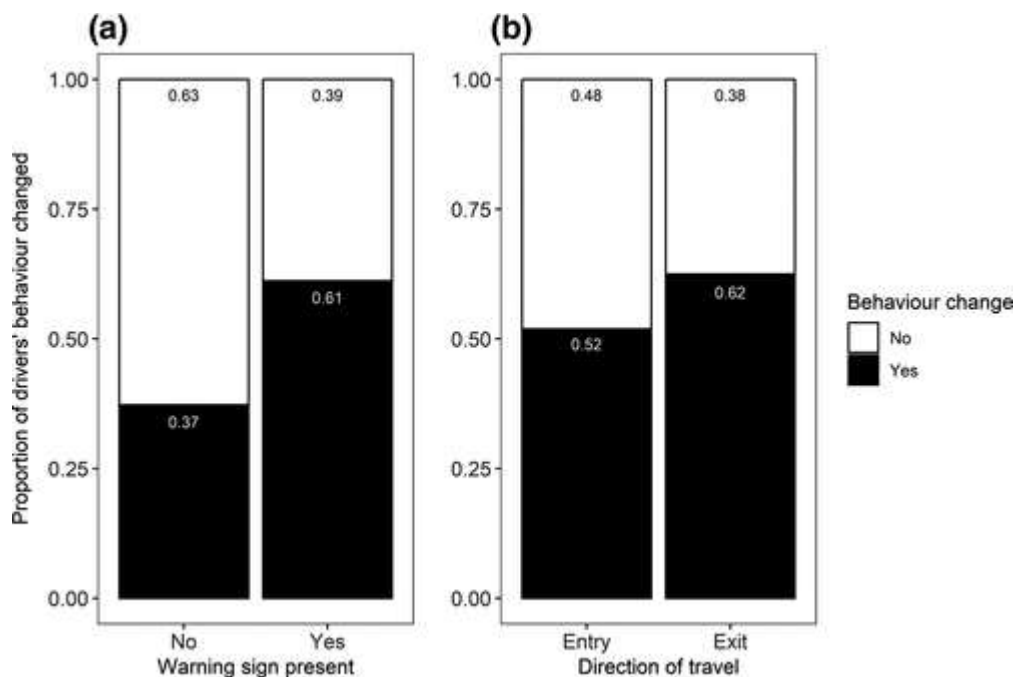


Figure 5. Proportion of drivers who change their behaviour in response to the dummy snake (a) after viewing warning sign, and (b) when entering or exiting the park.

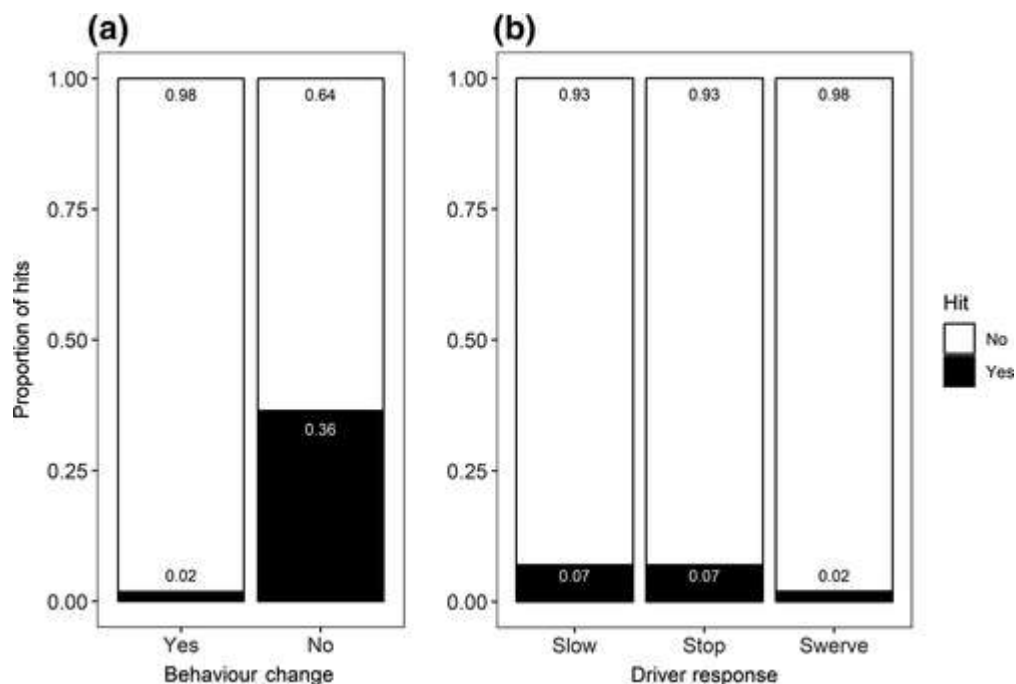


Figure 6. Proportion of wildlife collisions (a) when driver behaviour is changed upon sight of the dummy snake, and (b) following a change in behaviour.

An interaction between the animal depicted and distance before the dummy snake affected collisions, explaining 95% of the variation (Table 2). A wildlife-warning sign depicting a snake, and placed 100 m before the dummy snake, was most effective at reducing collisions (Fig. 7). When the sign was placed 100 m before the dummy snake, it was less likely to be hit if the sign depicted a snake ($\chi^2_{(1)} = 16.446$, $p < 0.001$; Fig. 7), but there was no difference in collision probability between images when the sign was placed 1 km before the dummy snake ($\chi^2_{(1)} = 0.061$, $p = 0.805$; Fig. 7).

Table 2. The six candidate models used to investigate which sign was most effect at reducing wildlife collisions. The top model is indicated in bold, where delta $AIC_c \leq 2$.

Rank	Model	df	LogLikelihood	AIC_c	Delta AIC_c	Weight
1	Animal*Distance	4	-2383.87	4775.74	0.00	0.95
2	Distance*Image	4	-2387.12	4782.26	6.52	0.04
3	Animal*Image	4	-2388.90	4785.80	10.06	0.01
4	Distance	2	-2390.95	4785.89	10.16	0.01
5	Animal	2	-2391.49	4786.98	11.24	0.00
6	Image	2	-2395.83	4795.67	19.93	0.00

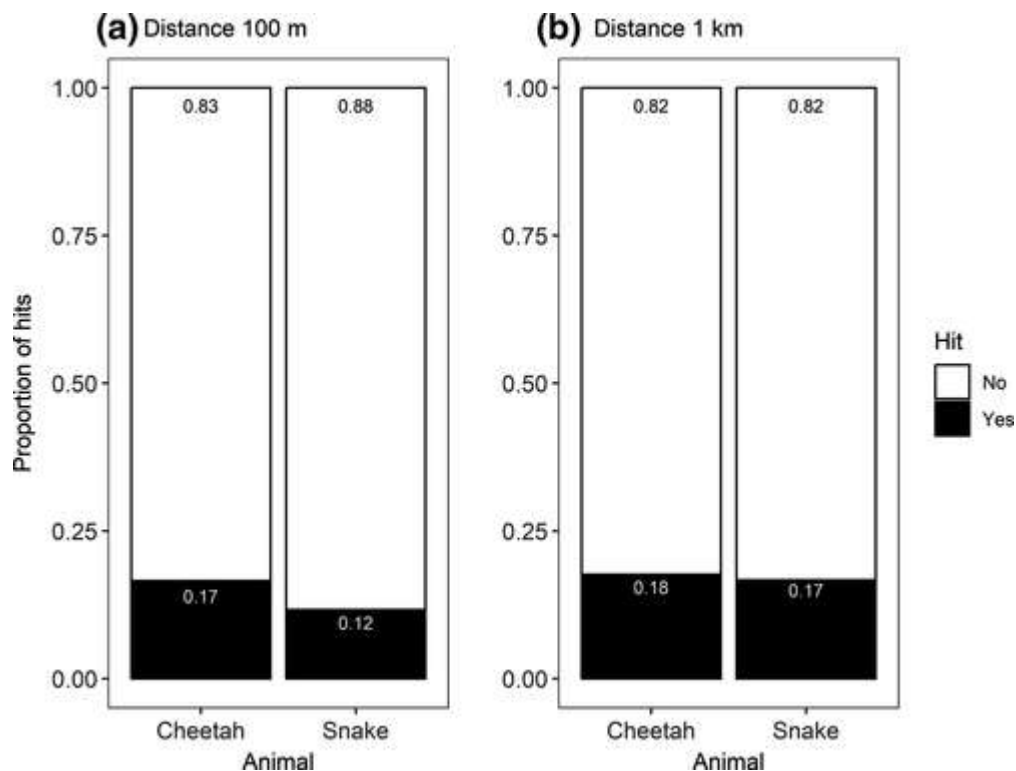


Figure 7. Proportion of wildlife collisions based on animal depicted in the sign at (a) 100 m, and (b) 1 km.

Discussion

Wildlife-vehicle collisions (WVCs) are of increasing concern within protected areas (Collinson pers. comm.). Our results show that visitors to national parks are more likely to cause WVCs than are staff, but this probability becomes similar – and higher overall – when the driver is speeding. We also show that changing behaviour in response to an animal in the road reduces WVCs, and appropriate warning signs can increase awareness of potential animals in the road over a short distance.

Staff are more familiar with driving within a protected area and are more likely to be looking at the road as opposed to game viewing (i.e. head side-facing). To our knowledge, no surveys have been undertaken that examine differences between staff and visitor driving behaviour within protected areas. Ad hoc reports via social media and personal communications (Collinson, 2017; unpublished data) have surmised that staff are most likely to cause WVCs, but our study is the first to investigate this specifically. However, our results show that, even when speeding, staff were less likely to cause WVCs than visitors. This is supported by many other studies showing that speeding contributes to WVCs (Gunther *et al.*, 1998; Bertwistle, 1999; Dique *et al.*, 2003; Hobday & Minstrell, 2008), most likely due

to a reduced ability to respond once the animal is seen. Our results also show that altering driver behaviour reduces WVCs, and so, mechanisms that increase awareness of small animals on the road are likely to result in fewer collisions (Huijser & McGowan, 2003; Seiler & Helldin, 2006; Grace *et al.*, 2015). Drivers exiting the park were more likely to change their behaviour in response to the dummy snake than those entering, but we found no interaction between direction of travel and the location of the sign depicted. The location of the sign did not affect driver's response to it, and drivers were more likely to change their behaviour when exiting the park. This is likely due to more focus on the road than on game viewing when exiting. In this study, we found that swerving was the most effective driver response in reducing WVCs. Although considered a dangerous response when driving on national roads with high speed limits and high traffic volumes, this response is more acceptable in a national park where speed limits and traffic volumes are low, and vehicles stopped in the road are common. As a result, we suggest that drivers in a protected area safely move around animals in the road to avoid WVCs.

Warning signs were more effective when placed 100 m before the dummy snake compared to 1 km. Driver memory and recall of wildlife-warning signage is poor (Fisher, 1992), and frequent signage leads to habituation, and therefore the placement of the signage can be critical for messages to be conveyed, understood, and retained by drivers (Gordon *et al.*, 2004). It is suggested that where drivers are novel to a region, signs maintain effectiveness over time (Hobday & Minstrell, 2008), which may be applicable for tourists visiting protected areas irregularly. Rather than frequent signage, we suggest the identification of WVC hotspots, and signs to be erected as drivers enter these hotspots (Bond & Jones, 2013).

Our social media survey (Supplementary Material) showed that the public felt they would more likely reduce WVCs if they saw a sign depicting a cheetah (a charismatic, large mammal), and reported that a snake (an often disliked and feared reptile) would be least likely to influence their behaviour. Secco *et al.* (2014) also demonstrated the dislike for snakes in a developing country (Brazil), where drivers deliberately hit a snake on the road. In contrast to the public opinion survey, we found that the sign depicting the snake was most effective at reducing WVCs, especially when placed closer to the

dummy snake. As snakes often utilise paved roads to bask (Branch, 1998), we postulate that a sign depicting a snake prompts drivers to be aware of snakes and other small animals on the road, compared to the cheetah which may divert attention to the search of large mammals (Gordon *et al.*, 2004; Rytwinski *et al.*, 2016; Grace *et al.*, 2017). It may also be that the drivers were less likely to hit a snake after passing a warning sign depicting a snake and, consequently, successful avoidance may be a result of image recognition. We suggest further investigation to fully understand this effect.

Throughout this study, the observer vehicle was visible to drivers, although we are confident that our results reflect natural behaviour as we were a distance away from the experiment (100 m) and vehicles are often stationary in protected areas. Furthermore, the vehicle was always parked on the same side of the road, facing the same direction. As direction of travel (entry/exit) was not significant in affecting WVC in this study, we do not believe that the location of the observer vehicle impacted WVC. We do acknowledge that the observer vehicle may be a potential limitation of the study, but unfortunately, it was not possible to hide the observer completely within a national park with off-road restrictions and wildlife that may be dangerous to observers on foot. High-tech solutions for remote data collection, for example real-time video surveillance, should be explored to better understand and control for this source of potential bias.

Despite the limited evidence of their effectiveness, wildlife-warning signs are the most commonly implemented mitigation measure of WVCs due to their low cost (Huijser *et al.*, 2009; Rytwinski *et al.*, 2016). Therefore, improving the potential effectiveness of this inexpensive option may aid in reducing the impacts of WVCs, as well as improving motorist safety (Huijser *et al.*, 2009). Furthermore, limiting these impacts may be particularly important where road mortalities to wildlife contribute to local population declines, if the landscape is unsuitable for other mitigation options (as may be the case in protected areas), or when funds are unavailable for more effective mitigation. In order to reduce WVCs within protected areas, we suggest steeper penalties for speeding and campaigns to increase awareness, specifically, with targeted signs placed in WVC hotspots.

Acknowledgements

Thanks to Pilanesberg National Park, Bridgestone South Africa, Mikros Traffic Monitoring and Copenhagen Zoo for supporting the initiative. Thanks too, to the citizen science volunteer network and Africa:Live, iSpot, Pilanesberg Honorary Officers, Pilanesberg Wildlife Trust and Makanyane Volunteers. Additional thanks go to: Steven and Perry Dell, Charlotte and Cobus Marais (Pilanesberg National Park), Innocent Buthelezi and Megan Murison (data collection), Lizanne Roxburgh and Tamsyn Galloway (GIS mapping), and Marion Burger (poster and flyer design).

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.

References

- Anderson, C.D., Epperson, B.K., Fortin, M.J., Holderegger, R., James, P., Rosenberg, M.S., Scribner, K.T., & Spear, S. (2010). Considering spatial and temporal scale in landscape- genetic studies of gene flow. *Mol. Ecol.* **19**, 3565-75.
- Andrews, K.M. & Gibbons, J.W. (2005). How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* **4**, 772–782.
- Barton, B.K. (2017). MuMIn: Multi-Model Inference. R package version 1.40.0.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**,1-48.
- Bertwistle, J. (1999). The effects of reduced speed zones on reducing bighorn sheep and elk collisions with vehicles on the Yellowhead Highway in Jasper National Park. In: *Proceedings of the Third International Conference on Wildlife Ecology and Transportation* FL–ER–73–99. Florida Department of Transportation, Tallahassee, pp 89-97.

Assessing driver behaviour to reduce roadkill

- Bond, A.R.F. & Jones, D.N. (2013). Wildlife warning signs: public assessment of components, placement and designs to optimise driver response. *Animals* **3**, no. 4, 1142-1161.
- Branch, B. (1998). *Field Guide to Snakes and other Reptiles of Southern Africa*, 3rd edition. (eds. P. Barker, H. Reid) Struik Publishers, Cape Town. ISBN 978-1-86872-040 8.
- Bullock, K.L., Malan, G. & Pretorius, M.D. (2011). Mammal and bird road mortalities on the Upington to Tsee Rivieren main road in the southern Kalahari, South Africa. *Afr. Zool.* **46** (1), 60-71.
- Burnham, K.P. & Anderson, D.R. (2003). Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.
- Caro, T., Dobson, A., Marshall, A.J. & Peres, C.A. (2014). Compromise solutions between conservation and road building in the tropics. *Curr. Biol.* **24** (16), 722-R725.
- Coelho, I. P., Kindel, A. & Coelho, A.V.P. (2008). Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. *Euro. J. Wildl. Res.* **54**, 589-699.
- Coffin, A.W. (2007). From roadkill to road ecology: a review of the ecological effects of roads. *J. Transp.Geogr.* **15**, 396-406.
- Collinson, W.J., Reilly, B.K., Parker, D.M., Bernard, R.T. & Davies-Mostert, H.T. (2015). An inventory of vertebrate roadkill in the greater Mapungubwe Transfrontier conservation area, South Africa. *Afri. J. Wildl. Res.* **45**, 301-311.
- D'Amico, M., Périquet, S., Román, J. & Revilla, E. (2016). Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *J. Appl. Ecol.* **53** (1), 181-190.
- Dique, D.S., Thompson, J., Preece, H.J., Penfold, G.C., de Villiers, D.L. & Leslie, R.S. (2003). Koala mortality on roads in south-east Queensland: the koala speed-zone trial. *Wildlife Res.* **30**, 419-426.

EWT. (2018). <https://www.facebook.com/EndangeredWildlifeTrust/> Accessed July 2017.

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecol. Soc.* **14** (1).

Fisher, J. (1992). Testing the effect of road traffic signs' informational value on driver behavior. *Hum. Factors* **34**, 231-237.

Forman, R.T.T. (2003). Road ecology: science and solutions. Island Press, Washington, DC.

Garriga, N., Santos, X., Montori, A., Richter-Boix, A., Franch, M. & Llorente, G.A. (2012). Are protected areas truly protected? The impact of road traffic on vertebrate fauna. *Biodivers. Conserv.* **21**, 2761-2774.

Gordon, K.M., McKinstry, M.C. & Anderson, S.H. (2004). Motorist response to a deer-sensing warning system. *Wildl. Soc. Bull.* **32**, 565-573.

Grace, M.K., Smith, D.J. & Noss, R.F. (2015). Testing alternative designs for a roadside animal detection system using a driving simulator. In: Seiler A, Helldin J-O (Eds) *Proceedings of IENE 2014 International Conference on Ecology and Transportation*, Malmö, Sweden. Nature Conservation 11, 61–77. doi: 10.3897/natureconservation.11.4420.

Grace, M.K., Smith, D.J. & Noss, R.F. (2017). Reducing the threat of wildlife-vehicle collisions during peak tourism periods using a Roadside Animal Detection System. *Accident Anal. Prev.* **109**, 55-61.

Gunther, K.A., Biel, M.J. & Robison, H.L. (1998). Factors influencing the frequency of road-killed wildlife in Yellowstone National Park. In: *International Conference on Wildlife Ecology and Transportation* (ICOWET 1998) Florida Department of TransportationUS Department of TransportationUS Forest Service Defenders of Wildlife, Jeju Island, South Korea, 16-18 March 2018 1998.

- Hels, T. & Buchwald, E. (2001). The effect of road kills on amphibian populations. *Biol Conserv.* **99** (3), 331-340.
- Hobday, A. J. & Minstrell, M.L. (2008). Distribution and abundance of roadkill on Tasmanian highways: human management options. *Wildl. Res.* **35** (7), 712-726.
- Huijser, M.P. & McGowen, P.T. (2003). Overview of animal detection and animal warning systems in North America and Europe. In: Irwin CL, Garrett P, McDermott KC (Eds) *Proceedings of the International Conference on Ecology & Transportation (ICOET)*. Center for Transportation and the Environment, North Carolina State University, Raleigh, 368–382.
<http://www.icoet.net/downloads/03AnimalVehicleCollision.pdf>
- Huijser, M.P., Duffield, J.W., Clevenger, A.P., Ament, R.J. & McGowen, P.T. (2009). Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: A decision support tool. *Ecol. Soc.* **14**.
- Huijser, M., Mosler-Berger, C., Olsson, M. & Strein, M. (2015). Wildlife warning signs and animal detection systems aimed at reducing wildlife-vehicle collisions. In *Handbook of Road Ecology* (Eds. R. van der Ree, D.J. Smith, and C. Grilo), pp. 198-212. John Wiley & Sons, United Kingdom.
- Jaeger, J.A. & Fahrig, L. (2004). Effects of road fencing on population persistence. *Conserv. Biol.* **18** (6), 1651-1657.
- Karani, P. (2008). Impacts of roads on the environment in South Africa. DBSA—Development Bank of Southern Africa, Midrand, South Africa [Online]. Available online at: <https://www.dbsa.org/EN/About-Us/Publications/Documents/Environmental%20implications%20of%20the%20road%20network%20in%20South%20Africa.pdf>. Accessed Dec 2016.

Keshkamat, J.M., Looijen, B. & Zuidgeest, M.H.P. (2009). The formulation and evaluation of transport route planning alternatives: a spatial decision support system for the Via Baltica project, Poland *J. Transp.Geogr.* **17**, 54-64.

Mucina, L. & Rutherford, M.C. (2006). *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19: pp. 1-807. South African National Biodiversity Institute, Pretoria, South Africa.

Pilanesberg National Park. (2018). <http://www.pilanesbergnationalpark.org/>. Accessed 13 March 2018

Road Traffic Management Corporation (RTMC) (1999). Section 3 of the RTMC Act, No. 20 of 1999. URL: <http://www.arrivealive.co.za/pages.aspx?i=2343> [accessed 15 November 2012].

Rheindt, F.E. (2003). The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution?. *Journal für Ornithologie*, **144** (3), 295-306.

Rytwinski, T., Soanes, K., Jaeger, J.A., Fahrig, L., Findlay, C.S., Houlahan, J., van der Ree, R. & van der Grift, E.A. (2016). How effective is road mitigation at reducing road-kill? A meta-analysis. *PLoS one* **11** (11), e0166941.

Secco, H., Ratton, P., Castro, E., da Silva Lucas, P. & Bager, A. (2014). Intentional snake road-kill: a case study using fake snakes on a Brazilian road. *Trop. Cons. Sc.* **7**, 561-571.

Seiler, A. & Helldin, J.O. (2006). Mortality in wildlife due to transportation. In *The ecology of transportation: Managing mobility for the environment* (pp. 165-189). Springer, Dordrecht.

Smith, D.J. (2003). The ecological effects of roads: theory, analysis, management, and planning considerations. PhD thesis, University of Florida, Gainesville, FL. 346.

Statistics South Africa. (2012). Census 2011: census in brief. Statistics South Africa. <http://www.statssa.gov.za/>. Accessed 19 October 2012.

Statistics South Africa. (2015). Tourism 2015. <http://www.statssa.gov.za/publications/Report-03-51-02/Report-03-51-022015.pdf>. Accessed 13 March 2018 .

Assessing driver behaviour to reduce roadkill

Taylor, B.D. & Goldingay, R.L. (2004). Wildlife road-kills on three major roads in north-eastern New South Wales. *Wildl Res.* **31** (1), 83-91.

Team RC. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Trombulak, S C. & Frissell, C.A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conser. Biol.* **14** (1), 18-30.

van der Ree, R., Jaeger, J.A., van der Grift, E.A. & Clevenger, A P. (2011). Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving toward larger scales. *Ecol.Soc.* **16** (1).