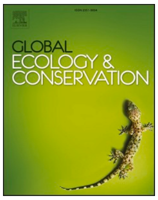
Global Ecology and Conservation 38 (2022) e02199

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



The role of environmental, structural and anthropogenic variables on underpass use by African savanna elephants (*Loxodonta africana*) in the Tsavo Conservation Area

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ARTICLE INFO

Keywords:
African elephant
Railway
Tsavo
Underpass
Wildlife crossing structure
Wildlife movement

ABSTRACT

Wildlife crossing structures are effective interventions for mitigating fragmentation of habitats by linear infrastructure. The 2017 construction of a new railway cutting through the Tsavo Conservation Area (TCA), home to the largest elephant population in Kenya, affected wildlife movement and habitat connectivity. Although numerous studies have investigated the use of wildlife crossing structures by a wide range of species, few have focused on their use by megaherbivores. In this study, we examined use of 41 wildlife crossing structures by African savanna elephants (*Loxodonta africana*) along a 133 km section of new railway in Tsavo, Kenya. We used a generalized linear mixed modeling approach to assess the relationship between elephant crossing rate over 28 months between July 2017 to April 2021 and explanatory factors including crossing structure attributes, livestock presence and proximity to highways, water points and human settlement. We found that structural attributes of crossing structures were most strongly associated with the elephant crossing rate, particularly height and its interaction with type of crossing structure (bridges, wildlife underpasses and culverts). Higher crossing structures were associated with higher crossing rate, with the largest influence of height at culverts and wildlife underpasses. Although bridges comprised only 19.5 % of the 41 available crossing structures, they accounted for a disproportionately high number of elephants crossing events (56 %). The results demonstrated the importance of bridges over designated crossing structures for elephants, with predicted seasonal counts of elephant crossings being 0.31 for average sized culverts, 2.88 for wildlife underpasses and 5.86 for bridges. The environmental and anthropogenic variables were not strongly associated with elephant crossing rate. Our findings have direct application for future siting and design of crossing structures across elephant ranges.

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https://doi.org/10.1016/j.gecco.2022.e02199
Received 11 April 2022; Received in revised form 15 June 2022; Accepted 15 June 2022

1. Introduction

In an increasingly industrialized world, linear infrastructure development is now a primary driver of habitat fragmentation (Roy and Sukumar, 2017), and construction of transportation infrastructure has emerged as a major threat to wildlife and ecosystem protection across Africa and in other continents (Laurance et al., 2009, 2015). Such infrastructure development drives the loss and fragmentation of wildlife habitat, causes increased wildlife mortality during crossing attempts, and creates barriers to wildlife movement and dispersal (Jackson, 2000; Forman et al., 2003; Smith, 2003). Of all the primary effects of transport infrastructure, the barrier effect is the most concerning for highly mobile wildlife species (Forman and Alexander, 1998; Seiler and Folkeson, 2006).

Despite the effects on wildlife, transportation networks are vital to modern economic activity and provide substantial societal benefits (Button and Hensher, 2001). Linear infrastructure provides connectivity for people and enables exchange of goods and services, underpinning development (van der Ree et al., 2011). Developing countries often have rich natural resources but poor infrastructure to capitalize on them, which leads to significant challenges in terms of balancing development with conservation (Hopcraft et al., 2015). Therefore, there is a need to achieve a compromise between infrastructure development for human communities and environmental conservation for wildlife (Ghent, 2018).

In cases where there are overriding reasons to build transport infrastructure through wildlife conservation areas, mitigating the negative impacts of linear infrastructure on wildlife movement and habitat connectivity is critical to maintain wildlife populations and key ecological processes (Beyer et al., 2016). The construction of wildlife crossing structures (WCS) has emerged as the primary approach to mitigate linear infrastructure impacts in natural areas. Effective crossing structures and exclusionary fencing to funnel wildlife to those structures can significantly reduce negative impacts on wildlife populations and maintain wildlife connectivity (Clevenger et al., 2001; Clevenger and Waltho, 2005; Simpson et al., 2016; Smith et al., 2015). A meta-analysis of road studies found that such mitigation measures reduced roadkill by 40 % (Rytwinski et al., 2016). The effectiveness of WCS to facilitate wildlife movement depends on a number of variables including dimensions, location, proximity to natural wildlife corridors, noise levels, substrate, habitat cover, fencing, moisture, temperature, light, and human disturbance (Jackson and Griffin, 2000; Ghent, 2018). Most of these studies on the effectiveness of WCS have been conducted in North America, Australia and Europe. Out of 123 studies on WCS reviewed by van der Ree et al. (2007), none were conducted in Africa. This information gap is particularly notable for a region that maintains such diverse and abundant populations of mobile wildlife, including megafauna.

In addition, the assessment of ecological impacts of linear infrastructure has largely focused on roads, given they are a leading cause of habitat fragmentation, loss of migratory corridors, and loss of connectivity among populations in many ecosystems around the world (Beckmann and Hilty, 2010; Simpson et al., 2016). Railways, although expected to impact wildlife in similar ways, have received far less research attention than roads, probably because one of their major impacts, train-animal collisions, is not visible to the general public (Wells et al., 1999; Cserkész and Farkas, 2015; Borda-de-Água et al., 2017). Although various studies have documented wildlife-train collisions (e.g., Krauze-Gryz et al., 2017; Roy and Sukumar, 2017; Nezval and Bíl, 2020), we know little about wildlife use of railway crossing structures.

Understanding the major attributes and covariates influencing the use of WCS by the endangered African savanna elephant (IUCN, 2021) is significant for the future development of mitigation measures of linear infrastructure cutting through elephant ranges. However, only a single study has comparatively analyzed characteristics correlated with use of different crossing structures by elephants (Pan et al., 2009), finding that 44 % of WCS were utilized by Asian elephants during a seven-month monitoring period and that WCS located on existing natural movement corridors were preferred. Nyaligu and Weeks (2013) and Green et al. (2018) studied the use of a fenced wildlife corridor with one underpass between Mt. Kenya and Laikipia in Kenya. Although primarily concerned with elephant use of the entire 14 km corridor, these studies gave initial empirical evidence of African elephants (*Loxodonta africana*) crossing a road through an underpass. Okita-Ouma et al. (2021) also found evidence of satellite tracked African elephants using underpasses in Tsavo ecosystem, in Kenya, showing that median hourly speeds significantly increased while crossing the railway, and that 78 % of the elephant railway crossing occurred at night. Yet the relocation data resolution was insufficient to identify which crossing structures were used, and no study to date has investigated WCS use by African elephants and factors influencing their use.

Planned development in Kenya (Kenya Vision 2030; Government of Kenya, 2007) is structured to address social, economic and health needs and to facilitate transition to a middle-income economy by the year 2030. Infrastructure development is part of this plan, with a goal to identify approaches to reduce negative environmental effects and conserve wildlife corridors and migratory routes. In 2017 construction of a standard gauge railway (SGR) from Mombasa to Nairobi was completed with 133 km of the route bisecting the Tsavo Conservation Area, a wildlife area comprising of 21,000 km^2 Tsavo National Parks. To facilitate wildlife movement and reduce wildlife-train collisions a set of WCS were constructed underneath the railway. Additional potential crossing structures, including bridges and culverts of varying size and dimension were also created, primarily to manage water flow through the feature. This resulting variation in the category, location and dimensions of potential WCS across the railway offered an opportunity to investigate the potential factors influencing use of these structures by elephants. Our goal was to combine information about each structure as well as the landscape context in which it occurred to determine key factors associated with crossing structure use by African elephants.

2. Materials and methods

2.1. Study area

This study was carried out along a 133 km section of the Mombasa – Nairobi SGR that cuts through the Tsavo Conservation Area (TCA) in south-eastern Kenya. The TCA is an area of approximately 44,000 km^2 (Gillson, 2004) and includes Tsavo East, Tsavo West

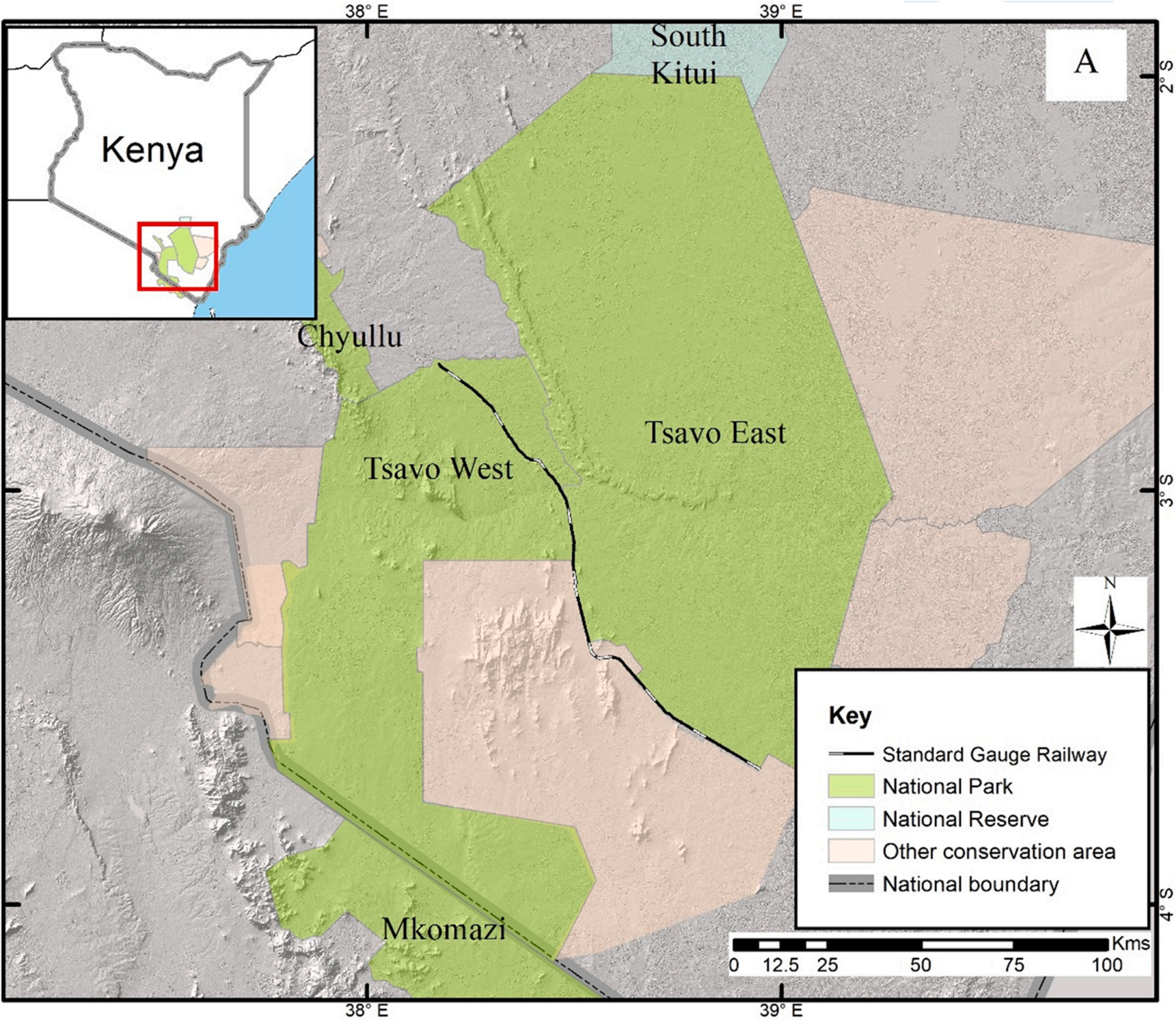

Fig. 1. The Tsavo Conservation Area (A) and the study area along the standard gauge railway (B), with all wildlife crossing structures (n = 41) used to monitor elephant crossing rates.

and Chyullu National Parks, South Kitui National Reserve, adjacent ranches, and community conservancies (Lala et al., 2021; Fig. 1A). Mkomazi National Park in northern Tanzania is connected to TCA. Adjacent and almost running parallel to the SGR are the Mombasa – Nairobi meter-gauge railway and the Mombasa – Nairobi highway (Fig. 1B). Out of a total of 130 potential WCS constructed under the SGR in the study area, 41 were open and available for wildlife use during the period under study. These open structures included 6 designated wildlife underpasses, 8 bridges and 27 culverts. The rest were fenced off by electric fence on both sides after completion and launch of the SGR. The designated wildlife underpasses resemble bridges structurally, but range from 60 to 70 m wide and 5.5–7 m high (Okita-Ouma et al., 2021) whereas bridges vary widely in dimension depending on their intended purpose (height range: 4–12 m; width range: 20–1960 m). Most of the bridges were designed to cross rivers and stream valleys, which are more frequent in the northern section of railway, while others spanned the older meter-gauge railway line or provided vehicle access. The culverts are concrete boxes, almost always smaller than bridges and wildlife underpasses, but also varying in their dimensions (height range: 2.4–5.5 m; width range: 2–6.8 m; Table A1; Fig. A1).

The most common large herbivores found in the TCA include African savanna elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), African buffalo (*Syncerus caffer*), hippopotamus (*Hippopotamus amphibius*) and Burchell's zebra (*Equus quagga*) (Ngene et al., 2017). The TCA has the largest single elephant population in Kenya; estimated at 14,964 individuals (Ministry of Tourism and Wildlife, Government of Kenya, 2021). Previous total aerial censuses in TCA have shown that the highest elephant abundance is in Tsavo East and Tsavo West National Parks, with the highest densities commonly found in south of Tsavo East (Ngene et al., 2017), south of Voi River.

TCA is a semi-arid area characterized by two annual rainy seasons. The "long" rains occur from March to May and the "short" rains

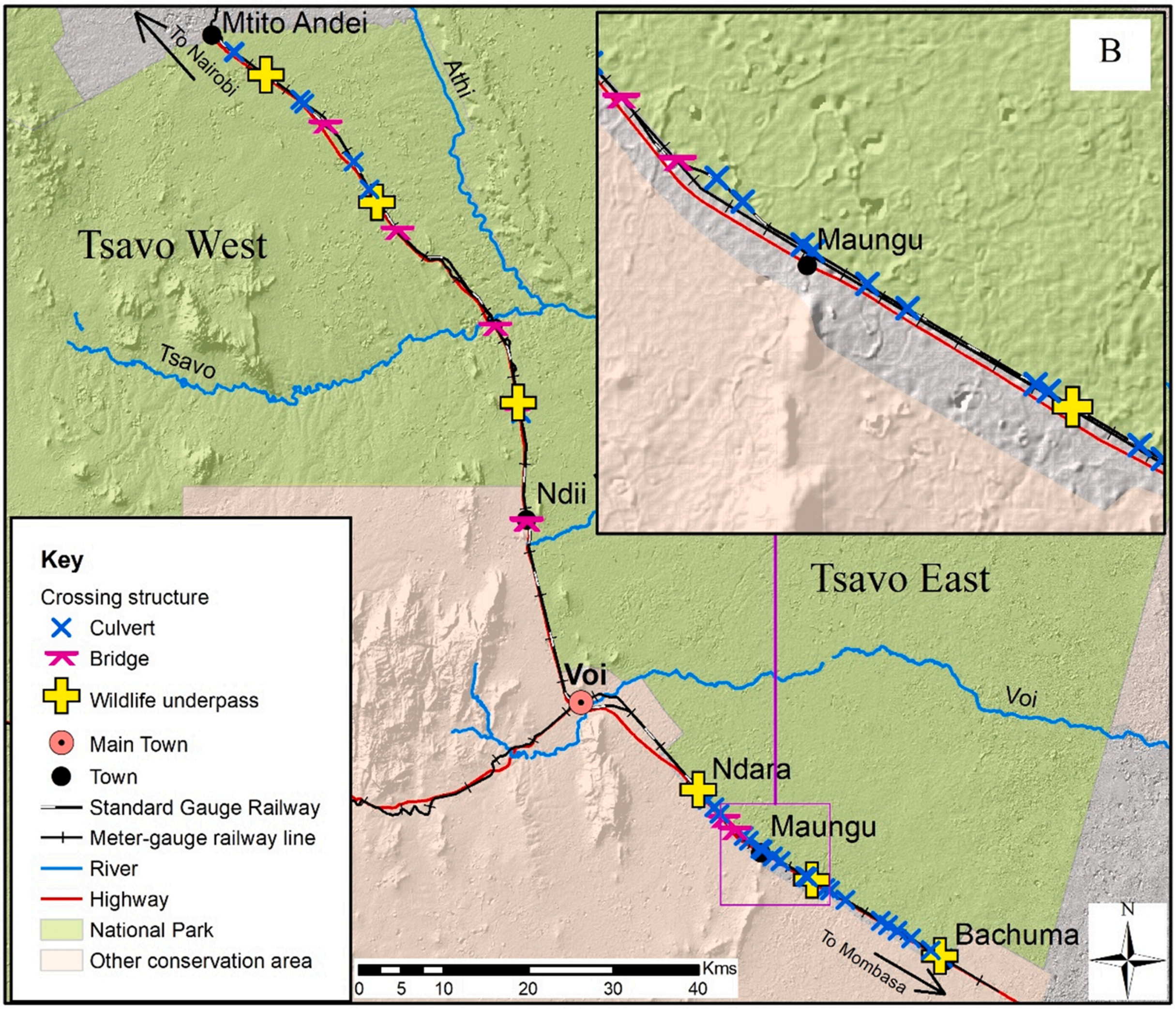

Fig. 1. (*continued*).

between November and December. The short dry season occurs in January and February while the long dry season extends from June to October (Leuthold and Sale, 1973; van Wijngaarden, 1985). This rainfall pattern is erratic and influenced by altitude, with annual rainfall in the highlands being over 1200 mm and the plains receiving an average of 500 mm annually (Munyao et al., 2020). Altitude also influences temperature in Tsavo, with highlands having temperatures ranging between 18 °C and 27 °C, and the lowlands between 23 °C and 35 °C (Munyao et al., 2020). The landscape is undulating with notable hills such as Taita hills, Yatta plateau and Sagalla hills. Vegetation in Tsavo varies from grasslands to dense wooded bushlands and is predominantly of *Commiphora* spp. and *Acacia* spp. plant communities (van Wijngaarden, 1985).

2.2. Data collection

2.2.1. Monitoring of wildlife crossing

From July 2017 to April 2021 (28 months), after completion and launch of the Mombasa – Nairobi SGR, we collected data on the wildlife and livestock utilization of the 41 SGR crossing structures that remained open to wildlife. The surveys were carried out by driving along the SGR inside Tsavo National Park from Bachuma to Mtito Andei. The 133 km railway length was divided into two sections for monitoring: Bachuma - Ndara and Ndii - Mtito Andei. Monitoring of wildlife crossings was done for one section per day. Underpasses were scheduled for surveys 6 times per month in a section, making 12 days per month of overall survey effort. The specific monitoring days varied due to occasional logistical challenges and some months were not surveyed at all (2018: January, February, June and December; 2019: January and February; 2020: January, February, April, May and June; 2021: February).

During each survey, the project staff inspected each crossing structure on foot to ascertain whether elephants had crossed since the previous survey based on presence of elephant signs including dung piles and footprints or occasionally direct observations of elephants using the underpass (Lala et al., 2022). The ground around the crossing structures was mostly bare, making elephant signs highly detectable, and all recorded signs was dusted and marked with white chalk to avoid double counting. Data on livestock use of these crossing structures was also collected and summarized following the same approach. Each sampling event was associated with a season (dry vs. wet) as described above.

2.2.2. *Crossing structure assessment*

The data on structural dimensions (height and width) of crossing structures were collected through field visits using a laser range finder, or in cases where the width was too large, a handheld GPS (Garmin etrex x20).

2.2.3. *Environmental and anthropogenic covariates*

Data on the location of water sources in the TCA, including boreholes, water pans, and water tanks and troughs which are not seasonal, was obtained from the Kenya Wildlife Service (KWS), the national wildlife agency. The Mombasa – Nairobi highway through the TCA was manually digitized using satellite imagery and distances from each crossing structure to the highway and the closest water source were calculated.

Human settlement data was collected in May 2018 by field mapping of houses on the railway corridor from Bachuma to Ndara, and from Ndii to Mtito Andei. The location of individual houses was georeferenced whereas clustered houses were counted and assigned to their center waypoint. Density of houses was calculated based on the number of houses within a 1 km buffer radius of a crossing structure.

In total we considered 9 separate variables and their potential association with frequency of use of crossing structures by elephants (Table 1). The covariate(s) explored were selected based on: a priori knowledge of structural attributes, human activities and environmental factors in Tsavo, and conclusions made by Okita-Ouma et al. (2021) in their analysis of elephant movements in relation to this railway. Other studies have also shown that environmental factors such as distribution of water sources and human activities influence elephant movements. Movement of African elephants in Tsavo was found to be more directed toward water sources in the dry season as compared to the wet season (Wato et al., 2018). Despite their involvement in crop raiding, elephant tracking locations and movement pathways have indicated a general avoidance of highly populated human settlements and villages in Botswana (Songhurst et al., 2016; Buchholtz et al., 2020).

All spatial data were projected to UTM 37S for overlay operations and distance calculations; all spatial data preparation and calculations were performed using ESRI ArcMap 10.7.1 (Esri Inc. ArcGIS 10.7.1. Redlands, CA: Esri Inc. 2019).

2.3. *Data analysis*

To investigate factors associated with use of railway crossing structures by elephants, we used generalized linear mixed models with a negative binomial error distribution and associated log link function. We assigned crossing structure ID as a random effect (random intercept), given that observations were repeated within crossing structures across seasons and years. To create our response variable, we pooled the counts of elephant and livestock crossing events within each season (wet vs. dry) and year, resulting in a total of 410 samples (WCS by season by year). We pooled surveys in this manner in part because of a suspected influence of season on elephant movement behavior (Wittemyer et al., 2007; Wato et al., 2018), and because individual surveys would be highly influenced by whether local and regional elephant herds were even present in the area. Pooling across seasons reduced the likelihood of “false” zeros, where zero counts of elephants were the result of the absence of elephants, rather than the avoidance of a particular crossing structure. To account for variable number of survey visits between the two sections of the railway, we included survey effort as an offset term in all models.

We first tested all continuous covariates for collinearity and considered any pair with a Pearson’s $r > 0.70$ to be problematic. This resulted in removal of the number of houses variable, as it was highly correlated with housing density (Fig. A1). Crossing structure width and housing density were $\log_{10}$-transformed to address large gaps in the data distribution. All continuous covariates were also standardized (centered and scaled), to improve model convergence.

Model building initially considered three categories of predictor variables: structural attributes, human activities, and environmental factors (Table 1), and began by first identifying the optimal model representing each of the three categories.

All combinations of variables were tested within each category and models with the lowest AICc value were considered optimal. We included interaction terms between width and category, and height and category, to allow the effect of width and height on crossing rate to vary by category. This allows, for example, structure height to be more strongly associated with elephant use for culvert

Table 1
Variables investigated for association with frequency of use of wildlife crossing structures across the SGR in the Tsavo Conservation Area.

Variable	Group	Unit	Abbreviation	Source
Underpass width	Structural	meters	Width	Field survey
Underpass height	Structural	meters	Height	Field survey
Underpass category	Structural		Category	Field survey
Proximity to highway	Environmental	kilometers	Dist Highway	Google satellite imagery
Proximity to water source	Environmental	kilometers	Dist Water	KWS
Livestock use	Human activity	count	Stock	Field monitoring
Proximity to houses	Human activity	kilometers	Dist House	Field mapping
Density of houses	Human activity	Per Sq. radius	HousesDens	Field mapping

structures than for bridges. Season was kept in all models as we suspected it played a role in elephant movements as earlier mentioned. Therefore, the season only model (with offset and random intercept) served as a baseline or null model for model comparisons within each category. Any non-nested models within 2.0 AICc were carried over to the final modeling stage where all combinations of these category models were considered. Individual variables within category top models were not separated from this point. We discuss any models from this final comparison within 2.0 AICc points of the top model.

We calculated a pseudo R^2 value for final models and performed a final check for multicollinearity based on the variance inflation factor (VIF). Adequate model fit was assessed through inspection of scaled simulated residuals in the DHARMa package (Hartig, 2017) and its associated tests for uniformity.

We performed all data exploration and analysis in the R environment (R Core Team, 2021). We used package *lme4* (Bates et al., 2014) to create regression models using the Laplace approximation to approximate likelihoods (Bolker et al., 2009) and "bobyqa" optimizer to avoid convergence issues. We used package *AICcmodavg* (Mazerolle, 2020) to assess and compare models, the *MuMIn* package (Barton, 2020) to calculate pseudo-R^2 and the *DHARMa* package (Hartig, 2021) to calculate and plot scaled residuals. All data plots were generated using *ggplot2*.

3. Results

Our 410 samples (season by year by WCS) resulted in 871 counts of elephant underpass use and 1921 counts of livestock underpass use. Elephant crossings during the wet season accounted for 51 % (n = 440) of the total. Total surveys on the Ndara – Bachuma section was 164, while on the Ndii – Mtito Andei section was 167. The three categories of crossing structures were not used according to their

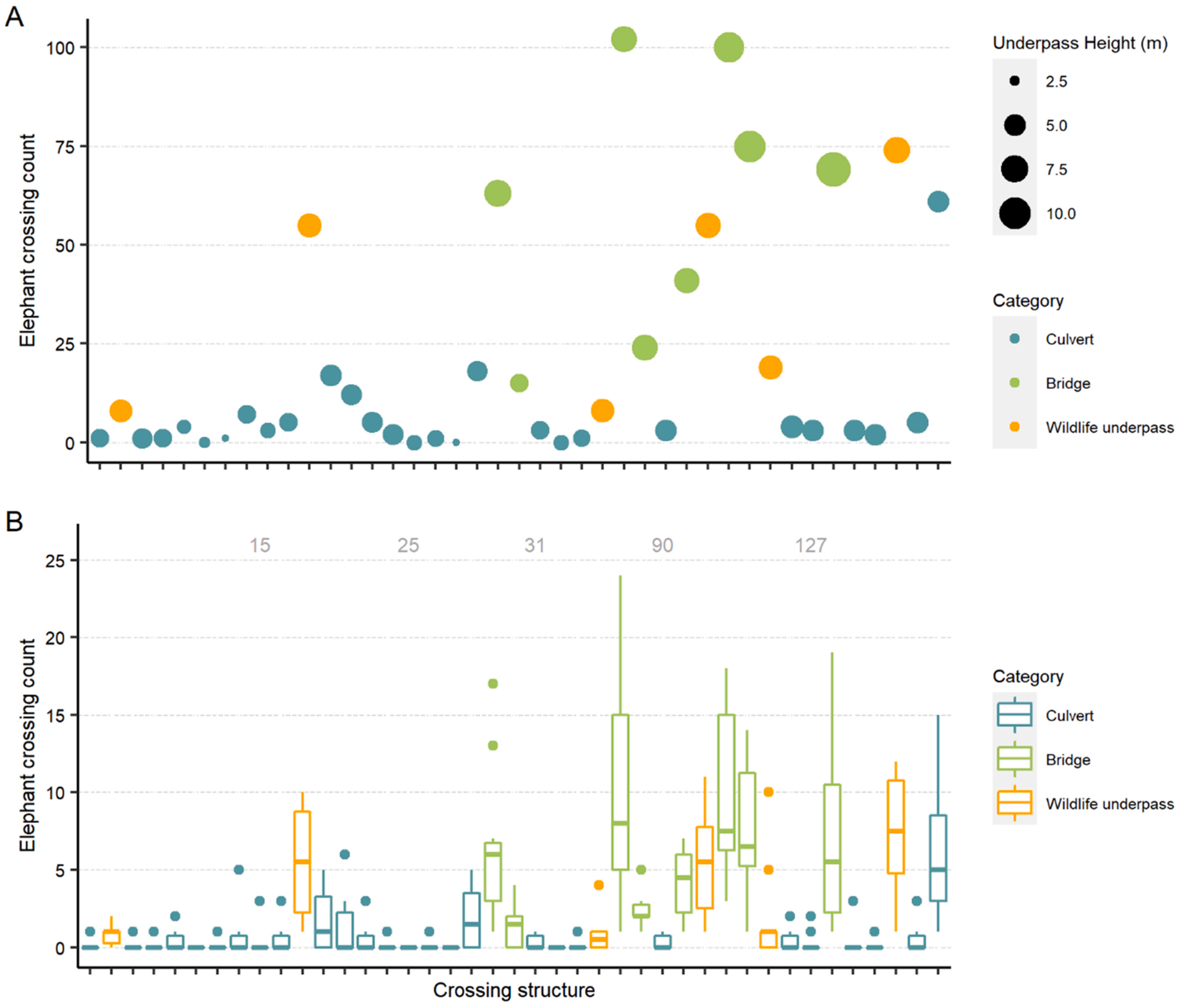

Fig. 2. The total recorded count relative to crossing structure height (A) and median count per sample (season/year) (B) across all 41 survey wildlife crossing structures along the SGR. Crossing structures are ordered as they appear along the railway, south – northwards and the distance (km) along the railway is indicated in gray, with zero at the southernmost point.

Table 2
Models of factors influencing African elephant use of railway crossing structures in Tsavo with number of parameters (K), corrected AIC (AICc), change in AICc compared to the best model (Δ AICc), AICc weight (AICcWt), log-likelihood (LL) and cumulative AICc weight (Cum.Wt). The lower the AICc, the better the model. Every model has season.

Model	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt
STR7: (Height * Category)	9	1109.79	0	0.50	-545.67	0.50
STR7 + HUMAN5	11	1110.80	1.01	0.30	-544.07	0.80
STR7 + HUMAN7	11	1111.64	1.85	0.20	-544.49	1
HUMAN5: (Stock + Dist House)	6	1149.81	40.02	0	-568.80	1
HUMAN7: (Stock + HousesDens)	6	1151.72	41.92	0	-569.75	1

[*] Denotes interaction effect. STR - Variable(s) related to structural attributes of a crossing structure. HUMAN - Variable(s) related to human activity. ENV - Variable(s) related to environmental factors.

Table 3
Estimates of regression coefficients for the best GLMM of variables influencing use of railway crossing structures by African elephants in Tsavo.

Predictors	Beta	se	CI	Statistic	p
Intercept	-3.15	0.27	–3.68 to –2.62	-11.66	<0.001
Height	1.90	0.48	0.97–2.84	3.99	<0.001
Category (bridge)	1.46	0.50	0.49–2.43	2.94	0.003
Category (wildlife underpass)	-0.26	0.75	–1.73–1.21	-0.35	0.726
Season (wet)	0.08	0.10	–0.11–0.27	0.80	0.421
Height: bridge	-1.55	0.53	–2.58 to –0.51	-2.92	0.004
Height: wildlife underpass	1.09	1.30	–1.45–3.64	0.84	0.400

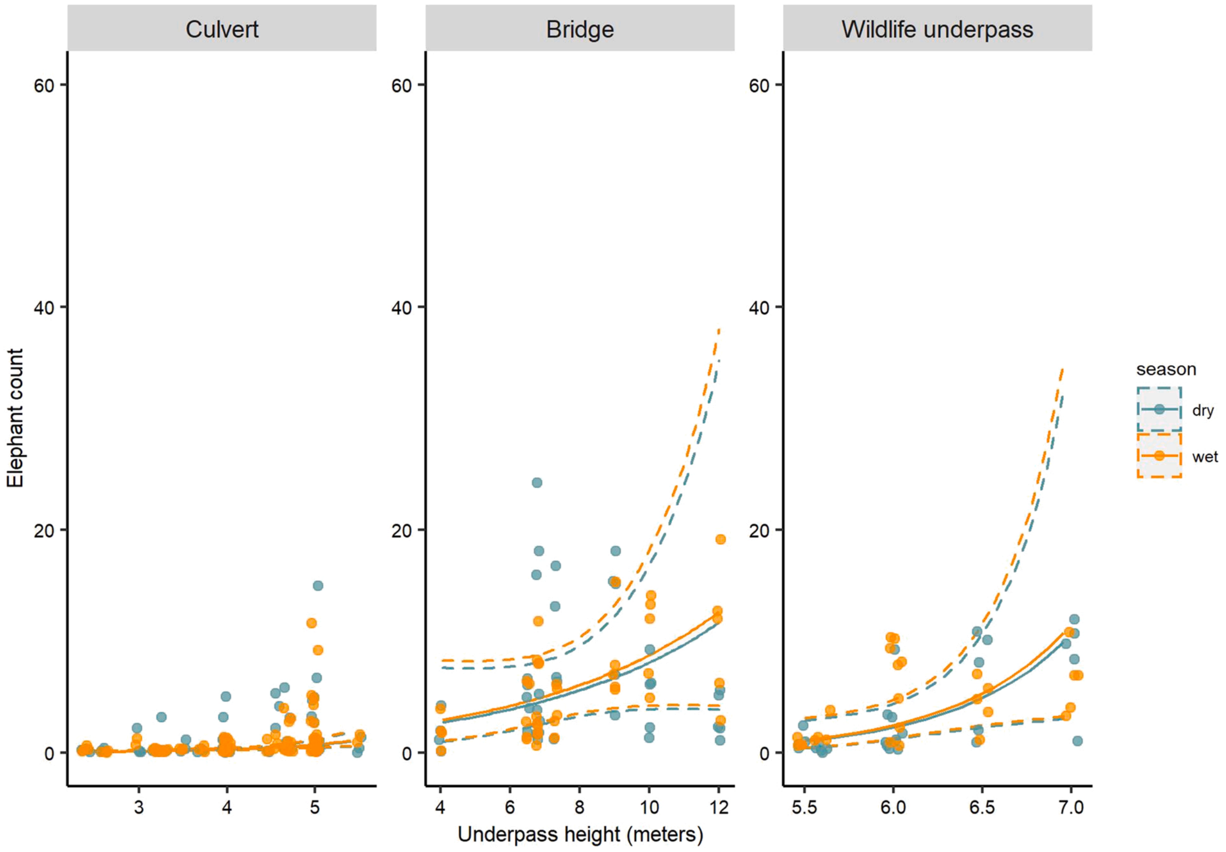

Fig. 3. Predicted relationship between crossing structure height and count of elephant crossing events at three different types of crossing structures and across two seasons, from a generalized linear mixed model approach (logit link, random intercept for underpass). Raw data points are jittered slightly along the x axis to allow viewing of points at the same height values.

availability. Wildlife underpasses, bridges and culverts made up 14.6 %, 19.5 %, and 65.9 % of crossing structures respectively, but 25 %, 56 % and 19 % of elephant crossings were recorded at each crossing category. Total recorded crossing events at a crossing structure ranged from 0 to 102 (Fig. 2A) with a median of 5 crossings (Fig. 2B). Four crossing structures recorded no elephant crossing at all and these were all culverts (Fig. 2A).

Initial model building from the sets of structural, environmental, and human-related covariates resulted in eleven, three and seven (Table A2i, TableA2ii, Table A2iii) unique models respectively in addition to the baseline, season-only model. From these three groups we brought forward four individual models to consider in 5 unique combinations for the final model set (Table 2).

Our top model included height and interaction with type of crossing structure (Table 2). The second-best model added livestock use count and distance to houses to the top-model predictors, but the addition of these predictors failed to improve the overall model ranking. Model coefficients (Table 3) indicated culverts and wildlife underpasses were used less frequently than bridges and that while height was positively associated with elephant crossing rate across all three categories, the influence of height on predicted crossing rates was strongest for wildlife underpasses and lowest for bridges. Across the range of heights recorded in our study, impacts of height differences on elephant crossing count were larger overall for wildlife underpasses and culverts. Whereas few elephant crossings were recorded at culverts below a height of 5 m, all wildlife underpasses and majority of bridges were taller than 5 m, with bridges reaching as high as 12 m (Fig. 3).

The marginal coefficient of determination (pseudo-R^2) of our top-ranked model (tri-gamma method) was 0.41. Generalized variance inflation factor estimates indicated no problematic multi-collinearity in our final model and plots of scaled residuals against fitted values of all potential predictors (regardless of inclusion in our optimal model) and random effect levels indicated no patterns or lack of fit. In the case of residuals vs. fitted values model fit was supported by a formal test of uniformity (One-sample Kolmogorov-Smirnov test, $D = 0.054$, $p = 0.175$).

4. Discussions

Our primary objective was to identify significant predictors associated with use of railway crossing structures by African elephants. Our findings indicate that structural attributes including height and type of crossing structure were more important than the levels of human activity, human development, or the environmental attributes of the surrounding landscape. Although we were unable to find any comparable studies outside of North America documenting factors influencing wildlife use of road or railway crossing structures, the relative importance of structural attributes is supported by numerous studies in North America. For example, crossing rates by mule deer (*Odocoileus hemionus*) were higher at overpasses compared to underpasses (Simpson et al., 2016) and structural characteristics and placement of wildlife underpasses were the most important factors associated with successful elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) crossing in Arizona, USA (Gagnon et al., 2011). Although some landscape factors were related to crossing structure use by various species in Banff National Park in Alberta Canada, Clevenger and Waltho (2005) found that structural attributes best explained crossing structure use of both predator and prey species.

Specifically, elephant use count in bridges was higher than that of culverts and wildlife underpasses, underscoring the importance of non-wildlife bridges in improving wildlife connectivity. As noted elsewhere (e.g., Sweden, Bhardwaj et al., 2020), wildlife use of structures not specifically designed for this use can play an important role in improving connectivity, particularly when designed or modified to meet certain structural thresholds. However, whereas culverts comprised the highest proportion of WCS in this study, they recorded the lowest proportion of elephant crossing. Here height clearly played a role, with culverts displaying the lowest height of all three categories. And whereas width of WCS did not add sufficient predictive power to our model, width was somewhat correlated with height ($r = 0.5$) and the typical dimensions of a culvert are incorporated into the category predictor of the model. We therefore speculate that width of culverts played some role in elephant usage of these features. An additional potential deterrent to the use of culverts may also be the primarily concrete substrate within them, as compared to a bridge's natural substrate, although culverts do accumulate dirt and soil over time.

Importantly, crossing structure height was not only a key predictor of elephant crossing rates, but support for an interaction between height and crossing category resulted in varying predictions of height effects for each category. Predicted counts of elephant crossings, across a season, for average-sized culverts, wildlife underpasses and bridges were 0.31, 2.88 and 5.86 respectively. The addition of 1 m of height to these structures is predicted to increase seasonal crossing counts by 0.52 (168 %), 10.48 (364 %) and 1.17 (19 %) events respectively. The relative influence of height changes on bridges is relatively small, likely because majority of the bridges were above the necessary height to encourage elephant use. The greatest gains from a structural standpoint then are in the improvements in height of culverts and wildlife underpasses, where relatively small increases in height (e.g., 1 m above average) are expected to increase crossings by 2.7 times and 4.6 times respectively. These gains translate into the largest increase in predicted elephant crossings for the wildlife underpasses. Foster and Humphrey (1995) pointed out that animals using an underpass should have an unobstructed view of the habitat on the far side of the underpass. Therefore, it is plausible that increasing height of a culvert has a greater impact on increasing the animal's horizon view more than the same increase in height of a bridge.

The shortest structures in the study allow us to predict the potential low height threshold for elephant use. To put this into perspective, the maximum observed shoulder height from a sample (170 males and 224 females) of elephants in Amboseli, Kenya (west of the study region, but linked by elephant movement), was identified as 3.18 m for one bull and 2.73 m for one cow (Lee and Moss, 1995). This study also showed that the asymptotic height, height when asymptote in height growth is reached, from the total sample of bulls was 3.04 m and that of females was 2.32 m. Therefore, we expect the low height threshold in WCS to be higher than the asymptotic and maximum shoulder height. Predicted crossing count drops below one elephant per season at approximately 5.4 m culvert height, and 5.5 m for wildlife underpasses, yet predicted seasonal crossing count at the lowest bridge height (4.0 m) was much higher at 2.7. This suggests there may be some additional benefit to the bridges not captured by our set of potential predictor variables. An upper threshold may also exist, beyond which few or no gains in crossing rate will be achieved with further increases in height. Visually there is some evidence from the raw data scatterplots (Fig. 3) that our data includes this threshold, with potential apparent plateaus in crossing rate for bridges and wildlife underpasses. We were unable to statistically estimate this upper threshold due to a relatively small sample of structures with high heights.

Our study found insufficient evidence that season of the year was related to elephant crossing structure use. This finding supports results from Okita-Ouma et al. (2021) finding no significant differences in wet and dry season diel crossings by African elephants in this same study area based on satellite tracking data. Seasonal variation in this region affects availability and abundance of both water and forage. African savanna elephants are known to prefer bushlands and woodland vegetation types (Mukeka, 2010; Okello et al., 2015) and these vegetation types are widely distributed over the landscape in Tsavo. Okello et al. (2015) also suggest that season was not a factor in elephant habitat selection in Amboseli, also in southern Kenya, due to the brevity and unpredictability of the rainy season (Obari, 2014). Given this, our definition of the wet and dry seasons by month of the year, as opposed to actual rainfall amounts may have disconnected our season categories from actual seasonal variation in water distribution on the landscape.

Although preliminary modeling (before addition of structural variables) indicated a negative association of livestock counts with elephant WCS use and higher elephant use of WCS further from houses (Table A2iii), these variables did not add sufficient information above that provided by the height and category variables to be included in our optimal model. Their lack of importance in this scenario may be explained by temporal partitioning of use of the WCS. Whereas, livestock are driven through the crossing structures primarily during the day when people are also more active, elephants have been shown to cross this railway primarily at night (Okita-Ouma et al., 2021). Earlier studies have found African elephants employ risk-avoidance behavior by shifting to nocturnal activity patterns and moving at higher speeds in human dominated areas in other scenarios, for example to minimize poaching risk (Ihwagi et al., 2018) or adapting their behaviour to exploit habitats within human -dominated landscapes (Graham et al., 2009). Our findings suggest that the human activity surrounding WCS, at least in our study area, are secondary to structural attributes of WCS in predicting elephant crossing rates.

There is potential for additional factors, unaccounted for here, to have influenced variable use of crossing structures by elephants. First, there is evidence that vegetation greenness/productivity indices generated from satellite imagery such as NDVI (Normalized Difference Vegetation Index) are associated with savanna elephant densities at both local and continental scales (Mukeka, 2010; Duffy and Pettorelli, 2012). Unfortunately, because our approach required pooling of crossing data across numerous months within a year, we were unable to investigate the potential impact of this factor on variation in crossing structure use. Second, the location of crossing structures near or on the natural elephant travel routes may also play a role in elephant crossing structure use. In this case, although 10 elephants (8 of which were year-round residents) were tracked with GPS collars in this study area, these animals were not tracked prior to construction of the new railway, and therefore knowledge of traditional travel routes by elephants in the TCA is not clearly documented. Broadly, the placement of SGR wildlife underpasses in Tsavo did have input from conservation organizations led by KWS (Okita-Ouma et al., 2016); therefore, siting of the wildlife underpasses specifically may have incorporated existing knowledge from various sources about the location of wildlife migratory and travel routes. Culverts and bridges, due to their design objectives, would not have accounted for this external information.

5. Conclusions

Understanding the factors that influence the use of WCS by different species is critical for sound management and conservation of individual wildlife species subjected to the potentially negative impacts of linear infrastructure. Knowledge about WCS features associated with increased use by focal wildlife species can guide design of future structures, particularly those crossing designated conservation areas, and existing WCS can be retrofitted in certain scenarios to maximize wildlife usage. Our study is the first to investigate variables related to use of WCS by African savanna elephants, and we have identified key structural characteristics, particularly height, most likely to influence elephant usage of these structures. Future planning of WCS in elephant ranges should consider crossing structure height as more important than structure width; and that the influence of crossing structure height depends on the type of WCS. Our results also underscore the importance of bridges not specifically meant for wildlife crossing. Therefore, connectivity gains may be highest where wildlife crossing structures are added to areas devoid of existing bridges, and future designs of non-wildlife bridges where linear infrastructure are cutting through elephant ranges should consider designs that accommodate elephant crossing and ensure that there is connectivity between the affected wildlife habitats.

CRediT authorship contribution statement

Michael Koskei: Conceptualization, Methodology, Data analysis, Writing – original draft, Writing – review & editing. Joseph Kolowski: Methodology, Data analysis, Writing – original draft, review & editing. George Wittemyer: Methodology, Writing – review & editing. Fredrick Lala: Writing – review & editing, Project administration. Iain Douglas-Hamilton: Writing – review & editing, Project administration. Benson Okita-Ouma: Conceptualization, Writing – review & editing, Supervision, Project administration.

Declaration of Competing Interest

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

Data availability

All data used in this research is available on request from Save the Elephants.

Acknowledgement

The Director of Wildlife Research and Training Institute is thanked for authorizing this research. We thank Wildlife Research and Training Institute staff from Tsavo East for assisting in data collection; especially Alex Mwazo, Dennis Kibara, Geraldine Mjomba, Lilian Apollo and Fridah Mwikamba. We appreciate administrative, technical and advisory support from Frank Pope, Festus Ihwagi, Chris Thouless, Lucy King and Wainaina Kimani of Save The Elephants. We also thank Elephant and Bees project team in Tsavo. This work was made possible by Save The Elephants through the Chief Executive Officer. Finally, we are grateful to the two anonymous reviewers for their insightful comments that improved the quality of this article.

Appendix A

See Appendix Fig. A1.

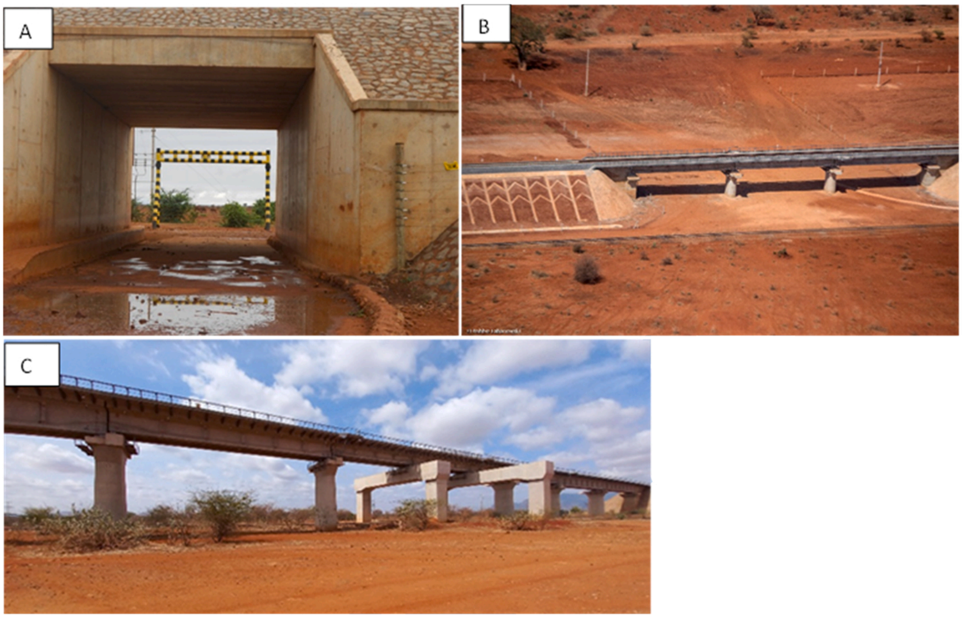

Fig. A1. Wildlife crossing structures: (A) culvert, (B) wildlife underpass, (C) bridge along the standard gauge railway in Tsavo Conservation Area.

See Appendix Tables A1 and A2i, A2ii, A2iii.

Table A1

Attributes of all 41 open wildlife crossing structures through the Standard-Gauge Railway (SGR) passing through the Tsavo Conservation Area, Kenya. For survey purposes the 133 km route was divided into the Bachuma-Ndara (BN) and Ndii-Mtito Andei (NM) sections. Crossing structure categories were culverts (C), bridges (B) and wildlife underpasses (W).

ID	X	Y	Category	Width (m)	Height (m)	Section
DK90 + 360	493488	9594459	C	6.8	4.0	BN
Bachuma corridor	493165	9594654	W	70.0	6.0	BN
DK92 + 071	492026	9595344	C	6.0	4.0	BN
DK94 + 800	489678	9596729	C	6.0	4.0	BN
DK96 + 653	488077	9597661	C	6.0	3.0	BN
DK97 + 900	487001	9598296	C	2.0	3.0	BN
DK98 + 900	486148	9598812	C	2.0	2.0	BN
DK103 + 759	481963	9601272	C	6.0	4.0	BN
DK105 + 893	480129	9602368	C	3.0	3.0	BN
DK106 + 507	479598	9602672	C	6.0	4.0	BN
Maungu corridor	478105	9603549	W	70.0	6.0	BN
DK108 + 909	477534	9603905	C	4.0	5.0	BN
DK109 + 242	477241	9604060	C	6.0	5.0	BN
DK112 + 627	474329	9605783	C	4.0	5.0	BN
DK113 + 692	473419	9606336	C	6.0	5.0	BN
DK115 + 126	472185	9607081	C	4.0	3.0	BN
DK115 + 420	471941	9607227	C	3.0	4.0	BN
DK117 + 100	470587	9608207	C	3.0	2.0	BN
DK117 + 893	470000	9608743	C	6.0	5.0	BN
Maungu rail crossing	469176	9609095	B	180.0	7.0	BN
Maungu water bridge3	467889	9610509	B	70.0	4.0	BN
DK121 + 873	467138	9611364	C	4.0	4.0	BN
DK122 + 832	466501	9612080	C	4.0	3.0	BN
DK124 + 001	465732	9612959	C	4.0	4.0	BN
Ndara corridor	464681	9614170	W	65.0	6.0	BN
Ndii water bridge	444662	9645220	B	60.0	7.0	NM
Ndii oil pipeline bridge	444632	9645378	B	25.0	7.0	NM
DK180 + 210	443705	9658258	C	4.0	5.0	NM
Manyani vehicle bridge	443508	9659371	B	20.0	6.0	NM
Manyani corridor	443482	9659511	W	70.0	6.0	NM
Tsavo River bridge	440944	9668185	B	1960.0	9.0	NM
Kenani rail crossing	429436	9679439	B	520.0	10.0	NM
Kenani corridor	426783	9683005	W	70.0	6.0	NM
DK213 + 765	425835	9684549	C	5.0	6.0	NM
DK217 + 510	423984	9687790	C	6.0	5.0	NM
Kanga bridge	420903	9691896	B	210.0	12.0	NM
DK226 + 599	418118	9694605	C	5.0	5.0	NM
DK227 + 198	417697	9695033	C	6.0	5.0	NM
Kanga corridor	413681	9697926	W	60.0	7.0	NM
DK236 + 741	409936	9700576	C	4.0	5.0	NM
DK236 + 909	409806	9700682	C	5.0	5.0	NM

Table A2i

Results of model comparisons (generalized linear mixed model with negative binomial error structure, log-link, and random intercept for crossing structure ID) within the structural attribute category, predicting count of elephant crossings at wildlife crossing structures across the SGR.

Model	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt
STR7: (Height * Category)	9	1109.79	0	0.64	-545.67	0.64
STR6: (Width + Height * Category)	10	1111.16	1.37	0.32	-545.31	0.97
STR10: (Height + Category)	7	1116.91	7.12	0.02	-551.32	0.99
STR4: (Height + Width + Category)	8	1118.99	9.19	0.01	-551.31	0.99
STR5: (Height + Width * Category)	10	1120.33	10.54	0.003	-549.89	1.00
STR1: Height	5	1121.50	11.71	0.002	-555.68	1.00
STR2: Width	5	1123.12	13.32	0.001	-556.48	1.00
STR9: (Height + Width)	6	1123.56	13.77	0.001	-555.68	1.00
STR3: Category	6	1125.10	15.30	0.0003	-556.45	1.00
STR8: (Width * Category)	9	1126.34	16.55	0.0002	-553.94	1.00
STR11: (Width + Category)	7	1126.35	16.55	0.0002	-556.03	1
Intercept Season	4	1156.45	46.66	0	-574.18	1

Table A2ii

Results of model comparisons (generalized linear mixed model with negative binomial error structure, log-link, and random intercept for crossing structure ID) within the environmental attribute category, predicting count of elephant crossings at wildlife crossing structures across the SGR.

Model	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt
Intercept Season	4	1156.45	0	0.39	-574.18	0.39
ENV2: Dist Water	5	1156.68	0.22	0.35	-573.26	0.73
ENV1: Dist Highway	5	1158.49	2.04	0.14	-574.17	0.87
ENV3: (Dist Highway + Dist Water)	6	1158.64	2.19	0.13	-573.22	1

Table A2iii

Results of model comparisons (generalized linear mixed model with negative binomial error structure, log-link, and random intercept for crossing structure ID) within the human variable category, predicting count of elephant crossings at wildlife crossing structures across the SGR.

Model	K	AICc	ΔAICc	AICcWt	LL	Cum.Wt
HUMAN5: (Stock + Dist House)	6	1149.81	0	0.34	-568.80	0.34
HUMAN4: (Stock + Dist House + HousesDens)	7	1151.20	1.38	0.17	-568.46	0.51
HUMAN2: Dist House	5	1151.30	1.49	0.16	-570.58	0.67
HUMAN7: (Stock + HousesDens)	6	1151.72	1.90	0.13	-569.75	0.80
HUMAN6: (Dist House + HousesDens)	6	1152.63	2.82	0.08	-570.21	0.89
HUMAN1: Stock	5	1153.13	3.31	0.06	-571.49	0.95
HUMAN3: HousesDens	5	1154.23	4.42	0.04	-572.04	0.99
Intercept Season	4	1156.45	6.64	0.01	-574.18	1

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