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Effectiveness of wildlife underpasses and culverts in connecting elephant habitats: a case study of new railway through Kenya's Tsavo National Parks

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Abstract

Transportation networks can be a major impediment to wildlife movements. We assessed the use of wildlife underpasses and culverts along a newly constructed railway in Kenya's Tsavo National Parks by African elephants (***L. africana***). We collared ten elephants with GPS satellite transmitters within 20 km of the railway in March 2016 and analysed their movement data to March 2019. Eight elephants used the underpasses although one did not cross the adjacent highway. The remaining two neither used the underpasses nor crossed the highway despite ranging in the vicinity. Their median speed significantly increased to 0.65 km/hr from 0.45 km/hr before crossing the railway, then slowed to 0.32 km/hr after crossing. Females in family groups moved faster than the lone bulls when using the underpasses. Seventy-eight per cent of all crossings made were at night. The fast speeds and the nocturnal patterns are behavioural responses of elephants in risky landscapes or under stress. Disturbance from vehicles traffic on the adjacent highway and from newly developed human settlements may have limited use of underpasses. Wildlife crossing structures, signage and speed bumps along the highway; relocation of the illegal human settlements; and inter-agency coordination are requisites for enhancing Tsavos' elephant habitat connectivity.

KEYWORDS

elephant tracking, highway, infrastructure, movement behaviour, policy, railway, Tsavo, wildlife underpass

Résumé

Les réseaux de transport peuvent représenter un obstacle majeur aux mouvements de la faune. Nous avons évalué l'utilisation de passages souterrains et de ponceaux pour la faune le long d'une voie ferrée récemment construite dans les parcs nationaux de Tsavo, au Kenya, par les éléphants d'Afrique (*L. africana*). Nous avons équipé dix éléphants avec des émetteurs de satellite GPS dans un rayon inférieur à 20 km de la voie ferrée en mars 2016 et analysé leurs données de mouvement jusqu'en mars 2019. Huit éléphants ont emprunté les passages souterrains bien que l'un d'eux n'ait pas traversé l'autoroute adjacente. Les deux autres n'ont ni emprunté les passages souterrains ni traversé l'autoroute malgré les distances de proximité. Leur vitesse médiane a augmenté de manière significative de 0,45 km/h à 0,65 km/h avant qu'ils ne traversent la voie ferrée, puis a diminué pour atteindre 0,32 km/h après la traversée. Les femelles des groupes familiaux se déplaçaient plus vite que les mâles adultes solitaires lorsqu'elles utilisaient les passages souterrains. Soixante-dix-huit pour cent de toutes les traversées effectuées se sont déroulées de nuit. Les vitesses rapides et les schémas nocturnes sont des réponses comportementales des éléphants dans des environnements à risque ou des situations de stress. L'utilisation des passages souterrains peut être relativement limitée dans les zones de perturbations causées par la circulation des véhicules sur la route adjacente et les établissements humains récemment développés. Des structures de passage de la faune, une signalisation adéquate, la mise en place de dos d'ânes sur l'autoroute, le déplacement des établissements humains illégaux et une coordination interinstitutions est nécessaire pour améliorer la connectivité de l'habitat des éléphants de Tsavos.

1 | INTRODUCTION

Linear infrastructure developments are one of the main human activities that threaten biodiversity (e.g. Sala et al., 2000; Sanderson et al., 2002). They may drive habitat loss and fragmentation, alter ecosystem dynamics and facilitate invasions by exotic species (Fahrig & Rytwinski, 2009). These infrastructures can interfere with animal movement patterns (Eftestøl et al., 2014; Frair et al., 2005), lead to changes in species distribution, habitat resource selection and population density (e.g. Fahrig & Rytwinski, 2009; Zeller et al., 2019) and increase wildlife mortality through vehicle collisions (Neumann et al., 2012; Zeller et al., 2018). Limiting the dispersal of individuals in isolated patches of habitats may also lead to a reduction in gene flow among wildlife populations (Rico et al., 2009). These detrimental impacts are set to increase as roads, rails and urban areas continue to expand by rapidly each year (Dulac, 2013; Seto et al., 2012). The greatest impact on wildlife will occur primarily in the tropics where there are high levels of biodiversity and pristine ecosystems (Laurance et al., ,2009, 2014; Torres et al., 2016).

Elephants are particularly sensitive to habitat disturbances due to their wide-ranging nature. Their movement is non-random (Loarie et al., 2009; Wittemyer et al., 2008) and is driven by the need for resources such as food, water and minerals (Chamaille-Jammes et al., 2007; Harris et al., 2008; Murwira & Skidmore, 2005; Wittemyer et al., 2007). Elephants may travel vast distances when resources are scarce and their spatio-temporal movement behaviour is mostly related to vegetation greenness (Bohrer et al., 2014; Bolger et al., 2008; Cushman et al., 2005). In areas of high human densities, elephants may alter their behaviour and adopt risk avoidance strategies such as travelling at night and moving faster through these areas, particularly increasing their speed when crossing busy roads (Blake et al., 2008; Cushman et al., 2005; Douglas-Hamilton et al., 2005; Graham et al., 2009).

Research is increasingly highlighting that linear infrastructures such as roads can act as barriers to elephant movement. Movement data from 28 elephants in the Congo basin showed that only one single individual made a road crossing during the entire study period, and this elephant only crossed once (Blake et al., 2008). A similar study in Central Africa showed that elephants did not cross roads at all, and some of the studied elephants would not even range close to the road (Granados et al., 2012). These responses were also observed in Malaysia where a road reduced elephant crossings by over 70% (Wadey et al., 2018). Nonetheless, the road also attracted several elephants due to the ecological factors of changes in vegetation structure and high food availability by the roadside (Wadey et al., 2018).

Kenya is a country rich in biodiversity with over 35,000 species of flora and fauna across varied ecosystems such as marine, mountains, grasslands, forests and savannahs (Ojwang et al., 2017). However, Kenya faces significant challenges of balancing linear infrastructural development and biodiversity conservation. There are ongoing efforts by the government to promote infrastructural development through the Kenya Vision 2030 programme launched in 2008 (GoK, 2007). This aims to help transform Kenya into a middle-income industrialised economy by 2030. One of the Vision 2030 flagship projects was the new 487 km Standard Gauge Railway stretching from Mombasa to Nairobi cities. Its construction took place between 2014 and 2017 and is without a doubt the most significant transport project in Kenya since the building of the original metre-gauge railway in the early 20th century. However, a section of the railway (133 km) is raised on an embankment and fenced on either side. Thus, cutting through key elephant range in the Tsavo Conservation Area. This poses a significant conservation challenge despite provisions of wildlife underpasses along this new railway.

In this study, we assessed the effectiveness of the wildlife underpasses and culverts along the new railway in enabling the movement

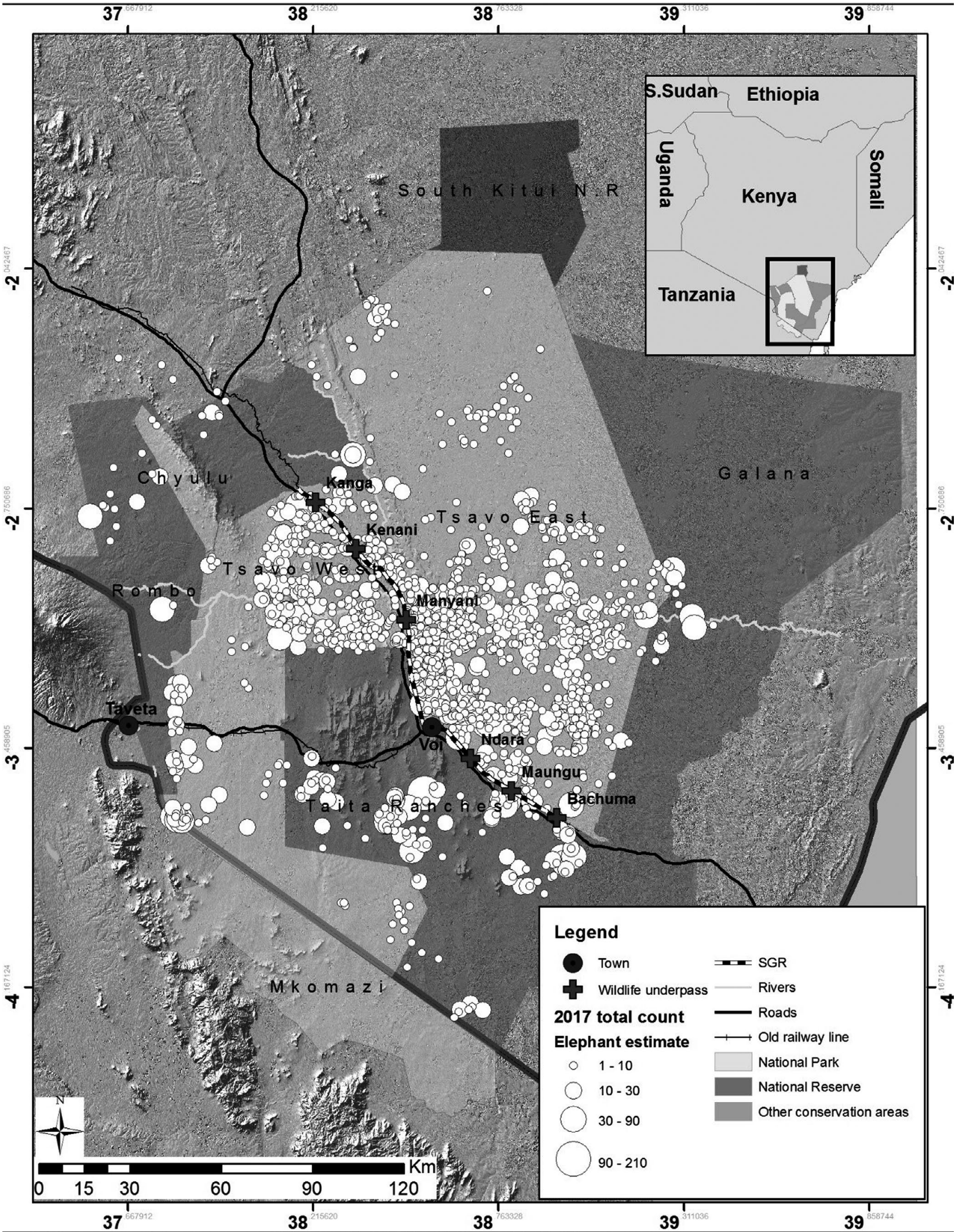

FIGURE 1 Tsavo Conservation Area and its constituent National Parks, other conservation and ranches. Elephant distribution as of the 2017 census is shown and the locations of the six official wildlife crossing structures/underpasses are labelled

and connectivity of African elephants (*L. africana*) in the Tsavo Conservation Area. We tested the hypothesis that the new railway's underpasses and culverts are not risk barriers to elephants by analysing GPS satellite tracking data of ten elephants. Specifically, we looked at: (1) the impact of the underpasses on elephant behaviour at periods of crossings (i.e. differences before, during and after crossing speeds and; (2) the temporal and seasonal patterns of railway crossings at individual and group levels. Our results will help guide future management decisions for habitat connectivity and infrastructure development.

2 | METHODS

2.1 | Study area

Our study site encompassed the new section of the railway (133 km) that cuts through the Tsavo Conservation Area (TCA), the largest protected area complex in Kenya covering *ca*. 42,000 km^2. There are three National Parks within the area; Tsavo East, Tsavo West and Chyulu Hills National Parks and a number of large community-groups ranches, which are important for wildlife dispersal and connectivity

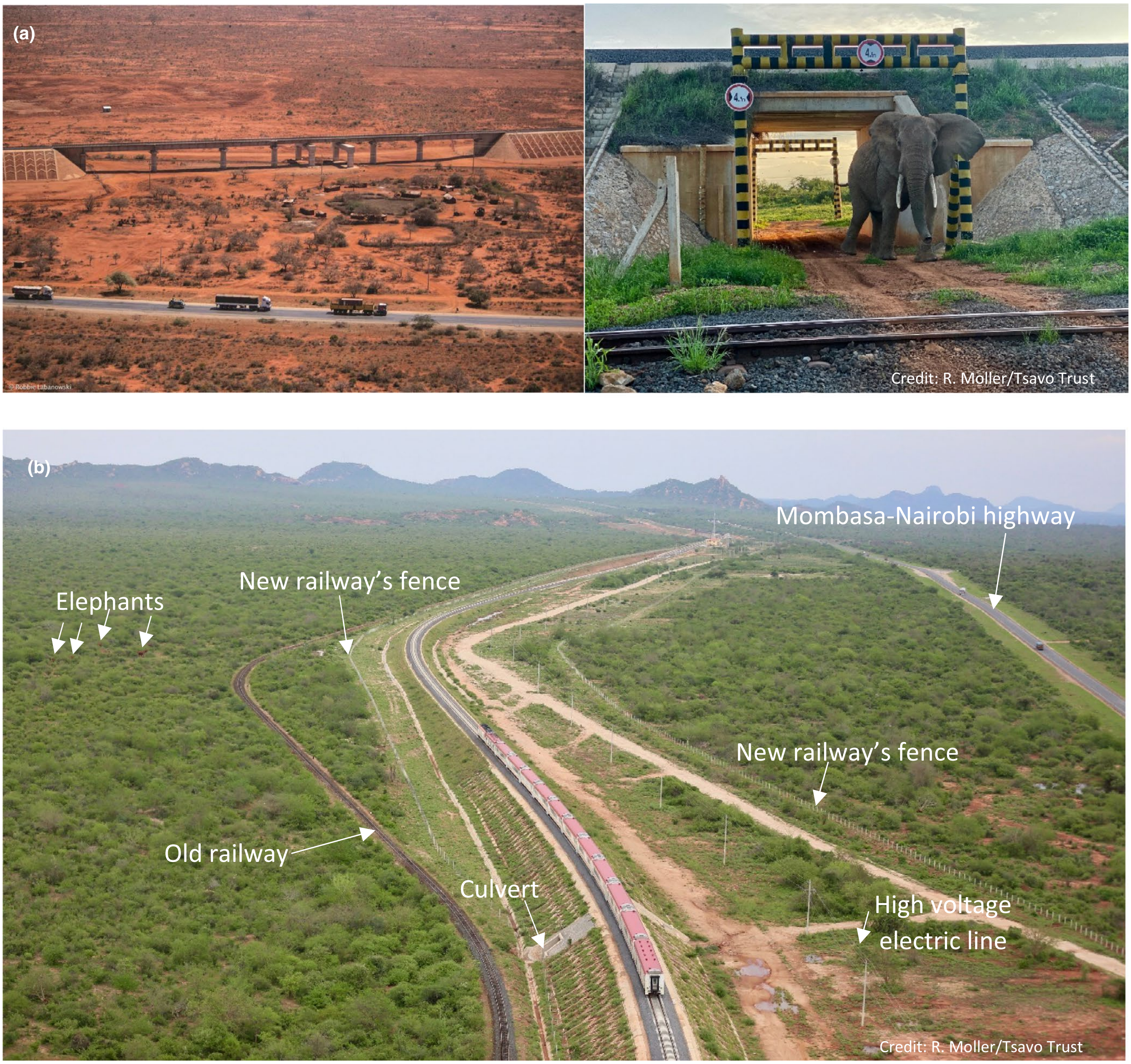

FIGURE 2 (a) A wildlife underpass with transient human settlements between it and the Mombasa–Nairobi Highway. To the RHS is an elephant using a multipurpose culvert/bridge under the new railway in the horizon. In the foreground is the old railway in Tsavo Conservation Area. (b) A section of the new railway line on a raised embankment with a fence running on both sides. Tsavo East NP and Tsavo West NP are the LHS and RHS of the Mombasa–Nairobi highway, respectively. A fenced-off culvert/bridge, the old railway, a high voltage electric gridlines and a few elephants are labelled in the area (Figure 1). The TCA is 70 to 250 km from the Kenyan coastline with altitude ranges between 200 and 1000 m. The area comprises of semi-arid bushland and acacia-savannah forest and is home to Kenya's largest single elephant population of approximately 12,843 (Ngene et al., 2017) to 16,681 individuals (Lamprey et al., 2020). Rainfall patterns vary considerably from year to year and month to month. However, in general the wet seasons occur between October and December and from March to May with an average monthly rainfall of 75 mm. The rest of the months are generally dry and hot with an average monthly rainfall of 15 mm (Leuthold & Leuthold, 1975; Tyrrell & Coe, 1974).

The communities living in the group ranches in Tsavo practice nomadic pastoralism, sedentary livestock keeping and small-scale farming. Commercial livestock keeping also occurs in the ranches of Galana and Kulalu. Small-scale farming dominates outside the protected areas and large-scale farming occurs in the west and central parts of the ecosystem. Tsavo Conservation Area is bound in the Northwest by densely human populated parts of Ukambani; to the Southwest by the Kilimanjaro, Pare and Usambara mountains; and to the Southeast by the moderately populated coastal hinterland. The Conservation Area borders Mkomazi National Park in Tanzania to the Southeast, enabling trans-frontiers movements of elephants in this region.

The entire section of the new railway through the TCA Area (except the wildlife crossings) is fenced-off to mitigate animal collision. The wildlife underpasses and drainage culverts are approximately 2–7 m long between Bachuma to Mtito Andei stations. A decision was made to fence off the 112 culverts to try and reduce encroachment into the National Parks by mainly illegal cattle grazing. Thus, these culverts are largely unusable for wildlife and people. There are six wildlife underpasses (70 m long and 6 m high) that connect Tsavo East and Tsavo West National Park. In addition to these six wildlife underpasses, there are also nine large bridges available for wildlife use. These include the: Tsavo river bridge (1980 m × 9 m); Kenani rail inter-crossing bridge (520 m x 10 m); Kanga bridge (210 m × 12 m); Maungu rail inter-crossing bridge (180 m × 7.3 m); Manyani vehicle bridge (20 m × 6.5 m); Ndii oil pipeline bridge (25 m × 6.8 m); Ndii water bridge (60 m × 6.8 m); Maungu water bridge 1 (70 m × 4 m); and Maungu water bridge 2 (95 m × 4.7 m) (Figure 2a). The construction of these bridges resulted in the wildlife underpasses being positioned on average every 9.5 km. Their placements were guided by best practices from elsewhere (e.g. FHWA, 2011) and by a joint inter-agency assessment report (KWS et al., 2014) that highlighted sections of the railway's route with high biological relevance. Their spacing is not equal as their placements were also determined by the engineering requirements for the railway.

Next to the new railway are five other types of mega-infrastructure: (1) the old railway which is 100 years old; (2) the old Mombasa-Nairobi highway, which marks the border between Tsavo East and Tsavo West National Parks. Along the highway is no wildlife crossing structure despite increasing traffic volume and speed; (3) two high voltage power gridlines; (4) two oil pipelines and; (5) the Mzima water pipeline. These infrastructures are within 200 m of each other and crisscross with the new railway in some places (Figure 2b).

TABLE 1 Dates of capture and locations of the ten study elephants and their family sizes

Tracking data period	Elephant ID name & sex	Estimated Age (yrs)	Capture location	Family size[a]
15/03/2016–15/03/2019	*Maungu (F)*	18	Maungu area in Tsavo East NP, 600 m east of the new railway, approx. 1 km north west of Maungu town	16
15/03/2016–15/03/2016	*Ndara (M)*	25	Ndara area in Tsavo East NP, 600 m east of the new railway	5
16/03/2016–09/07/2016	*Kenani (M)*	30	Kenani area in Tsavo East NP, 3 km east of the new railway, approx. 17 km north west of Tsavo River Bridge	1
16/03/2016–16/03/2019	*Kamboyo (F)*	25	Kamboyo area in Tsavo West NP, 20 km west of the new railway, approx. 16 km south west of Mtito Andei town	10
16/03/2016–16/03/2019	*Manyani (F)*	35	Manyani area in Tsavo East NP 1 km east of the new railway	4
16/03/2016–16/03/2019	*Tsavo Bull (M)*	35	Manyani area in Tsavo West NP, 800 m west of the new railway	1
17/03/2016–03/11/2018	*Rukinga (M)*	28	Rukinga Ranch south east of Maungu town, approx. 7 km from the new railway	3
17/03/2016–17/03/2019	*Taita (F)*	30	*Taita* Ranch south east of Maungu town, approx. 7 km from the new railway	15
31/01/2018–05/02/2019	*Sagalla (M)*	40	Sagalla area approximately 4 km from Tsavo East NP and new railway. The animal had a record of frequent crop raiding in the Sagalla community area and was among some 500 elephants that were stranded in Tsavo East NP during the construction of the new railway causing a spike in human elephant conflict in December 2018/January 2019. It was collared in 2018.	1
23/02/2018–05/02/2019	*Saidimu*	35	*Saidimu* was translocated to Tsavo Conservation Area in 2018 to mitigate human elephant conflict in Lewa Downs Conservancy approximately 600 km away. It was released onto Tsavo West NP in the rhino Intensive Protection Zone, 20 km west of the new railway	1

[a]This may not be the core family group number as this figure is from the time of the capture. Family numbers change throughout the year.

TABLE 2 Railway and highway crossings made by the 10 GPS collared elephants between March 2016 and March 2019 in the Tsavo Conservation Area

Elephant ID (sex *M*: male, *F*: female)	Number of new railway crossings	Number of Mombasa-Nairobi highway crossings	Observations in relation to the use of railway underpasses
Maungu (F)	85	0	Crossed the railway frequently mainly through the Maungu rail crossing bridge from Tsavo East NP but did not cross the highway into the ranches and onto the Tsavo West NP. *Maungu* roamed around the Ndara underpass but did not use it.
Ndara (M)	0	0	Did not cross the railway from Tsavo East NP into the ranches and into Tsavo West NP.
Kenani (M) (4 months of data only)	104	45	Crossed the railway more often than the highway mainly around the Kenani area in Tsavo West NP, implying the highway was more restrictive to its movement compared to the railway. *Kenani* was poached in July 2016.
Kamboyo (F)	0	0	Did not cross the highway from Tsavo West NP, and thus the railway into Tsavo East NP despite it getting as close as 100 m or less to the railway
Manyani (F)	11	53	Crossed the highway more frequently than it crossed the railway around Manyani area and at Tsavo River bridge.
Tsavo Bull (M)	43	748	Crossed the highway more frequently than the railway mainly around Manyani area via the Manyani underpass. It often crossed back into Tsavo West NP.
Rukinga (M)	41	35	Crossed the railway mainly around Ngutuni and at Maungu areas more than it crossed the highway into the ranches and Tsavo West NP. *Rukinga* is a frequent crop raider in the Sagalla community area. Its collar failed in November 2018.
Taita (F)	20	24	Almost all railway crossings, mainly via the Maungu underpass and Maungu rail crossing bridge, were followed with highway crossings into the ranches and Tsavo West NP. *Taita's* range extends into Mkomazi NP in Tanzania.
Sagalla (M)	2	6	Crossed the highway more than the railway (mainly around Ngutuni area).
Saidimu (M)	9	37	Crossed the highway more often than the railway (mainly around Kanga bridge).
Total (10 animals)	315	948	Much higher highway crossings compared to railway crossings, implying low efficacy of the railway crossing structures/underpasses.

The construction of the new railway left only 10% of the original connectivity available to animals along this corridor posing both ecological and human safety challenges. For example, according to Kenya Wildlife Service's unpublished data, 32 train/vehicle–elephant collisions were recorded during the construction of the new railway between 2015 and 2017. The collisions occurred when elephants crossed the old railway or the Mombasa–Nairobi highway, panicked and then got trapped between the new railway's fence or embankment, and the old railway or highway. This was a 256% increase from a total of nine collisions between 2012 and 2014 before the new railway construction began. Three vehicle-elephant collisions on the highway and zero train collisions were recorded between 2018 and July 2020. This was a 67% decline in collisions compared to the 2012 to 2014 period. Similar declining trends in train/vehicle wildlife collisions were observed for other animal species on the old railway and the highway after the new railway became operational from 2018 (*KWS unpublished data*). At least three human fatalities, several injuries and significant economic losses were linked to the reported collisions.

2.2 | Collaring data

Ten GPS satellite collars were fitted on five adult male and five adult female elephants in March 2016 during the construction of the new railway. Group size of the collared elephants ranged from 1 to 16 individuals. Eight of the elephants were collared within 20 km of the new railway to specifically study the effectiveness of the wildlife underpasses. The other two (not included in this study) were collared for another related study. In order to increase our sample size, we also used data from two additional elephants who were fitted with collars in 2018 close to the new railway (Table 1).

The collars deployed in 2016 were AWT (African Wildlife Tracking) (https://awt.co.za/) satellite while the 2018 collars were Henrik GL200 (http://www.savannahtracking.com/). All the tracking collars were set to acquire GPS fixes at every 60-min interval.

Selection of the animals for the study, their capture locations and the month of capture were designed to maximise the chances of elephants using the underpasses and culverts from

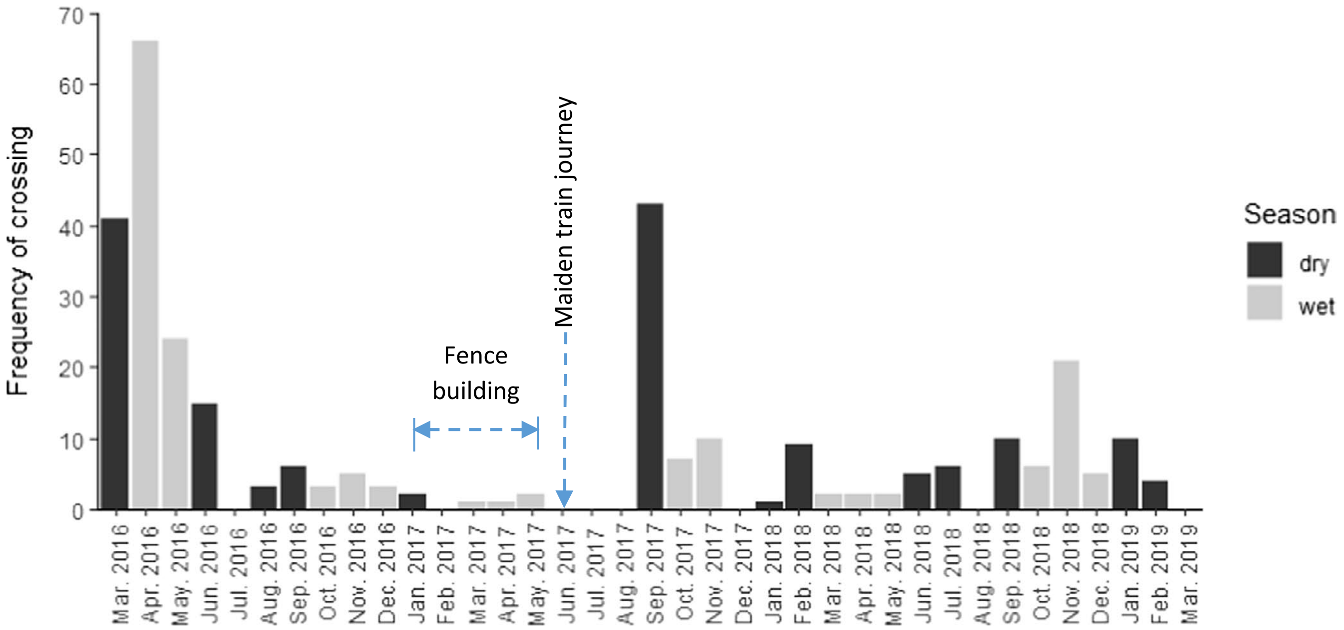

FIGURE 3 Monthly new railway crossing frequencies of eight collared elephants and their families between March 2016 and March 2019, Tsavo Conservation Area

both sides of the railway. This would enable us to study sexual differences and increase the chances for seasonal movements at least during dry/wet transitional month of March. The sampling range (20 km each side of the railway) for the collaring was within the >1500 km^2 historical ranging area for elephants in the TCA (Leuthold & Sale, 1973). We did not have data for ranging patterns for the collared animals before the construction of the railway. Capture and general handling of the animal followed procedures described in KWS (2016), Okita-Ouma et al. (2016) and Okita-Ouma et al. (2008).

2.3 | Analyses

2.3.1 | Data preparation and visualisation

Elephant movement data were retrieved using the 'STE Downloader' programme. The Downloader programme connects to the ESRI service using an internet protocol. Here data are transferred via the Internet and updates a locally stored ESRI geodatabase with tracking data from the server Animal Tracking database (Wall, 2015). The programme interface within the Downloader lets users conduct advanced selection and filtering operations on stored locations and extract data for further analyses. Elephant GPS data collected from collars were therefore filtered using an upper, biologically based threshold speed of 7 km/h (elephant hourly movement distances do not exceed 6.5 km) to glean out erroneous fixes caused by GPS error. All spatial data analyses and map creation were carried out in ArcMap and projected to Universal Transverse Mercator (UTM) WGS-84 reference system (Zone 37S). All elephant movement tracks were visually explored to determine which elephants crossed the new railway and to identify potential barriers for those that did not cross. Dry and wet seasons were guided by the long-term seasonal patterns as already described (Leuthold & Leuthold, 1975; Tyrrell & Coe, 1974).

2.3.2 | Elephant railways crossing speeds

The downloaded elephant tracking data already have movement paths calculated, complete with straight-line distances and speeds for every individual animal throughout the tracking period. Further spatial data manipulation were carried out in ESRI ArcMap 10.5.1 (Esri Inc. ArcGIS 10.5.1. Redlands, CA: Esri Inc. 2016). Individual elephant movement trajectories were extracted using selection and query tools in ArcMap. Shapiro–Wilk tests showed that the hourly travel speeds recorded before, during and after railway crossings were not normally distributed between March 2016 and March 2019. A non-parametric paired Wilcoxon signed rank test was then performed to test for the differences between the speeds. Variations in crossing speeds between males and females were analysed using Wilcoxon rank sum test, while differences in crossing speeds across individuals were performed using a Kruskal–Wallis test. Statistical analyses and tests were carried out in R 3.6.3 /RStudio (R Core Team, 2020).

2.3.3 | Diel and seasonal railway crossing patterns

Railway crossing times were extracted from segment midpoint times from the downloaded elephant tracking data. The recorded segment

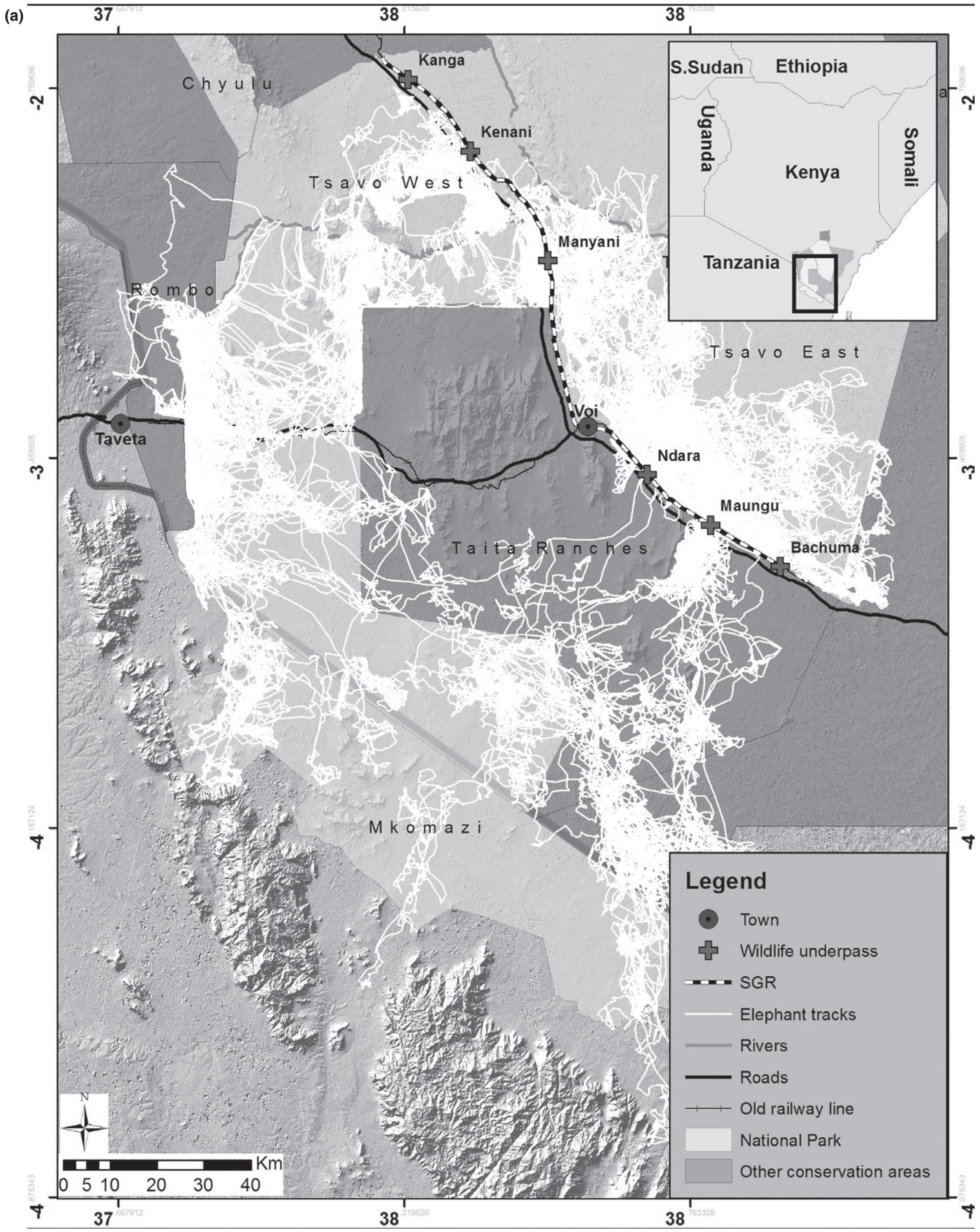

FIGURE 4 (a) Aggregated movements of the ten collared study elephants. Restricted elephant movement is highlighted by the railway, highway and infrastructures such as the National Park's boundary fences on the North of Taita ranches and East of Taveta (erected to mitigate human–wildlife conflicts). (b) Ranging pattern of *Ndara* (M), *Maungu* (F) and *Rukinga* (M) as restricted by the new railway, the Mombasa–Nairobi highway and human settlements. The insert map shows *Maungu* crossing under a culvert by the human settlements, but not crossing the highway. (c) Movement patterns of *Manyani* (F), *Tsavo Bull* (M) *and* Kamboyo (F). *Kamboyo's* movements are restricted by the Mombasa–Nairobi highway, the rhino sanctuary fence line, hills and partly by the Tsavo River; *Manyani* (F) and *Tsavo Bull* (M) ranging patterns are restricted by the new railway and the Mombasa–Nairobi highway. The tracks across all maps show that three animals, *Ndara* (M), *Maungu* and *Kamboyo* (F) did not cross to either sides of the new railway or the highway between March 2016 and March 2019

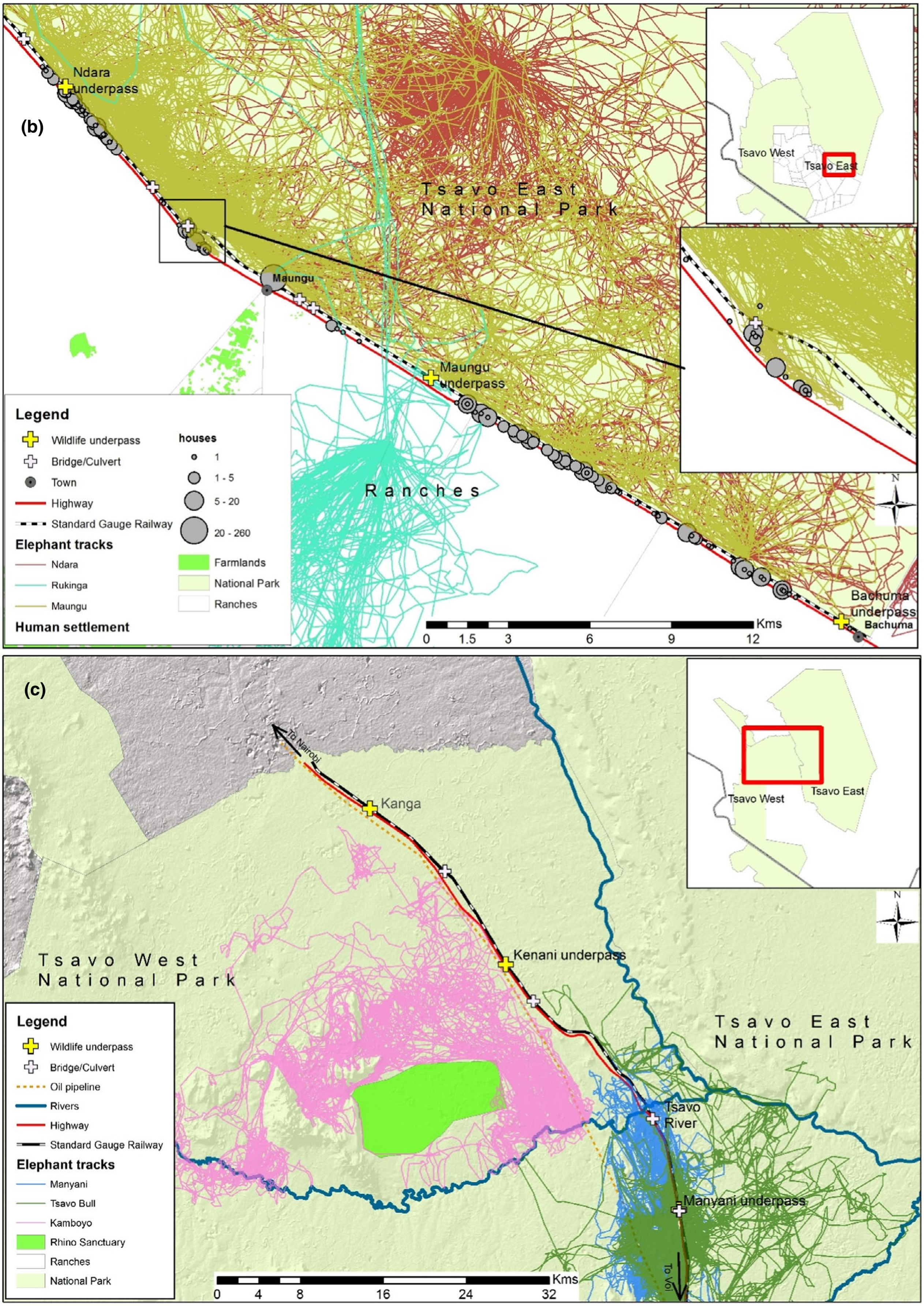

FIGURE 4 (Continued)

time included date, month and year. Specific times when the elephant crossed the railway were computed using VB Script field calculator in ArcMap. We further aligned the time of crossing the railway to sunrise, sunset and zenith. Additionally, we examined possible changes in crossing patterns in relation to large seasonal changes based on long-term rainfall patterns by calculating the frequency of elephant crossings for the dry (January–February and June–September) and wet (October–December and March–May) using the track segment midpoint times. Kruskal–Wallis tests were conducted to examine the differences between dry and wet season crossing times.

3 | RESULTS

3.1 | Elephant railway crossing frequency and movement patterns

During the three-year study period, we collected 176,184 GPS fixes (median = 25,670, range = 2,694–30,357) and recorded a total of 315 uses of the underpasses or culverts by the collared elephants. Eight of the ten collared elephants crossed the new railway using the designated wildlife crossing structures. *Ndara (M)* and *Kamboyo (F)* came within 100 m or less to the railway, but did not cross from Tsavo East NP. Visual observations of their tracks showed that the new railway, the Mombasa–Nairobi highway, human settlements and other hard boundaries seemed to restrict their movements (Figure 4a). *Maungu (F)* crossed the railway several times on the Tsavo East NP side but did not cross the Mombasa–Nairobi highway into Tsavo West NP on the other side of the railway (Table 2).

Elephant railway crossing frequencies were high (36 crossings per month) between March and June 2016, but were dominated by the individual *Kenani* (M) (71%), who crossed mainly in the areas between Kanga, Kenani and Tsavo River Bridge. These crossings occurred when the railway fence and underpasses were still under construction. Unfortunately, *Kenani* was poached on 9 July 2016. This was then followed by a sharp decrease to <2 railway crossings per month between August 2016 and August 2017 and no crossings at all between June 2017 and August 2017. Crossings suddenly increased to 43 times in September 2017, followed by a drop to seven crossings in October 2017. More regular crossings averaging 6 times per month were recorded for 16 months thereafter up to February 2019 (Figure 3).

All 43 crossings made in September 2017 were by *Maungu* (F) and her family group through one crossing structure (the Maungu rail crossing bridge). *Maungu* also approached the Ndara underpass (within 50 m) but did not use it to cross the railway. She made 85 railway crossings at Maungu rail crossing bridge during the study period, but did not cross the Mombasa–Nairobi highway into Tsavo West NP (Figure 4b, inset). The highway also probably confined movement of *Kamboyo* (F) and her family group to Tsavo West NP (Figure 4c) having roamed 19 times within 200 m of it during the study period. *Ndara* (M) came with 200 m of the Maungu Water Bridge 2, during 74 occasions totalling 18 hours, but did not use the underpasses. On numerous occasions, *Manyani* (F), *Taita* (F), *Rukinga* (M) and *Tsavo Bull* (M) paced within 200 m of the new railway and the highway prior to their successful use of the underpasses. *Sagalla* (M) paced within 200 m of the new railway 28 times before using the underpasses and bridges between Ndara and Ngutuni sections.

3.2 | Elephant railway crossing speeds

The 1 hr before, 1 hr during and 1 hr after railway crossing speeds were not normally distributed ($W = 0.83$, df = 943, $p < 0.05$). The median speeds of elephants before, during and after crossing were 0.45 km/hr, 0.65 km/hr and 0.32 km/hr, respectively (Figure 5). Elephant speeds during one hour of crossing were significantly higher than one hour before crossings ($V = 16236$, $Z = -5.3$, $p < 0.025$, one-tailed) and one hour after crossings ($V = 15327$, $Z = -5.8$, $p < 0.025$, one-tailed).

There was significant variation in the elephant railway crossing speeds across individuals and between sexes (Figure 6). Individual median crossing speeds ranged from 0.26 km/hr to 1.36 km/hr with significant difference across individuals ($X^2 = 46.957$, $p < 0.005$, df = 7). Median crossing speeds of females ranged from 0.73 km/hr to 1.36 km/hr while for males it ranged from 0.26 km/hr to 1.19 km/hr (Figure 6). Females crossed significantly faster than males ($W = 13394$, $p < 0.05$).

3.3 | Elephant day and night seasonal railway crossing patterns

Seventy-eight per cent of elephant crossings occurred during the night with the highest frequency between sunset and midnight (Figure 7 and Figure A1) when trains stop running. There was a higher proportion of night time crossings to daytime crossings during the wet season (54.3%), compared to the dry season (24.1%). Crossings during the night in the dry season were relatively evenly spread between sunset and sunrise, compared to night crossing during the wet season, which tended to be peak between sunset and midnight then decreased from midnight to sunrise (Figure 7). These dry and wet seasons diel crossing hours were not significantly different ($X^2 = 0.868$, $p = 0.35$, df = 1). *Maungu* (F) made the highest number (40%) of crossings in the daytime (Figure A2).

4 | DISCUSSION

4.1 | Ecosystem connectivity and railway crossing patterns

During the study, two elephants (*Ndara – (M) & Kamboyo – (F)*) did not use the underpasses, bridges or culverts. *Maungu (F)*, from a family of 16, used one particular underpass but did not cross the Mombasa–Nairobi highway. These elephants represented 30% of the sample size ranging close to the linear infrastructures, but not crossing them into either side

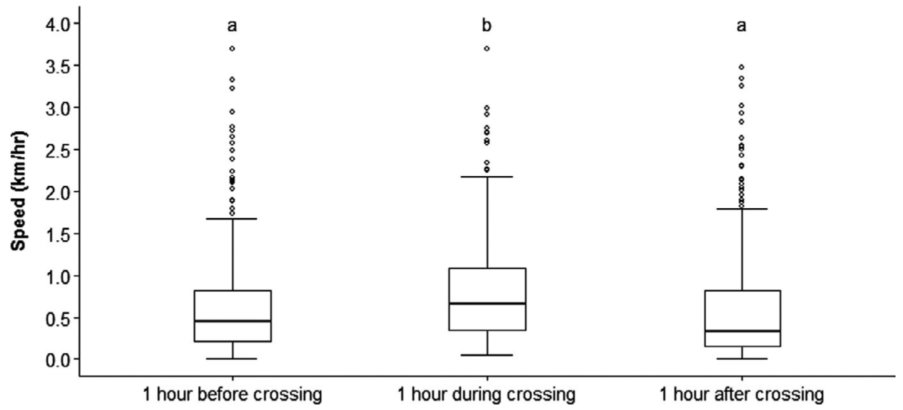

FIGURE 5 Speed distributions of eight elephants crossing the new railway (n = 315) in Tsavo Conservation Area between March 2016 and March 2019. The 'a' and 'b' letters above the box plots indicate differences between speeds. Significantly different speeds ($p < 0.05$) are denoted by different letters whereas speeds that are not significantly different ($p > 0.05$) are denoted by the same letter

of the National Parks. Previous studies have shown that elephants move throughout the entire TCA have large home ranges of >1500 km^2 and are strongly influenced by seasonal variation in water and food distribution (Leuthold & Sale, 1973; Ojwang et al., 2017; Wato et al., 2018). Thus, the highway's traffic volumes and other disturbances from transient human settlements at the railway underpasses may have restricted elephants' use of the underpasses. Anecdotal information also indicates that some elephants in the TCA are reported to never cross the Mombasa–Nairobi highway (A. Mwazo 2020 *Pers. Comm*). This highlights that some elephants will avoid roads completely (Blake et al., 2008; Granados et al., 2012). Elephants made approximately 1:3 railway to highway crossings further supporting our assertion that transient human settlements at the underpasses limited their effectiveness in enabling elephant movements (Koskei et al., 2018; Okita-Ouma et al., 2016, 2017). However, elephants may have crossed the highway more frequently than they crossed the new railway because of possible favourable vegetation structure changes, high food availability or plant available moisture by the roadsides as observed in Malaysia (Wadey et al., 2018).

4.1.1 | Elephant railway crossing frequencies and use of underpasses

Elephant crossing frequency was high between March and June 2016, which was most likely because the railway and fence line was still under construction enabling regular elephant crossings. However, as the railway construction advanced to completion in May 2017, a barrier had been created leaving 10% of the original connectivity points for the animals to use. This also explains the low crossing frequencies between August 2016 and May 2017, and the very few crossings between February 2017 and May 2017, followed by no crossings between May and August 2017. The trains started to run on the 31 May 2017, but before that the construction and noise from the machinery and workmen were at their peak and could have also contributed to those few crossings. This period was followed by a sudden increase in frequency of crossings in September 2017. This then regularised possibly after the animals learnt the locations of the underpasses.

Low elephant crossing frequencies were recorded in December 2018 to January. This coincided with a period of high human–elephant conflict cases in the Sagalla community, which is located approximately 1.5 kilometres from the railway. The number of crop raiding incidents during that period increased compared to previous years (King et al., 2017) leading to uproars by the affected communities (KNA, 2018; Mkanyika, 2016). Over 500 elephants in Sagalla community ranches including *Sagalla* (M), a known crop raider, were blocked by the railway's fence from accessing Tsavo East National Park (K. Hellyer 2020 *Pers. Comm*).

It took 3 to 4 months (i.e. in August/September 2017) after the new railway construction was completed for the collared elephants to start making regular use of the underpasses and bridges. This is a relatively positive result, as in China, it took the Tibetan antelope (*Pantholops hodgsonii*) more than 10 years to learn where the underpass locations of the Qinghai–Tibet railway were (Ruan et al., 2005; Xia et al., 2007). This fast learning is indictive of elephant's high intelligence and has also been documented in Mount Kenya where elephants began to use the underpass on the Nanyuki–Isiolo road within two weeks after its construction (G. Chege 2020, *Pers. Comm*). The longer learning time in our study can be attributed to the wide distances between the bridges and the time it took to construct the railway.

4.2 | Increase in elephant speeds at railway crossing

The elephants increased their speeds when using the underpasses and bridges then slowed down to normal speeds after crossing. The fastest female and male median crossing speeds of 1.36 km/hr and 1.19 km/hr, respectively, were similar to the 1.1 km/hr speeds observed by Douglas-Hamilton et al. (2005) of elephants moving in strip-like corridor areas outside protected 'safe' areas. The median crossing speed (0.65 km/hr) of all the elephants was similar to the 0.7 km/hr speed of elephants moving in risky landscapes (Ihwagi, 2019; Ihwagi et al., 2018). The median speeds before (0.45 km/hr) and after crossing (0.32 km/hr) were similar to elephant speeds recorded in other areas with little human disturbances (Douglas-Hamilton et al., 2005; Ihwagi et al., 2018; Wall et al., 2013). These increases in speeds during crossing followed by normal walking speeds are expressions of risk avoidance behaviours, as observed in other wildlife species crossing railways or roads (Barrientos et al., 2019).

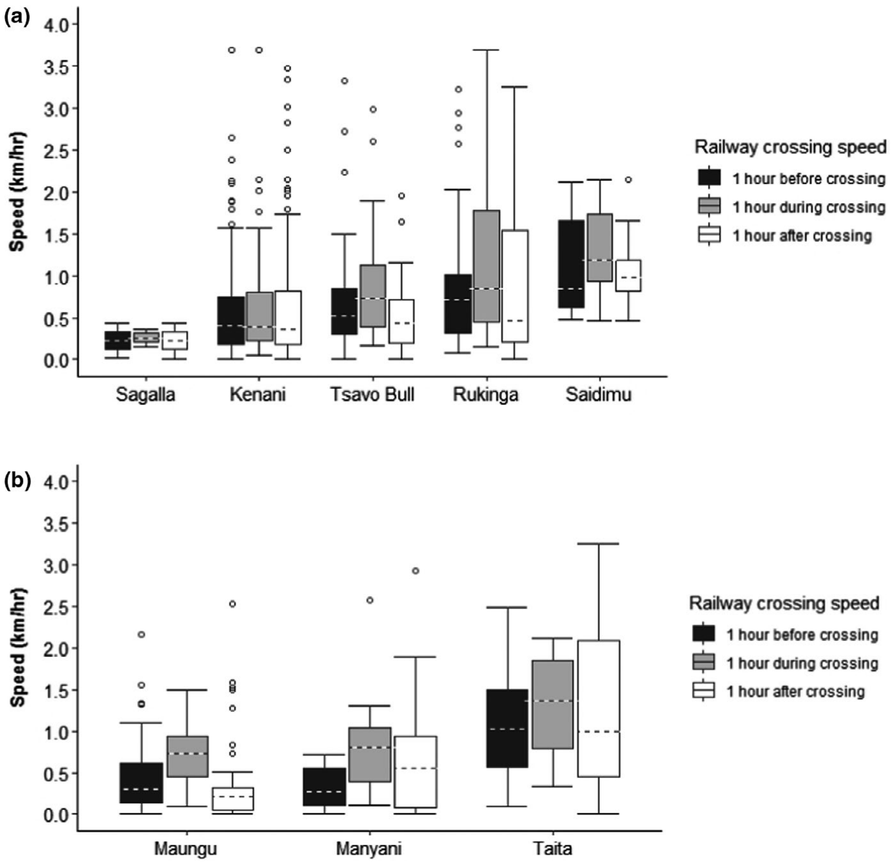

FIGURE 6 Individual speeds of (a) five male elephants and (b) three female elephants before, during and after crossing the new railway between March 2016 and March 2019, Tsavo Conservation Area

Thus, elephants may perceive the underpasses and bridges as risky areas, but they have to use them to access vital resources.

Our results showed that female elephants travelled at faster speeds when crossing the railway compared to males. Females invest heavily in their offspring and are protective of family members. Thus, the railway is more of a perceived risk for females, and there is more of a need to cross the railway as quickly as possible to ensure safety to all the family members compared to males. The propensity of risk-taking in males has been attributed to higher variance in reproductive success, which has led to selection pressures favouring risky strategies (Chiyo et al., 2011; King et al., 2017). For example, crop raiding is risky as it can easily lead to injury or death but the reward of crop raiding is highly nutritious food, which can lead to gains in body size and mating success (Chiyo et al., 2011). However, this perception of risk does not account for an animals willingness to cross, physiological cost or reduction in survival (Stevens et al., 2006; Zeller et al., 2012). Also, the movement paths between 60-min GPS satellite fixes in our study were unknown and therefore had to be inferred. Our diel underpass uses supported our speed results.

4.3 | Elephant diel and seasonal railway crossing patterns

We found that the elephants used the underpasses predominately at night, which indicates another risk avoidance strategy, as elephants are largely active during day time hours. Travelling more frequently at night has also been observed in areas of high poaching (Ihwagi et al., 2018). One exception to the results was the elephant called *Maungu*, who used one particular underpass during the day. This may have been due to the safety in numbers theory as she travelled in a large family group (3–40 individuals). *Maungu* used a wildlife underpass with increasing transient human settlements between it and the highway. This may gradually completely block the underpass from wildlife use if not managed quickly. Thus, it will be important to monitor any change in *Maungu's* underpass utilisation strategy in the future.

There were no significant differences in seasonal crossings, or in day and night crossings in the dry or wet season. However, the equal spread of night crossings during the dry season could be because the animals have to balance the search for scarce food/water resources to meet their energy demands, while avoiding hot ambient temperatures and risks by the underpasses. In the wet seasons, food/water resources and ambient temperatures are favourable. Therefore, nighttime crossings are due to risk avoidance rather than for the search of food or keeping cool. This also may explain the slight skew of wet season crossings towards the early part of the night (sunset to midnight), whereas the dry season crossings were evenly spread throughout the night (sunset to sunrise). When human activities are low, animals may alter their diel and seasonal movements to maximise habitat utilisation, as observed in black bears (*Ursus americanus*) (Zeller et al., 2019).

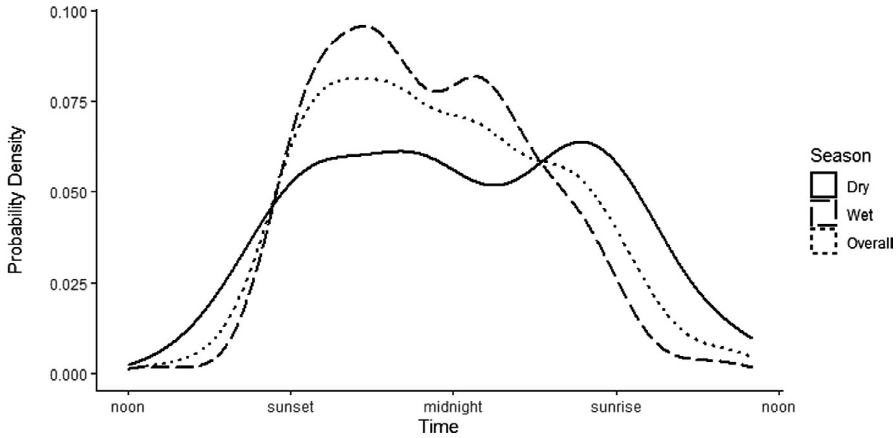

FIGURE 7 Day and night patterns (n = 315) as probability density functions, of the new railway crossings by eight satellite-collared elephants (and their families) between March 2016 and March 2019, Tsavo Conservation Area

4.4 | Policy implications

Transportation networks are key for connectivity in today's economy and society. However, infrastructure comes at a cost to wildlife and the environment. We are faced with the challenge of balancing the needs of development with conservation. Trying to find a compromise requires systematic research and partnerships between conservationists and linear infrastructure developers. Our results lend support to the TCA Management Plan, which emphasises stricter limits on human development and more effective methods of managing and limiting human use within the National Parks (KWS, 2008). A progressive retrofit of wildlife crossing structures, speed bumps, warning signs of wildlife crossings along the highway; management of the illegal human settlements along the rail and road wayleaves; and inter-agency partnerships are requisites for enhancing the effectiveness of the underpasses and sustaining ecosystem connectivity.

5 | CONCLUSION

This novel study is the first to investigate the effectiveness of wildlife underpasses in connecting elephant habitats in Africa. Understanding the complex use of an animal's range is crucial for infrastructure planning and sustainable development. Thirty per cent of the studied elephants did not cross the railway despite moving close to the underpasses and bridges. Crossing the railway underpasses was clearly a risk for the elephants, as documented by the faster speeds crossing the underpasses and their nocturnal crossing patterns. There must be a gain including accessing vital resources for them to take the risk. We isolate the risks to be the transient disturbances from the high daytime traffic volume and speeds along Mombasa–Nairobi highway, the human settlements by the underpasses and from the construction workers and their machinery in the initial phases of construction.

The limitations of our study stem from the lack of data prior to the construction of the railway and accounting for other forms of ongoing disturbances in the vicinity, such as increasing settlements and traffic volume and speeds. We therefore recommend future research to collect such data and investigate the immediate and long-term ecological implications of such barriers to the elephant in the TCA. These could include implications on population dynamics, migration and home-range patterns, access to food and water sources (Ito et al., 2013; Olson & van der Ree, 2015; Ruan et al., 2005), gene flow (Yu et al., 2017), bottlenecks in life-history adaptation on calf survival (Bolger et al., 2008), deterioration in animal health (*See* review in Iosif (2012) and Rautsaw et al. (2018) and human–wildlife co-existence strategies.

Our findings present an opportunity to learn to design and develop a country while keeping its national heritage intact. Partnerships between conservationists and infrastructure developers are requisites for future developments in conservation areas. We must not lose this chance to influence how such development and conservation can work together.

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CONFLICT OF INTEREST

The authors declare no conflict of interest in relation to this work.

AUTHORS' CONTRIBUTIONS

BO-O, LK and ID-H initially thought of the idea to monitor the effects of the railway on the movements of elephants. BO-O, ID-H and LK designed the collaring methods and coordinated the collaring work with FL and RM. MK curated the monitoring data from Save the Elephants tracking system, produced the graphs, maps and undertook statistical analyses in consultation with RA and LT. BO-O led the writing of the manuscript with contributions from MK, RA and LT. ID-H provided useful guidance and input alongside those of LK, RM and FL. All authors have read and approved the final version of the manuscript.

DISCLAIMER

Findings, opinions conclusion and recommendation expressed in this material are those of the author(s) and the funding agencies do not accept any liability in this regard.

DATA AVAILABILITY STATEMENT

All data used in this research are available on request from Save the Elephants. Data especially on individual locations may be shared only by the permission from the Kenya Wildlife Service due to the sensitivity surrounding conservation of such information.

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APPENDIX 1

Times of crossing the new railway between March 2016 and March 2019 by individual elephants in the Tsavo Conservation Area.

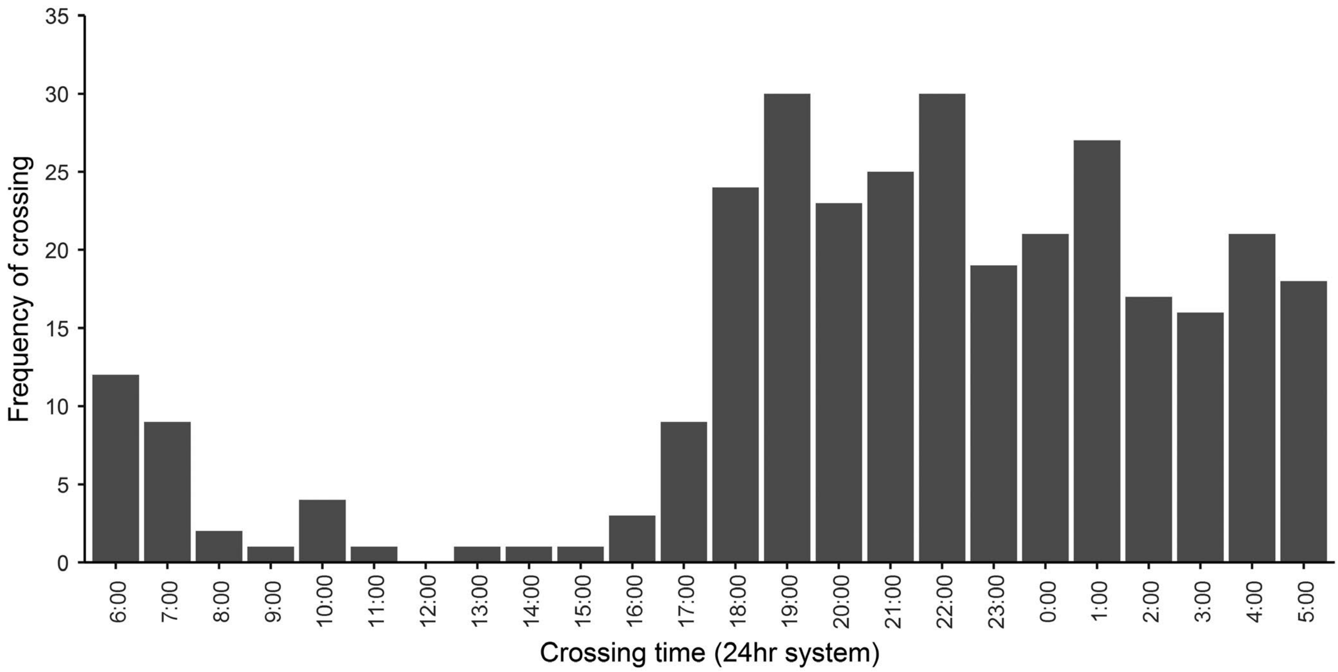

Figure A1 Day and night crossing frequency (n = 315) of the new railway by eight elephants and their families between March 2016 and March 2019 in the Tsavo Conservation Area

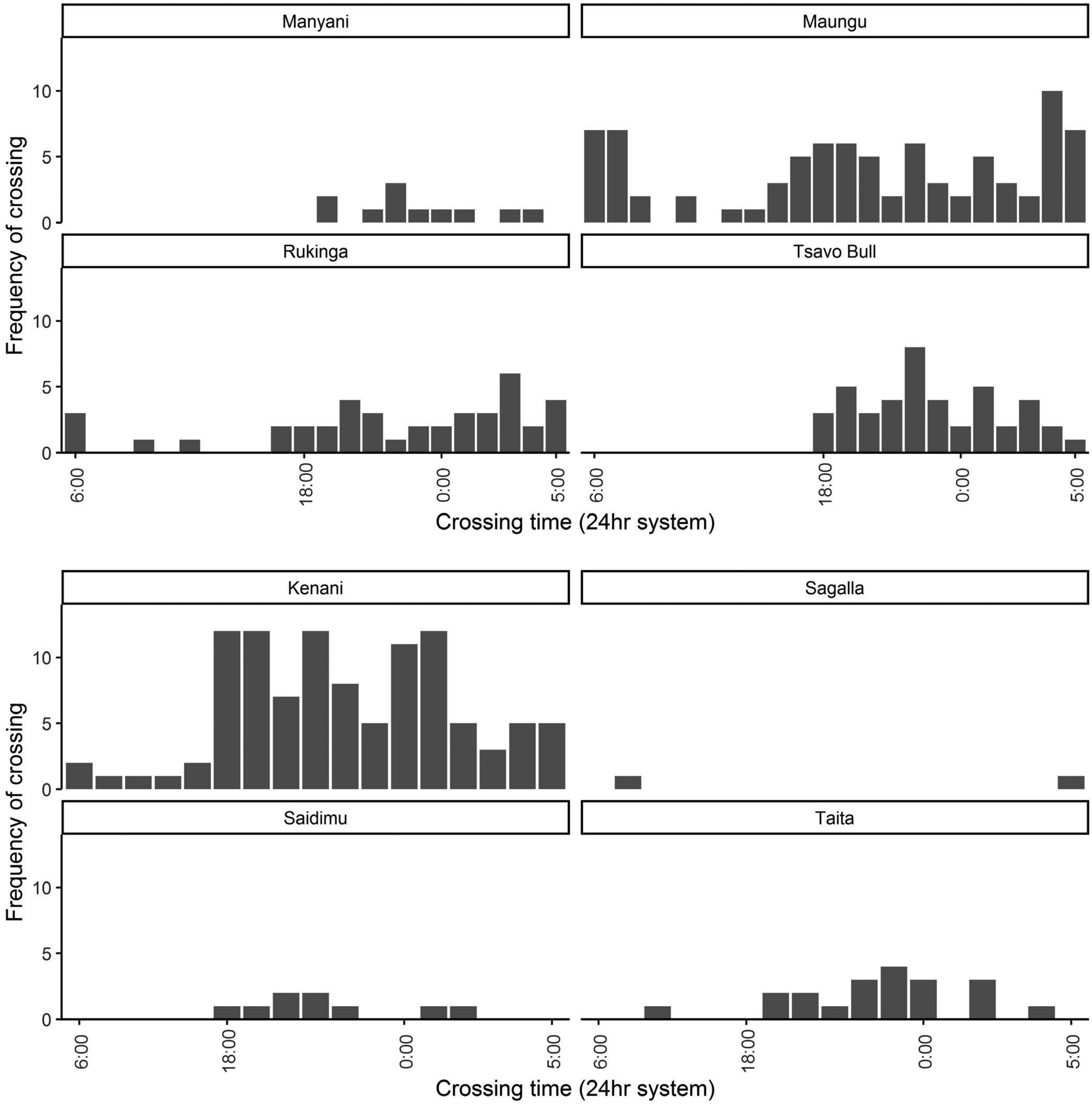

Figure A2 Crossing times of the new Mombasa-Nairobi standard gauge railway between March 2016 and March 2019 by eight individual elephants and their families