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Do wildlife corridors link or extend habitat? Insights from elephant use of a Kenyan wildlife corridor

Siân E. Green[1,2] | **Zeke Davidson**[2] | **Timothy Kaaria**[3] | **C. Patrick Doncaster**[1]

[1]Biological Sciences, University of Southampton, Southampton, UK

[2]Marwell Wildlife, Colden Common, Winchester, UK

[3]Lewa Wildlife Conservancy, Isiolo, Kenya

Correspondence
Siân E. Green, Beer Mill, Clawton, Devon, EX22 6PF, UK.
Email: sian.green92@outlook.com

Abstract

Human encroachment on wildlife habitats is leading to increased fragmentation; hence, there is an increasing focus on improving connectivity between remaining habitat. Large, wide-ranging species such as the African elephant, (*Loxodonta africana*), are particularly vulnerable due to their extensive habitat requirements. Wildlife corridors have been created to facilitate movement, with little knowledge to date on whether they serve their intended function as transit routes, or whether they simply extend the available habitat for occupancy. We collected data on elephant behaviour in the Mount Kenya Elephant Corridor, with the aim of quantifying the utility of the corridor. A grid of 25 camera traps was used to survey the 478 ha corridor over 11 weeks. Cameras recorded over 43,000 photos with 694 separate events triggered by elephants. Patterns of use varied spatially and temporally, indicating that certain areas were treated as habitat extension, while others were predominantly for transit. These differences were likely due to variation in vegetation cover and levels of human disturbance. Corridor use differed amongst individuals, suggesting that use may depend on both the characteristics of the corridor itself and the social or resource needs of individual elephants.

Résumé

L'envahissement des habitats naturels par les hommes entraîne un accroissement de la fragmentation, et l'on s'intéresse de plus en plus à l'amélioration de la connectivité entre les habitats restants. Des espèces de grande taille, qui font de grands déplacements, comme les éléphants *Loxodonta africana* sont particulièrement vulnérables parce qu'elles ont besoin de grands espaces. Des corridors ont donc été créés pour faciliter les déplacements, sans que l'on sache bien, jusqu'à présent, s'ils remplissent bien leur fonction de voies de transit ou s'ils agrandissent simplement l'habitat disponible. Nous avons récolté des données sur le comportement des éléphants dans le Corridor des éléphants du mont Kenya, afin de quantifier l'utilité de ce corridor. Un réseau de 25 pièges photographiques a permis de surveiller les 478 ha de ce corridor pendant 11 semaines. Les appareils ont enregistré plus de 43,000 photos et 694 événements différents ont été déclenchés par des éléphants. Les schémas d'utilisation variaient dans l'espace et le temps, ce qui veut dire que certains endroits étaient considérés comme une extension de l'habitat alors que d'autres servaient surtout au passage. Ces différences étaient probablement dues à des variations du couvert végétal et au niveau de perturbations humaines. La fréquentation du corridor différait selon les individus, ce qui suggère que l'utilisation peut dépendre des caractéristiques du corridor lui-même et des besoins sociaux ou de ressources de chaque individu.

KEYWORDS

African elephants, camera trapping, connectivity, corridor

1 | INTRODUCTION

Current species extinction rates far exceed the natural background rate (Ceballos et al., 2015), with a major driver for this being habitat loss. Habitat loss can be further compounded by isolation and fragmentation of remaining habitat (Crooks, Burdett, Theobald, Rondinini, & Boitani, 2011) and simply protecting habitat is not proving adequate to cope with ongoing biodiversity loss (Mora & Sale, 2011). There is now strong evidence that habitat fragmentation and lower dispersal ability can contribute substantially to extinction risk (Crooks et al., 2011; Flather & Bevers, 2002; Thomas et al., 2004).

Wildlife corridors vary greatly in structure, ranging from hedgerows to tracts of riparian forest and can increase movement, and thus promote connectivity, between sites for a range of taxa including birds (Castellón & Sieving, 2006; Lees & Peres, 2008), butterflies (Haddad & Tewksbury, 2005; Haddad et al., 2003) and mammals (Dixon et al., 2006; Gilbert-Norton, Wilson, Stevens, & Beard, 2010; Mech & Hallett, 2001). Corridors facilitate gene flow between populations, thereby increasing population persistence and reducing inbreeding (Dixon et al., 2006; Mech & Hallett, 2001) and can provide the further benefit of additional habitat, and thus resources (Bennett, 2003). Increased gene flow can have negative consequences, such as outbreeding, reduced local adaptation and decreased fitness (Lebas, 2002). Increased connectivity could increase potential for disease transmission (Hess, 1996) and narrow passage structures may act as prey traps. Corridors may serve other functions than those for which they were created, such as occupancy rather than transit. Use can depend on characteristics such as length and width of a corridor, with wider corridors being occupied more heavily (Brodie et al., 2014; Hilty & Merenlender, 2004). In some instances there may be some discrepancy between corridor “use” and “function” where the corridor itself is utilized as additional habitat with no corresponding increase in connectivity between populations (Horskins, Mather, & Wilson, 2006).

Despite these concerns, improving connectivity may be crucial to conservation efforts, particularly for wide ranging and migratory species such as the African elephant (*Loxodonta africana).* Their requirements for water and sufficient forage means they may travel great distances to access resources (Ngene et al., 2010; Shannon, Page, Slotow, & Duffy, 2006; Wall, Wittemyer, Klinkenberg, LeMay, & Douglas-Hamilton, 2013). A restricted or homogenous habitat is unlikely to provide for their seasonally changing needs. Elephant numbers have suffered significant declines over the last 100 years, although populations and ranges are now starting to increase in parts of East Africa (Litoroh, Omondi, Kock, & Amin, 2012; Ngene et al., 2013). This expansion is hindered by a growing human population. Elephants are sensitive to anthropogenic disturbance, making them susceptible to human activity blocking traditional routes (Epps, Wasser, Keim, Mutayoba, & Brashares, 2013; Graham, Douglas-Hamilton, Adams, & Lee, 2009; Kioko et al., 2015). Where humans and elephants do interact, it can lead to conflicts such as crop raiding and retaliatory killings (Gadd, 2005; Mackenzie & Ahabyona, 2012; Thouless, 1994).

Wildlife corridors can help to alleviate conflict, while increasing connectivity, by directing animals through designated safe passage routes. In Kenya, East Africa, conservation targets now include creation of new corridors (Litoroh et al., 2012). The Mount Kenya Elephant Corridor (MKEC) was constructed to link protected areas of the mountain to historic dispersal areas in Laikipia and Samburu, via private and community conservancy land. Mt Kenya National Park and Reserve is home to approximately 3,700 elephants while the Samburu/Laikipia ecosystem hosts an additional 7,400 elephants (Litoroh et al., 2012). Prior to the creation of this corridor, the Mount Kenya population had been functionally isolated by agriculture and peri-urban development surrounding the base of the mountain. Only a few individuals regularly traversed the slopes between these habitats. The damage to agriculture caused by their passage was the main impetus behind the implementation of the corridor.

While elephants have regularly been recorded using the MKEC, not all those entering the corridor traverse its entire length, with some returning to the same end which they entered and many taking longer than necessary simply for transit (N. Winmill, unpublished data, 2014). A better understanding of behaviour is needed if corridors are to serve a valuable purpose (Lapoint, Gallery, Wikelski, & Kays, 2013). We know of no studies to date that have sought to quantify corridor function for elephants from empirical data.

Data from radio and GPS collars are often used to study movement, yet such data can result in underestimation of travel distance, particularly when obtained with low sampling frequencies (Rowcliffe, Carbone, Kays, Kranstauber, & Jansen, 2012). Here we describe a study using camera traps set at 500 m intervals throughout the MKEC to monitor its use by elephants. Elephants have been found to move through corridor zones at speeds of ~1 km/h (Douglas-Hamilton, Krink, & Vollrath, 2005) meaning they could pass from one study camera to the next in ~30 min. The cameras therefore have potential to record elephant locations at greater frequencies than many collars (Douglas-Hamilton et al., 2005; Graham, Douglas-Hamilton, et al., 2009; Shannon, Page, Duffy, & Slotow, 2010). Use of cameras also meant all members of the population using the corridor had the potential to be captured. Our aim was to quantify the utility of the corridor itself and determine whether it was primarily used as an access route or as home range. By modelling detection of elephants within the corridor and examining movements of identified individuals from sequential camera trap photos, we were able to obtain detailed data on elephant behaviour within this corridor relevant to evaluating its primary function.

2 | METHODS

2.1 | Study site

All data were collected within the fully fenced Mount Kenya Elephant Corridor (WGS 84 UTM 37N 330146, 11749), situated on the northern slope of the mountain. The 14-km-long corridor traverses elevations of approximately 2,000 m in the North up to 2,700 m in the South, and connects the Mount Kenya National Park and Reserve (MKNP 212,400 ha) to the Ngare Ndare Forest Reserve (NNFR 5,540 ha). Corridor width varies from just over 1 km down to 7 m at a concrete underpass. This underpass allows elephants to safely pass beneath the Nanyuki—Meru A2 highway, which is the larger of two public roads bisecting the corridor. There are plans for a second underpass to be built at the smaller, unpaved D481. Other than this, the narrowest point of the corridor is 27 m, and average corridor width is approximately 400 m.

Small scale farms line the eastern boundary of the corridor. Commercial wheat farms extend similarly along the western boundary. Elephants must traverse a small portion of Kenya Forestry Service (KFS) land before entering the contiguous MKNP. The Ngare Ndare is an area of indigenous forest openly connected to the 25,090 ha Lewa Wildlife and Borana Conservancies. Elephants can move between these private conservancies and the northern rangelands through wildlife fence gaps in their perimeters.

The southern part of corridor is dominated by open grassland (*Pennisetum strontium*) where cattle are regularly grazed during the day but removed at night. The northern half is mixed native bushland and forest, with some small patches of commercially planted bluegum trees (*Eucalyptus globulus*). A non-perennial river runs through the corridor from South to North. The corridor is managed by a joint team involving Marania and Kisima commercial farms, KFS and Lewa Wildlife Conservancy and led by the Mount Kenya Trust.

2.2 | Data collection

Twenty-five Bushnell HD™ camera traps were set out in a 500 m^2 grid design, on recognizable elephant trails. Cameras were programmed to take three photos per trigger and were in place between 22 February and 6 May 2016. One camera was moved during the study due to modification of the corridor fence line. Three further cameras were moved due to excessive false triggers. Where cameras were moved during the course of the study only data from the second location was used for occupancy analysis, as this was where vegetation and GIS data were collected from. Images were entered into a database designed to work with the Zoological Society of London's data organization package, the Camera Trap Analysis Tool (CTAT) (Davey, Wacher, & Amin, 2015). Species present in the image were identified and recorded, and time and date of each image were extracted using EXIFextractor (BR Software, 2016). Livestock, vehicles and other human presence captured by the cameras were recorded and used as indicators of disturbance. For all species and disturbances an image was defined as a new capture event if it occurred after a 30-min interlude from previous photos; this was to avoid single camera crossings being counted as multiple events. Elephant images were split into diurnal and nocturnal occurrences. Images were recorded as diurnal if they were taken after 06:06 and before 19:12 as these were the earliest and latest times when the sun was less than 6 degrees below the horizon (Time and Date, 2016). Elephants were identified as male or female, and to individual where possible. Where females could not be identified to individual level, it was often still possible to identify them to family group level. Family groups consisted of adult females with offspring and juvenile males.

Vegetation assessments were made at 23 of the 25 camera trap sites, as two sites were inaccessible. At the remaining sites, a 100-m transect was walked and, at ten random points per transect, the point-centred quarter method was used to assess tree density (Mitchell, 2007). Within each quarter, distance to nearest tree, within a 10-m radius, and elephant damage to that tree were recorded. Absolute density of trees was calculated following methods described by Mitchell (2007). Due to truncated sampling, some quarters were empty so a correction factor was used following Warde and Petranka (1981). GIS analysis with ArcMap 10.3.1. (ESRI, 2015) was used to measure the straight-line distance from roads and the straight-line corridor width at each camera site. SRTM (Shuttle Radar Topography Mission) digital elevation data at a 90-m resolution was downloaded freely from The CGIAR (Consultative Group on International Agricultural Research) Consortium for Spatial Information (Jarvis, Reuter, Nelson, & Guevara, 2008) and was then used to calculate inclination of slope in degrees using ArcMap. These variables were then employed as predictors to determine which factors most influenced detection of elephants.

Time taken for identified elephants to move between cameras was used to indicate speed of progress through the corridor. Straight-line distances were calculated between each camera trap on ArcMap, representing the minimum distance travelled between each camera. The distance between cameras was then divided by time taken between photo recaptures to give an estimate of speed of travel between the two sites. These distances and the times between subsequent trapping incidences for identified individuals were used to calculate speeds of movement through different parts of the corridor. For bull elephants, time taken between recapture incidences was calculated from the time of last photo at a camera site to time of first photo at the subsequent camera. On some occasions, there was a considerable time lapse between first and last members of a family group passing a camera. In order to avoid overestimating the speed of individuals, time taken between capture incidents for family groups was calculated from the time of the first photo of a capture event to the time of the first photo of the subsequent capture event. Speeds were used to provide further insight into corridor use, with fast speeds indicating transit as the primary use, and slower speeds indicating use as habitat extension.

The collated vegetation data, site descriptions and photographs taken in the field indicated that the corridor could be split into three sections, defined by general classes of vegetation cover: (i) open grassland and (ii) narrow (corridor width <500 m) mixed forest bushland and 3) wide (corridor width >500 m) mixed forest bushland.

2.3 | Data analysis

All analyses were performed in R, version 3.4.2 (R Core Team, 2017).

Initial observations showed cattle presence during the day to be a regular form of disturbance at particular sites. To test whether this regime might be causing any temporal avoidance, sites were divided into two categories: cattle present during the day and cattle absent. Numbers of events during the night and during the day were then compared for these two categories using a Pearson's chi-squared test.

Presence-absence matrices were generated using CTAT, recording detection or non-detection within each 24-hr survey period. One-species single-season occupancy models run using the R package "unmarked" (Fiske & Chandler, 2011) were used to determine the influence of environmental variables on detection, as an indicator of frequency of site use by elephants (Mackenzie et al., 2002). Our analysis of the response by elephants to environmental influences was limited to detection due to lack of spatial variation in site occupancy, as all sites were visited at some time during the course of the study (Figure 1). Width of corridor, density of trees, distance to the nearest road, slope of ground and disturbance were modelled in various combinations as predictors to determine which factors influenced detection of elephants. Occupancy analysis included only camera-trapping sites with data on all variables (n = 23 sites). Models were ranked according to AIC values, where there was uncertainty over the best model, model averaging was used and parameter estimates are given based on averaging of models with ΔAIC < 2.

Journey speeds were calculated for three easily recognizable adult bulls, and for all identified family groups. Journeys were recorded as separate events when an individual or group was believed to have left and re-entered the corridor on the basis of detections near the corridor entrance or exit following or preceding a 24-hr period of non-detection. For each journey, average speeds were calculated for movements within each of the vegetation classes. A repeated-measures ANOVA with vegetation class as a fixed factor and elephant ID as a random factor tested for differences in average speed amongst these classes. Analysis was performed on square-root transformed data in order to improve homogeneity of variances.

Elephant trapping rates were calculated as the number of independent photo capture events at a site divided by the number of active camera trapping days. Proportion of trees showing elephant damage was arcsine-root transformed for analysis and regression was used to test for a relationship between damage and trapping rate. Sites with no trees were excluded from analysis.

3 | RESULTS

Throughout the study there was a combined 1,588 successful trapping days. Over 43,400 photographs were analysed, which included 2,070 trapping events triggered by one or more of 22 identified mammal species and 1,379 disturbance events (435 from vehicle activity, 238 from livestock and 706 from human activities other than camera services). Elephants were captured in 694 events, of which 444 occurred at night and 250 in daylight. In 562 events, elephants were identified either as adult bulls (457 events) or as members of family groups (105 events). Images from remaining events were insufficiently clear to confidently assign a gender.

It was possible to clearly distinguish two family groups using the corridor. One of these, the "Liqueurs" a known resident family on Lewa Wildlife Conservancy (LWC) (S. Rouse, unpublished data), was recorded only in the northern part of the corridor and did not pass through the open grassland area in the south. The other group was unfamiliar, and was detected entering the corridor from the south and traversed its full length. This group has not previously been recorded in LWC (S. Rouse, unpublished data).

Relative frequencies of diurnal and nocturnal events differed between sites with and without cattle disturbance ($X^2 = 84.89$, $df = 1$, $p < 0.001$). At sites where cattle were present, a higher proportion of capture events occurred during the night. Where cattle were absent similar proportions of capture events occurred during the night and day (Table 1).

All camera traps detected elephants. One camera detected only diurnal activity and one only nocturnal, all other cameras detected elephants both nocturnally and diurnally (Figure 1). As there was a difference in nocturnal versus diurnal use patterns (Table 1) separate models were run based on detections during the day and during the night within each 24-hr survey period. The highest ranking diurnal model had reasonable support, with no other model coming within Δ AIC < 2 (Table 2, Appendix). Model output on logit scale gives an occupancy estimate of 3.09 (±1.03 SE), which when back-transformed indicates a 0.957 probability for site occupancy. Detection was negatively influenced by disturbance, corridor width, slope of ground and tree density (Table 3). There was more uncertainty as to the best nocturnal model, with the top three models all within Δ AIC < 2, (Table 2). Model average outputs shows an occupancy estimate of 3.19 (±1.13 SE) which equates to a 0.96 probability for site occupancy. Detection patterns at night differed slightly to during the day (Figure 1) and distance to nearest road had more of an influence, with more detections at closer distances to the road. Disturbance had a smaller effect, and slope had no influence on nocturnal detection (Table 3).

Elephants travelled at different speeds in different areas of the corridor ($F_{2,7} = 13.19$, $p < 0.01$, Figure 2). Speeds were fastest

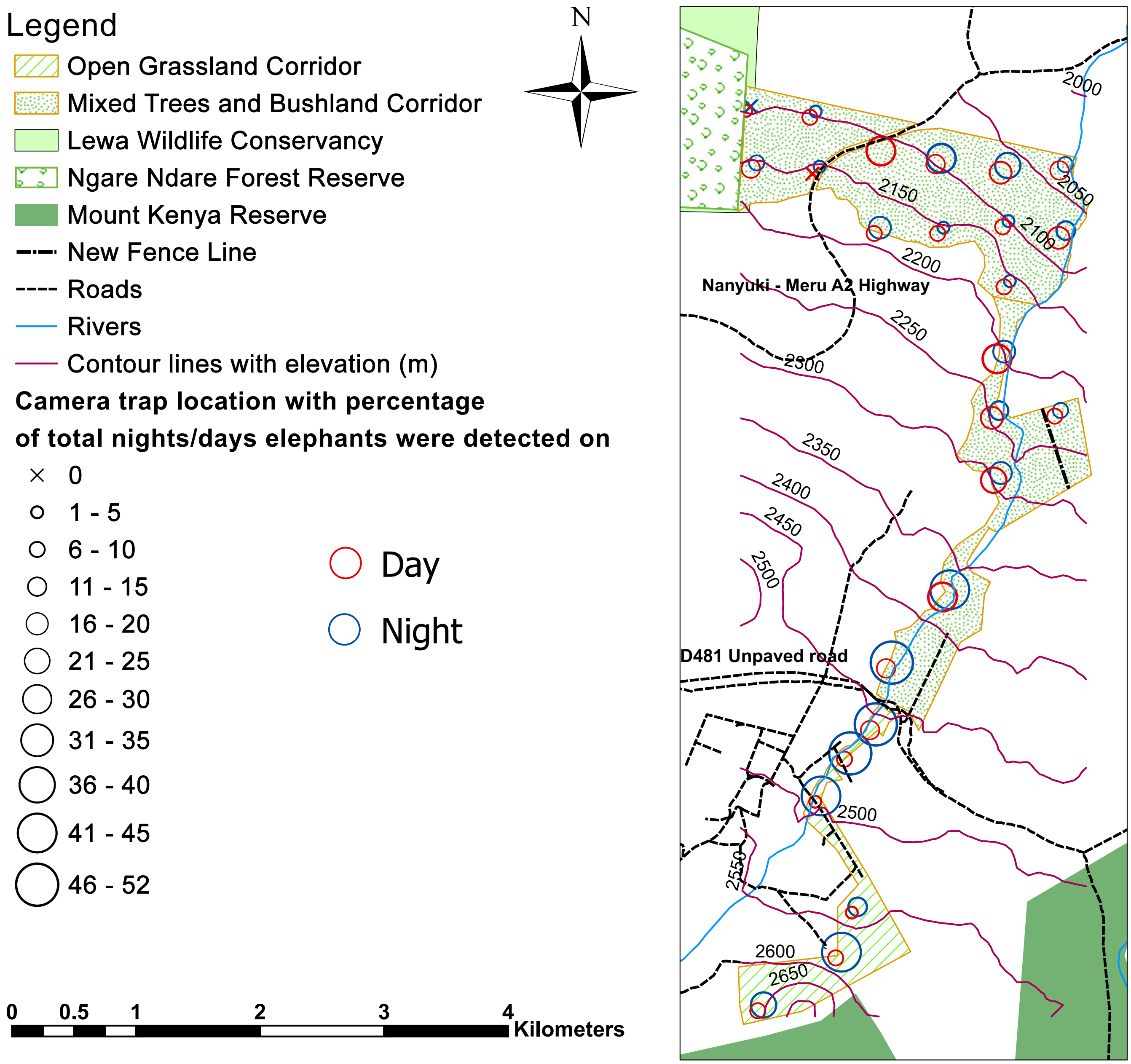

FIGURE 1 Position of camera traps within the Mount Kenya Elephant Corridor, Meru County, Kenya, showing the percentage of active trapping days and trapping nights during which elephants were detected [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Number of trapping events and proportion of nocturnal and diurnal elephant capture events that occurred at sites with and without cattle regularly present

	Cattle present		Cattle absent	
Time	Trapping events	Proportion	Trapping events	Proportion
Day	33	0.13	217	0.49
Night	215	0.87	229	0.51

through vegetation class one (mean = 1.38 km/h ± 0.31 SE), intermediate through class two (mean = 0.94 km/h ± 0.16 SE) and slowest through class three (mean = 0.49 km/h ± 0.12 SE). Individuals also varied in speed ($F_{4,7} = 16.84$, $p < 0.01$). Average speed of family groups was higher (mean = 1.24 km/h ± 0.24 SE) than for adult bulls (mean = 0.65 km/h ± 0.10 SE). The highest speed calculated was 4.26 km/h, for a family group travelling through vegetation class one. The lowest speed was 0.03 km/h for an adult bull travelling through vegetation class three. Average slope was steeper within classes three (mean = 7.47° ± 0.73 SE) and two (mean = 8.42° ± 1.25 SE) than within class one (mean = 5.15° ± 0.93 SE). Range of slope values was greater within class three (max = 14.37°, min = 3.96°) than classes two (max = 12.40°, min = 5.33°) and one (max = 8.65°, min = 3.72°).

TABLE 2 Model selection results for covariate effects on detectability. Top five models and the global model are given for each of diurnal and nocturnal data sets

	Model	AIC	Δ AIC	AIC weight	Cumulative AIC weight
Diurnal models	Width + Tree*Disturbance + Slope	1046.59	0.00	0.59	0.59
	Width + Road + Tree*Disturbance + Slope	1048.58	2.00	0.22	0.81
	Width + Tree*Disturbance	1049.77	3.18	0.12	0.93
	Width + Road + Tree*Disturbance	1050.91	4.32	0.068	0.99
	Width + Tree + Disturbance + Slope	1058.38	11.79	0.002	1.00
	Null Model	1081.44	34.85	<0.001	1.00
Nocturnal models	Width + Road + Tree + Disturbance	1302.48	0.00	0.48	0.48
	Width + Road + Tree*Disturbance	1304.24	1.76	0.2	0.69
	Width + Road + Tree + Disturbance + Slope	1304.34	1.86	0.19	0.88
	Width + Road + Tree	1306.02	3.53	0.083	0.96
	Width + Road + Tree + Slope	1307.44	4.96	0.041	1.00
	Null Model	1461.41	158.93	<0.001	1.00

TABLE 3 Covariate effects on detection probability based on model averaging of models with $\Delta AIC < 2$

Covariate	Estimate	*SE*	*Z*	*p*
Diurnal				
Intercept	0.204	0.515	0.0396	0.692
Corridor Width	−1.331	0.326	−4.08	<0.001
Disturbance	−1.062	0.21	−5.06	<0.001
Slope	−0.106	0.048	−2.2	0.028
Tree density	−0.061	0.017	−3.62	<0.001
Tree density : Disturbance	0.129	0.034	3.82	<0.001
Nocturnal				
Intercept	0.783	0.273	2.865	0.004
Corridor Width	−1.974	0.316	6.24	<0.001
Distance to nearest road	1.602	0.235	6.81	<0.001
Disturbance	−0.286	0.127	2.25	0.025
Slope	−0.0004	0.007	0.06	0.956
Tree density	−0.067	0.016	4.11	<0.001
Tree density:Disturbance	0.002	0.013	0.17	0.869

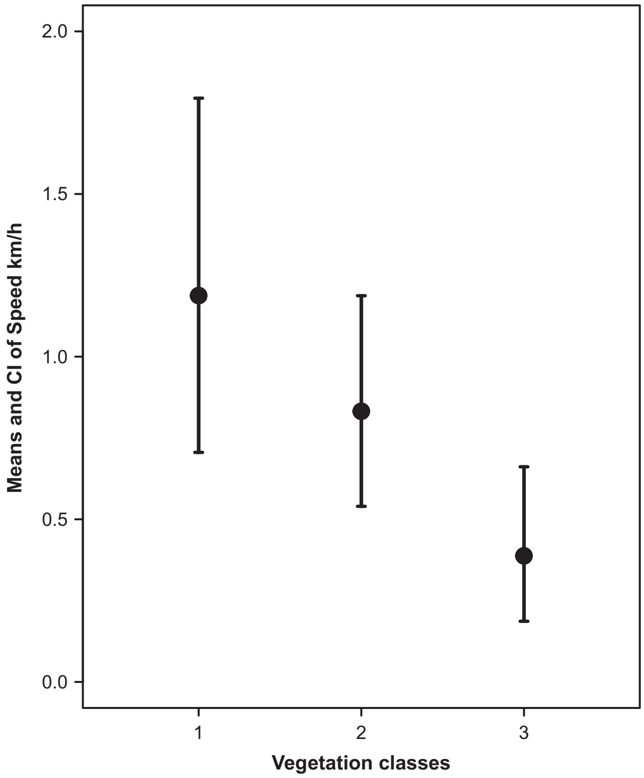

FIGURE 2 Means and 95% CI of speeds calculated for elephants moving through different sections of the Mount Kenya Elephant Corridor, as defined by vegetation classes: (1) open grassland, (2) <500 m corridor width mixed forest bushland (3) >500 m corridor width mixed forest bushland. Figure shows back-transformed values from analysis of square-root data

The proportion of trees showing elephant damage regressed positively with elephant trapping rate ($r^2 = 0.27$, $F_{1,18} = 6.52$, $p = 0.02$, Figure 3).

4 | DISCUSSION

Wildlife corridors can have mixed success and slow uptake (Druce, Pretorius, & Slotow, 2008; Haddad et al., 2003; Kioko & Seno, 2011). In the case of the MKEC, elephants were using the corridor and the underpass within a week of its opening in 2010 (Chege, 2011). A minimum of 60 different elephants use the MKEC and 52% of these are, at least on some occasions, travelling the full length of the corridor. Some of these elephants make separate, partial journeys in addition to full journeys. This means that overall, more journeys into the corridor are partial rather than full, at a ratio of 2:1 (N. Winmill, unpublished data 2014).

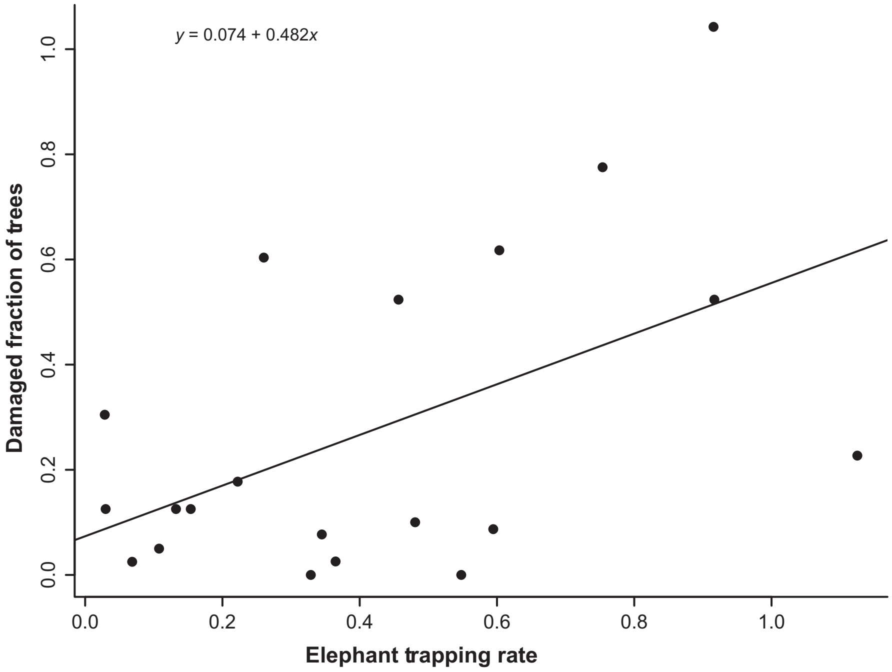

FIGURE 3 The arcsine-root transformed proportion of trees surveyed that had suffered elephant damage at a site in relation to trapping rate of elephants at that site

During our study we recorded elephants in 694 capture events distributed throughout the corridor. This demonstrates that the corridor is clearly valuable as it is heavily utilized and successfully connects two protected areas. Nevertheless, our data show detection as well as speed of movement varies throughout the corridor, indicating that different parts of the corridor have different primary functions for elephants.

Occupancy models can be used to answer a range of biological questions (Mackenzie et al., 2002; Royle & Nichols, 2003). One assumption of a single-season occupancy model is that of closure, i.e. no movement into or out of sites between surveys. Where this assumption is not met, occupancy can be interpreted as probability of use (Kéry & Royle, 2015). In the MKEC, probability of site occupancy was 0.96 for diurnal and nocturnal models. Interpreting this as use rather than occupancy indicates a very high probability that all sites within the corridor are used during the day and night. This lack of variation in occupancy precluded meaningful modelling of it, and so covariates were used to model detection. Our use of detection to model elephant site preferences within the corridor is akin to using presence only data or trapping rates. These methods assume perfect detection, so it is hard to separate detectability from actual rate of use. Nevertheless, such data still perform well in predicting species distributions, and can provide biologically meaningful results for populations with high detection probabilities (Lazenby & Dickman, 2013; Rood, Ganie, & Nijman, 2010; Van Bommel & Johnson, 2016). Elephants are large and so relatively easy to detect and, as all cameras were positioned on known elephant trails, it is likely that elephants using a site would be detected over the course of a survey period. Ignoring the influence of abundance on detection may cause as much bias as ignoring the effects of non-detection (Welsh, Lindenmayer, & Donnelly, 2013). Therefore, interpretation of the effects of the modelled covariates on detectability should be done with caution, but should not be dismissed as they can provide a meaningful indication of intensity of use.

During the day, elephants preferred sites with lower disturbance, and were detected more regularly in the northern part of the corridor, where human activity is lower. Width of corridor is known to influence corridor use, with wider corridors being preferred (Hilty & Merenlender, 2004). Conversely, in the MKEC, width of corridor correlated negatively with elephant detections. It is possible that detections were higher at sites in narrow parts of the corridor as animals were funnelled past the cameras. Despite some sections of corridor being very narrow, this did not seem to prevent use of these areas or inhibit passage through the corridor, indicating that even small areas of protected land can help provide connectivity. These narrow sections are short and intermittent, however, and therefore unlikely to be representative of how elephants might use a wholly narrow corridor.

During the night, pattern of use shifted and sites closer to roads were used more frequently. Although elephants have been known to avoid roads (Blake et al., 2008), traffic reduces at night, particularly on the small, non-paved roads in this remote area. Removal of cattle would have further reduced overall disturbance levels in the corridor. Disturbance had a smaller effect during the night, likely due to reduction in disturbance level, although its effect indicates more disturbed sites are still avoided. Increased nocturnal activity is a well-documented strategy employed by elephants to avoid contact with humans (Cook, Henley, & Parrini, 2015; Galanti, Preatoni, Martinoli, Wauters, & Tosi, 2006; Graham, Douglas-Hamilton, et al., 2009). It is likely some temporal avoidance of anthropogenic activity by elephants is occurring, and that they are passing sites that are more heavily disturbed during the day, such as near roads, at night in order to avoid disturbance. This is supported by the lower trapping rates during the day at sites where cattle were grazed.

Another strategy used to avoid anthropogenic disturbance is increased transit speed (Douglas-Hamilton et al., 2005; Graham, Douglas-Hamilton, et al., 2009). Although there was some variation between individuals, elephants generally moved more quickly through vegetation class one, suggesting that it presented a higher perceived risk. As navigation of steep slopes can be costly for elephants in terms of energy and injury risk (Wall, Douglas-Hamilton, & Vollrath, 2006), differences in slope between our vegetation classes may have confounded data slightly. This would still not fully explain the difference in speed between classes one and three. While average incline in class three was greater than in class one, highest average incline was through class two, where intermediate speeds were recorded. Moreover, there is considerable variability in slope throughout class three so not all movement in this area required traversal of steep slopes. If the costs of navigating slopes were dramatically influencing movement, elephants would be expected to use sites with steeper slopes less frequently. Within our models of corridor use, slope had some effect on use during the day but not during the night, implying that it was not simply the gradient of the land that was influencing detection and other factors may be more important.

Bulls often travel at faster speeds (Duffy, Dai, Shannon, Slotow, & Page, 2011; Ngene et al., 2010), yet, in our study, the fastest speed was shown by a family group. The slight variation in calculation methods for bull and family group speeds does not explain the lower speed for bulls, as any slight bias would have increased bull speed relative to family group speed. Family groups are generally more cautious than adult bulls, participating less in crop raiding and expanding into new areas more slowly (Chiyo & Cochrane, 2005; Druce et al., 2008; Hoare, 1999). The high transit speed is likely to be a reflection of this cautious behaviour. Cameras were able to pick up fine scale movement where these higher speeds were logged, with identified elephants recorded by different cameras within 30 min. Overall, movement speed was underestimated, as distances were calculated as straight lines between cameras, which does not reflect exact paths taken. While speed over the ground is not accurate, it is indicative of movement behaviour and suggests that elephants were spending more time in areas with good cover, increased browsing opportunities and lower disturbance.

Elephants will spend more time in areas where forage is available (Gara et al., 2016) and travel more slowly when feeding (Ngene et al., 2010), so slow speeds may reflect increased foraging behaviour in vegetation classes two and three. This idea is supported by the positive relationship between elephant trapping rate and proportion of trees showing damage, as this suggests that elephants could be using favoured areas more intensely in order to forage. Although tree density had a slight negative effect in our models, tree density as a measure of vegetation may have been distorted by the presence of shrubs and forbs. These were not included in the survey but provided additional cover and food resources in some areas where tree density was low. Grasses can also be an important food source for elephants (Cerling et al., 2006; Codron et al., 2011) and they were photographed feeding in the open grassland at night. Our results suggest that the areas of the corridor where movement was slowest are being treated primarily as habitat extension and that the areas which are traversed at higher speeds have limited value as habitat, due to increased disturbance and lower forage diversity (Codron et al., 2011; De Boer, Ntumi, Correia, & Mafuca, 2000) but are used primarily for transit.

Electrified fencing is increasingly used to successfully alleviate human–elephant conflict (Graham, Gichohi, et al., 2009; Kioko, Muruthi, Omondi, & Chiyo, 2008). Fencing areas comes at the cost of restricting movement, which may involve obstruction of historic corridor routes (Graham, Gichohi, et al., 2009). Restriction of movement raises the potential for overexploitation of resources (Guldemond & Van Aarde, 2008), and thereby increased human–wildlife conflict as elephants turn to crop raiding to fill their nutritional needs (Cook et al., 2015; Galanti et al., 2006). Many reserves now face the problem of managing high densities of elephants and associated overexploitation of vegetation (Lombard, Johnson, Cowling, & Pressey, 2001; Van Aarde & Jackson, 2007). In the case of the MKEC, there are already concerns regarding overexploitation of vegetation on LWC and in Ngare Ndare forest (LWC, 2015; Mwambeo & Maitho, 2015). Prior to construction of the MKEC fence the corridor route was used by some elephants, leading to repeated crop raiding incidents. By fencing the corridor, it can enhance connectivity, thus reducing ecological impacts of fencing a reserve, while reducing risk of human–wildlife conflict.

Overall, the evidence suggests that the more open, southern part of the corridor is predominantly used by elephants for travel, and that this occurs mostly during the night. The northern section of the corridor has a more diverse function and serves as additional forage and cover, effectively as an extension of the contiguous NNFR habitat. This idea is supported by the observations of identified family groups. As the “Liqueurs” only used the northern part of the corridor, it appears that their use of the corridor was primarily as an extension of habitat. Conversely the other family appear to traverse the corridor in order to access resources within the corridor itself and the NNFR. For this group, the corridor provides both additional habitat and a safe transit route. Regardless of the nature of the movement our data clearly indicate that elephant have access to additional resources because of the corridor and that it successfully connects the MKNP populations with those further north, in the landscape beyond the corridor.

It has been suggested that some parts of the corridor are not used by elephants, and corridor size has been reduced since its original construction. Our study found this idea to be inaccurate, and showed that all parts of the corridor are utilized. Several recommendations can be made to encourage sustained use of the corridor and promote elephant movement through the entire corridor length. These include protecting the corridor width and managing human activity within the corridor. It may be prudent to create additional corridors linking Mount Kenya to other areas of elephant habitat surrounding the mountain. As human activity can lead to reduced corridor functionality (Jones et al., 2012; Kioko & Seno, 2011) protection of land may be necessary in order to maintain benefits provided by corridors.

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ORCID

Siân E. Green http://orcid.org/0000-0003-0513-8490

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APPENDIX

Model outputs from top 5 diurnal and nocturnal models based on AIC ranking, showing occupancy (ψ) and estimated coefficients of covariates used to model detection given on the logit scales with associated standard errors. Back-transformed occupancy estimate is given to show probability that a site is occupied (ψ probability).

Model			Covariate	*Estimate*	*SE*	*Z*	*p*
Diurnal 1							
ψ (SE)	3.09 (1.03)	Detection:	Intercept	0.204	0.515	0.0396	0.692
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.331	0.326	−4.078	<0.001
			Disturbance	−1.062	0.210	−5.060	<0.001
			Slope	−0.106	0.048	−2.199	0.028
			Tree density	−0.061	0.017	−3.620	<0.001
			Tree density: Disturbance	0.129	0.034	3.815	<0.001
Diurnal 2							
ψ (SE)	3.09 (1.03)	Detection:	Intercept	0.203	0.516	0.394	0.694
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.332	0.330	−4.041	<0.001
			Distance to road	0.008	0.270	0.030	0.976
			Disturbance	−1.060	0.214	−4.959	<0.001
			Slope	−0.107	0.053	−2.024	0.043
			Tree density	−0.061	0.017	−3.503	<0.001
			Tree density: Disturbance	0.129	0.034	3.797	<0.001
Diurnal 3							
ψ (SE)	3.13 (1.06)	Detection:	Intercept	−0.826	0.214	−3.86	<0.001
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.087	0.309	−3.520	<0.001
			Disturbance	−0.773	0.162	−4.770	<0.001
			Tree density	−0.057	0.017	−3.400	<0.001
			Tree density: Disturbance	0.105	0.031	3.390	<0.001

(Continues)

APPENDIX (Continued)

Model			Covariate	*Estimate*	*SE*	*Z*	*p*
Diurnal 4							
ψ (SE)	3.11 (1.04)	Detection:	Intercept	−0.629	0.299	−2.103	0.035
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.095	0.311	−3.525	<0.001
			Distance to road	−0.232	0.249	−0.929	0.353
			Disturbance	−0.857	0.185	−4.633	<0.001
			Tree density	−0.061	0.017	−3.529	<0.001
			Tree density: Disturbance	0.111	0.032	3.497	<0.001
Diurnal 5							
ψ (SE)	3.09 (1.02)	Detection:	Intercept	−0.417	0.473	−0.88	0.379
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.071	0.315	−3.400	<0.001
			Disturbance	−0.645	0.171	−3.770	<0.001
			Slope	−0.063	0.045	−1.400	0.161
			Tree density	−0.032	0.014	−2.210	0.027
Nocturnal 1							
ψ (SE)	3.18 (1.11)	Detection:	Intercept	0.769	0.258	2.98	0.003
ψ probability (SE)	0.96 (0.04)		Corridor WIDTH	−1.969	0.315	−6.250	<0.001
			Distance to road	−1.595	0.229	−6.950	<0.001
			Disturbance	−0.279	0.119	−2.330	0.020
			Tree density	−0.066	0.015	−4.330	<0.001
Nocturnal 2							
ψ (SE)	3.24 (1.21)	Detection:	Intercept	0.849	0.307	2.76	0.006
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.998	0.322	−6.215	<0.001
			Distance to road	−1.653	0.262	−6.299	<0.001
			Disturbance	−0.327	0.156	−2.092	0.037
			Tree density	−0.072	0.021	−3.485	<0.001
			Tree density: Disturbance	0.015	0.032	0.487	0.626
Nocturnal 3							
ψ (SE)	3.18 (1.12)	Detection:	Intercept	0.898	0.431	2.085	0.037
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.998	0.323	−6.184	<0.001
			Distance to road	−1.536	0.277	−5.538	<0.001
			Disturbance	−0.303	0.137	−2.216	0.027
			Slope	−0.018	0.049	−0.374	0.709
			Tree density	−0.066	0.015	−4.317	<0.001
Nocturnal 4							
ψ (SE)	3.12 (1.05)	Detection:	Intercept	0.253	0.132	1.92	0.055
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.724	0.295	−5.850	<0.001
			Distance to road	−1.338	0.200	−6.680	<0.001
			Tree density	−0.047	0.012	−3.780	<0.001
Nocturnal 5							
ψ (SE)	3.13 (1.06)	Detection:	Intercept	0.108	0.231	0.469	0.639
ψ probability (SE)	0.96 (0.04)		Corridor width	−1.708	0.297	−5.751	<0.001
			Distance to road	−1.487	0.283	−5.263	<0.001
			Slope	0.032	0.043	0.759	0.448
			Tree density	−0.050	0.013	−3.799	<0.001