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RESEARCH ARTICLE

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Estimating elephant density using motion-sensitive cameras: challenges, opportunities, and parameters for consideration

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Abstract

With extinction rates far exceeding the natural background rate, reliable monitoring of wildlife populations has become crucial for adaptive management and conservation. Robust monitoring is often labor intensive with high economic costs, particularly in the case of those species that are subject to illegal poaching, such as elephants, which require frequent and accurate population estimates over large spatial scales. Dung counting methods are commonly employed to estimate the density of elephants; however, in the absence of a full survey calibration, these can be unreliable in heterogeneous habitats where dung decay rates may be highly variable. We explored whether motion-sensitive cameras offer a simple, lower cost, and reliable alternative for monitoring in challenging forest environments. We estimated the density of African savanna elephants (*Loxodanta africana*) in a montane forest using the random encounter model and assessed the importance of surveying parameters for future survey design. We deployed motion-sensitive cameras in 65 locations in the Aberdare Conservation Area in Kenya during June to August in 2015 to 2017, for a survey effort of 967 days, and a mean encounter rate of 0.09 ± 0.29 (SD) images/day. Elephants were captured in 16 locations. Density estimates varied between vegetation types, with estimates ranging from 6.27/km^2 in shrub, 1.1/km^2

in forest, 0.53/km^2 in bamboo (*Yushania alpine*), and 0.44/km^2 in the moorlands. The average speed of animal movement and the camera detection zone had the strongest linear associations with density estimates ($R = -0.97$). The random encounter model has the potential to offer an alternative, or complementary method within the active management framework for monitoring elephant populations in forests at a relatively low cost.

KEYWORDS

abundance, camera traps, capture mark recapture, density estimation, elephants, random encounter model

Reliable estimates of population numbers are fundamental for the effective conservation of wildlife (Zero et al. 2013). In the absence of information on changes in population size, it is difficult to assess conservation status, identify key threats, or assess interventions within an active management framework (Manzo et al. 2012). Density estimates are particularly challenging for species with clumped spatial distributions, which necessitates monitoring over large spatial scales (Jones 2011).

Across the African continent, montane forests act as dry-season refugia for African savanna elephants (*Loxodanta africana*) and African forest elephants (*Loxodanta cyclotis*) and subsequently harbor significant populations (Bohrer et al. 2014). But forests with poor visibility and steep topography present a significant challenge to monitoring (Barnes et al. 1997). Indices derived from indirect survey methods give a relative measure of abundance derived from encounter rates (e.g., dung, acoustic calls), and are often the only feasible option in these environments (Hedges 2012). Encounter rates can be combined with production rates (defecation, decay) to estimate actual density; however, the reliability of these models is heavily dependent on estimates of production and decay rates (for dung), which can vary substantially between areas (Narain et al. 2005, Hedges 2012). Accurate calibration of production and decay rates are therefore necessary for individual survey sites if reliable estimates are to be achieved (Walsh and White 2005, Kuehl et al. 2007, Vanleeuwe 2009). Calibration of these rates can be labor intensive, requiring 6 months for accurate estimates (Amin et al. 2019), potentially increasing to 12 months depending on environmental conditions and resources (Hedges et al. 2013). Consequently, dung count surveys are particularly expensive to conduct, especially if frequent monitoring is required over large spatial scales, or in heterogeneous habitats (Hibby and Lovell 1991, Hedges et al. 2013).

In the face of persistent and increasing threats from poaching, habitat loss, and human-wildlife conflict (Blanc 2008, Graham et al. 2010, Maisels et al. 2013), there is a significant need for a multi-country, high quality census of elephants in forests (Chase et al. 2016). Remote sensing using cameras offers the potential to overcome the problems with indirect methods and the high costs associated with genetic surveys in large populations (Miller et al. 2005). They are non-invasive and provide a lower cost alternative for monitoring species that are not easily observable (Carbone et al. 2001, Rowcliffe and Carbone 2008, Manzo et al. 2012). While cameras have been used to document elephant presence (Gray and Phan 2011), population dynamics (Varma et al. 2006), and habitat use (Green et al. 2018), there is a lack of information on their effectiveness in estimating densities of elephants, particularly in forests.

Capture-mark-recapture (CMR) models are commonly employed to derive density estimates from cameras; however, they require individual recognition, which can be difficult to achieve. Distinguishable individuals may represent only a small portion of the sampled population, if at all (Carbone et al. 2001, Manzo et al. 2012, Caravaggi et al. 2016). Spatially explicit capture-recapture (SECR) models can be used when a subset of the population can be uniquely identified, but these require large sample sizes with frequent recaptures to achieve precision (Chandler and Royle 2013, Rich et al. 2014, Caravaggi et al. 2016). Consequently, the development of motion-sensitive camera methods such as the random encounter model (REM; Rowcliffe et al. 2008) and distance sampling (Howe et al. 2017) can estimate density without the need to distinguish between individuals. The REM estimates density by modeling random encounters between cameras and subject animals. Currently, it has been employed only in a limited range of species and landscapes (Manzo et al. 2012, Zero et al. 2013, Rahman et al. 2017, Schaus et al. 2020), and is yet to be validated in forests or with elephants. Studies that have cross-validated REM estimates with complete census data, CMR models, and distance sampling show promising results in terms of accuracy and precision (Rowcliffe et al. 2008, Zero et al. 2013, Anile et al. 2014).

We examined the suitability of using motion-sensitive cameras for estimating the density of African savanna elephants in forests. The intention was to provide a viable, lower cost, and less resource intensive alternative, or complementary option to the currently employed dung count method, enabling conservation organizations to continuously monitor elephant populations in challenging forest ecosystems. We quantified and compared the effects of each of the REM parameters on the overall density estimates calculated to identify important aspects of survey design for the monitoring of elephants in montane forests.

STUDY AREA

The Aberdare Conservation Area (ACA) lies southwest of Mount Kenya (36°43′E 0°25′S), forming the eastern rim of the Great Rift Valley in the Central Province of Kenya (Figure 1). Comprising the Aberdare National Park and the surrounding Aberdare Forest Reserves, the area covers 1,748 km^2. Identified as a biodiverse hotspot, this Afro-montane area became isolated during glacial maxima and the recurrent expansions and contractions of the forest, providing dry-season refugia for a variety of taxa (Demos et al. 2014) including African savanna elephants and the Cape buffalo (*Syncerus caffer caffer*). Altitude varies from 1,800 m to 4,000 m, resulting in 4 main vegetation zones: moorland consisting of alpine heathland, hagenia (*Hagenia abyssinica-Hypericum revolutum*) forest, bamboo (*Yushania alpina*) forest, and woody forest and shrubland (Lambrechts et al. 2003). Climate was typical for the ecoregion, characterized by a uniform climate with temperatures averaging 17°C, and experiencing 2 wet seasons: long rains from March until May and short rains between October and December (Morrison et al. 2018). The ACA is situated in a matrix of human settlement. To protect the forest and reduce human wildlife conflict, an electric wildlife fence surrounding the perimeter was completed in 2009, with the area now containing a confined population of savanna elephants.

METHODS

Camera placement

Data used in this study formed part of an extensive camera survey in the study area under permits obtained from the National Commission for Science, Technology and Innovation of the Republic of Kenya. We used a subset of the camera data to apply the REM on the savanna elephant population. We deployed cameras (Natureview; Bushnell, Overland Park, KS, USA) during the dry season between June and August for 2015 to 2017 with a survey effort of 967 days over 65 locations (Table 1). We assumed the population was closed because movement was curtailed by the perimeter fence and periods between survey years were short in relation to elephant longevity and gestation periods. Additionally, Kenya Wildlife Service ranger patrols did not report excessive mortality over the study period. We selected camera grid locations based on vegetation type and altitude, and placed cameras a minimum of 1 km apart (Figure 2). To ensure that surveying effort (camera days) in each vegetation type was representative of its

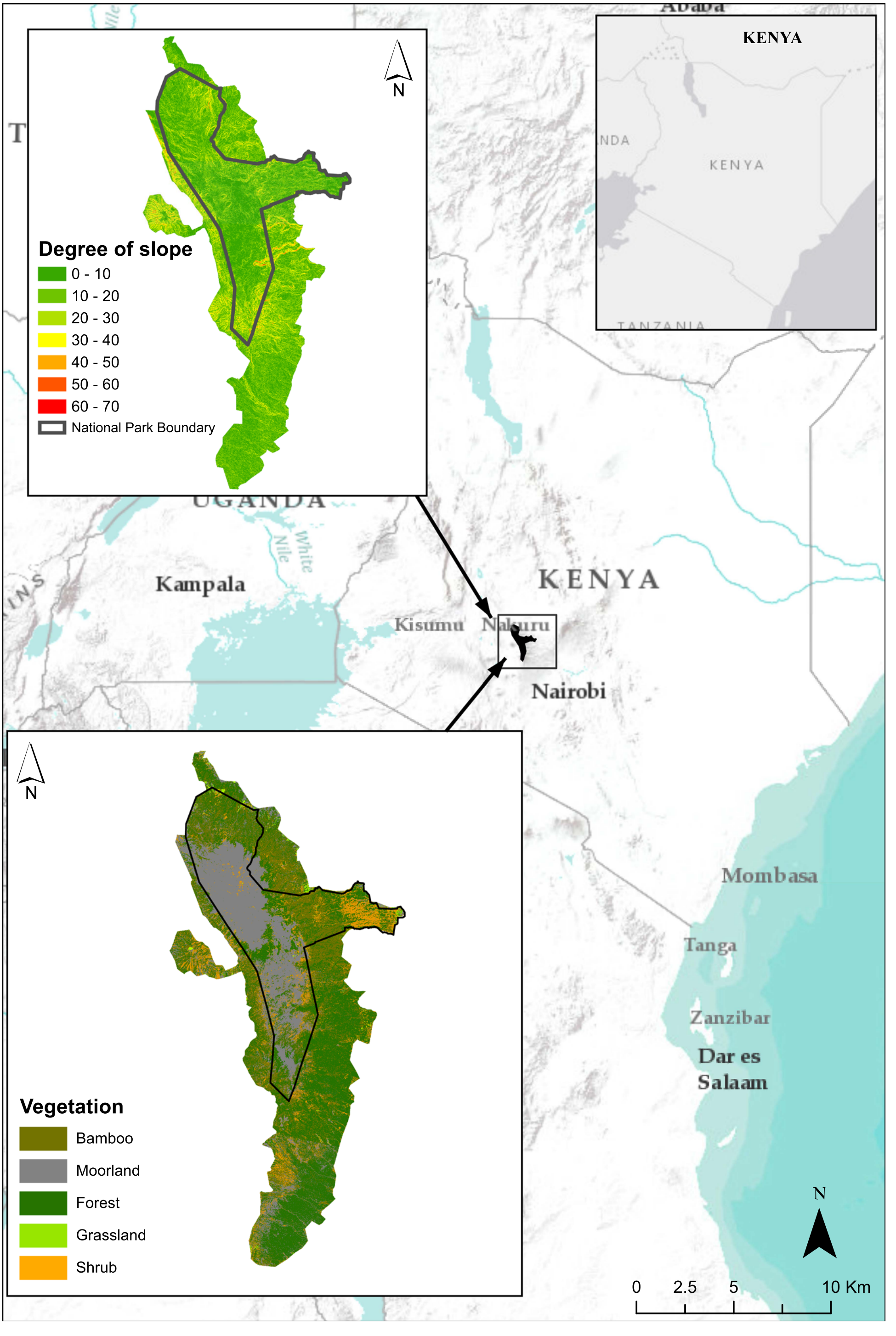

FIGURE 1 Location of the Aberdare Conservation Area, Kenya

THE JOURNAL OF WILDLIFE MANAGEMENT THE WILDLIFE SOCIETY

TABLE 1 Summary of motion-sensitive cameras placed in the Aberdare Conservation Area, Kenya, 2015–2017, to detect African elephants. The surveying effort is displayed in days for each vegetation type and year. The number of cameras deployed to achieve the surveying effort is displayed

Year	Vegetation type	Number of cameras in place	Surveying effort (days)
2015	Bamboo	4	40
	Moorlands	5	50
	Forest	8	80
	Shrub	10	100
2016	Bamboo	7	70
	Moorlands	7	70
	Forest	13	130
	Shrub	0	0
2017	Bamboo	3	121
	Moorlands	3	121
	Forest	4	146
	Shrub	1	39

coverage across the study site, we used Landsat 8 satellite images (https://earthexplorer.usgs.gov, accessed 26 Feb 2017) to produce a land-cover vegetation map. We classified vegetation types from ground truth data, and recorded global positioning system (GPS) locations as a reference. We performed a supervised classification (Figure 1) in the R package RStoolbox (Leutner et al. 2017) using a random forest model, achieving accuracy of 79%. The area was stratified into 4 vegetation types: woodland (closed canopy forest, and hagenia dominated); moorlands, shrub, and bamboo (Figure 1). We selected cameras for the REM from the larger dataset based on the number of camera days (survey effort) required in each vegetation type (Figure 3). We selected the subset of cameras in each vegetation type by randomly generating a list of motion-sensitive camera identification numbers within R version 4.0.2 (R Core Team 2020). To achieve a sufficient number of camera days in each vegetation type for proportional sampling, and to increase the spatial coverage of the area, we deployed additional cameras in 2017. When placing cameras, we selected locations using the landcover map within ArcGIS 10.3.1. (Esri, Redlands, CA, USA) downloaded into GPS devices for positioning in the field. We selected suitable areas based on accessibility (within 3 km of road access), and positioned cameras within a 100-m radius of the GPS point. We placed cameras on trees 1.5–2.5 m high and programmed them to be active 24 hours/day, taking 3 consecutive photos with a 2-second delay once triggered by motion. We recorded camera identification, time and date, vegetation type, and minimum distance to intersecting dense vegetation and downloaded final GPS locations onto the site map in ArcGIS 10.3.1. We were unable to place cameras in the southern area of the Forest Reserve managed by the Kenya Forest Service because of commercial tree felling, and extensive conversion to agricultural land.

Random encounter model (REM) and sensitivity analysis

The REM obtains density (D) estimates from camera encounter rates without the need for individual recognition (Rowcliffe et al. 2008):

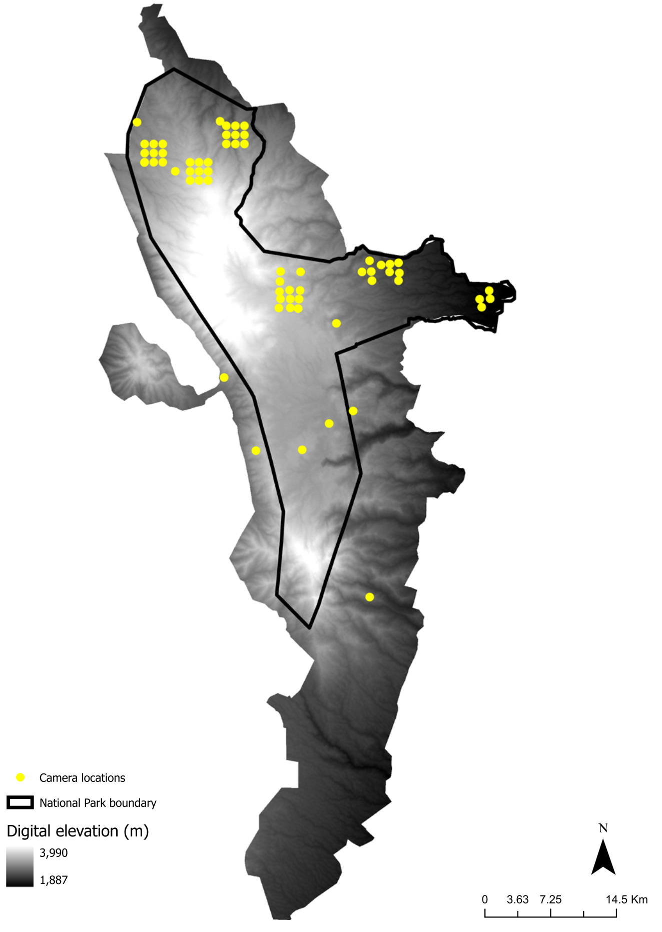

FIGURE 2 Location of the motion-sensitive cameras used to detect African elephants on a digital elevation model of the Aberdare Conservation Area, Kenya, 2015–2017

$$D = \frac{y}{t}\frac{\pi}{vr(2 + \theta)}$$

whereby y is the number of independent images, t is the total survey effort (days), v is the average speed of animal movement per day (km), and r (detection distance) and θ (camera angle) are used to calculate the camera's detection zone. Despite being herd animals, we decided not to calculate density based on group encounter events as it would be difficult to obtain unbiased, independent estimates of group size (Rowcliffe et al. 2008, Zero et al. 2013). Dense vegetation presents difficulties in observing all individuals, and elephant herd dynamics are heavily influenced by the availability of resources (Fishlock and Lee 2013). Attempting to count the average herd size of elephants at easily visible locations such as water points, would likely result in an over-estimation of group size and inflate the density estimates (Varman and Sukumar 1995). Although the integrated REM, an extension to the REM, allows more flexibility for animals that move in groups, it is not without limitations. For species traveling in large groups where the distance to the center of the group is unobservable to the camera, model assumptions may be violated and model fitting computer-intensive (Jourdain et al. 2020). We counted individual elephants from the group images and calculated encounter rates by combining sequential photographs into a single event. We deemed events independent when it was clear that a herd had moved through the field of view; we therefore classified consecutive images of elephants remaining in front of the cameras as the same event (Zero et al. 2013, Cusack et al. 2015).

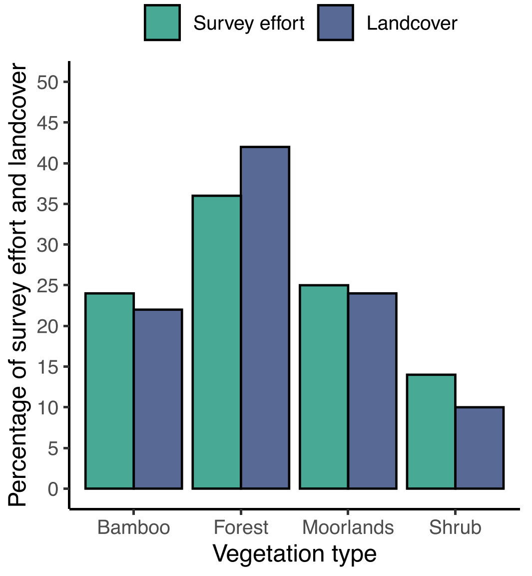

FIGURE 3 Stratified sampling of camera placements used to detect African elephants in the Aberdare Conservation Area, Kenya, 2015–2017, showing the percentage of landscape cover of each vegetation type, and the percentage of surveying effort throughout the study

To quantify animal daily movement range per day, we used telemetry data from the Kenya Wildlife Service of a male savanna elephant in the nearby Mount Kenya Forest Ecosystem. We obtained data collected over 5 months during the same season as the sampling period within our study. Daily movement was based on sampling frequencies of 1 GPS fix every 59 minutes over 24 hours. Although short-interval fixes are preferable to reduce potential issues of under-estimation of distance traveled (Rowcliffe et al. 2012), we were constrained by the setup used in existing long-term monitoring. Mean daily range was 6.5 km, which is comparable to movement data of collared forest elephants in a forest in Gabon (Mills et al. 2018), and wet season movement of male and female savanna elephants in Zimbabwe (Chamaillé-Jammes et al. 2013).

We calibrated the camera detection zone in a series of *ex situ* trials in captive elephants at Chester Zoo, United Kingdom. We placed motion-sensitive cameras ($n = 4$) around the enclosure for 6 hours, and calculated the detection distance by recording when the camera was first triggered by an elephant approaching from the front. We measured distance from the camera using a rangefinder and permanent features in the landscape as a reference. To estimate the camera angle, we recorded perpendicular approaches of the elephants to each side of the sensor (left and right) at the first trigger and took a bearing to the location using a compass placed at the camera location (Cusack et al. 2015).

Because of dense vegetation in the ACA study site, not all cameras were capable of achieving the detection distance of 12.9 m calculated during the calibration. As such, we averaged cameras that had shorter distances to intersecting dense vegetation with the calibration trial data. Therefore, the detection arc for the survey yielded a detection distance of 9.4 m, and an angle of 0.89 radians. We computed REM density estimates in R using the remBoot package (Caravaggi 2017; Code file S1, available online in Supporting Information). We calculated confidence intervals of elephant density for each of the strata using non-parametric bootstrapping, re-sampling camera encounter rates (y/t) with replacement 10,000 times (Rowcliffe et al. 2011, Manzo et al. 2012). We conducted a Kruskal-Wallis test in R version 4.0.2 (R Core Team 2020) to compare encounter rates between the various vegetation types.

We performed a sensitivity analysis on a subset of data (forest vegetation type) to measure the effect of each of the REM parameters on the resulting density estimates. Simulations (n = 500) examined the effects of a 1–10% (±) change in each parameter (v, r, θ), after removing the linear effect of all other parameters in each simulation. We conducted analysis in the pse package in R (Chalom and Prado 2017; Code file S2, available online in Supporting Information).

We downloaded the advanced spaceborne thermal emission and reflection radiometer, global digital elevation model at 30-m resolution from the United States Geological Survey (https://earthexplorer.usgs.gov, accessed 3 Mar 2017). We calculated the 3-dimensional surface volume for the study area using the global digital elevation model raster layer and ACA boundary polygon. We extracted volumetric calculations and computed them for the areas using the surface volume tool in ArcGIS version 10.3.1 to quantify the total area (km^2) for each vegetation type in the study area for accurate stratification.

RESULTS

Over the study area, we obtained 84 elephant images captured over 967 camera days. The mean encounter rate was 0.09 ± 0.29 (SD) photographs/day, with elephants being photographed in 16 of the 65 camera stations (Figure 4). The encounter rate was influenced by vegetation type (χ^2_3 = 9.094, P = 0.028). We calculated mean encounter rates of 0.02 ± 0.05 in bamboo, 0.02 ± 0.03 in moorlands, 0.03 ± 0.07 in forest, and 0.39 ± 0.63 in shrub.

Elephant densities varied between vegetation types based on the REM. Density was highest (6.27 elephants/km^2, 95% CI = 6.22–6.33) in shrub, followed by forest at 1.1/km^2 (95% CI = 1.08–1.11), bamboo at 0.53/km^2 (95% CI = 0.52–0.54), and moorlands at 0.44/km^2 (95% CI = 0.43–0.45). The overall density estimate for the ACA based on the proportionate sampling of vegetation types was 1.54 (95% CI = 1.54–1.56) elephants/km^2.

The animal movement and detection distance parameters had the strongest linear associations with the resulting density estimate based on partial rank correlation coefficients after removing the effects of all other parameters (r = −0.97 for both parameters; Figure 5). Simulations revealed that a 10% change in the average speed of animal movement and camera detection distance, resulted in a 10.1 ± 1.43% difference in density. The association between camera detection angle and density was weaker (r = −0.73); a 10% change in parameter input resulted in a 3.09 ± 0.14% change in density estimates (Figure 5).

DISCUSSION

Monitoring threatened populations is important for the development of management strategies and the allocation of conservation resources. Despite being a requirement under the Convention on International Trade in Endangered Species 'Monitoring the Illegal Killing of Elephants' programme, forest populations remain particularly difficult to monitor, with many traditional approaches to estimating population numbers unsuitable to employ in these environments. The most commonly used method in montane ecosystems is the dung count method; however, this was developed for lowland forests (Barnes et al. 1997). When applied in montane environments, this method can be problematic because of large variations in decay rates in higher altitudes. Our objective was to evaluate the use of motion-sensitive cameras as an alternative, or complementary approach, that is less resource intensive.

With the absence of true population size data for the area, it was not possible to cross validate the results from the REM; however, the density estimates calculated are comparable to a dung count survey that was conducted in 2017 at the study site by the Kenya Wildlife Service (Kenya Wildlife Service 2017). Results from the dung count survey generated average densities of 2.25 elephants/km^2 (Kenya Wildlife Service 2017), similar to those calculated using the REM, which varied between 0.44/km^2 and 6.27/km^2 dependent on vegetation type. Elephant densities vary across their extent and our results lie within the expected range (Chase et al. 2016). Higher annual vegetation

THE JOURNAL OF WILDLIFE MANAGEMENT
THE WILDLIFE SOCIETY

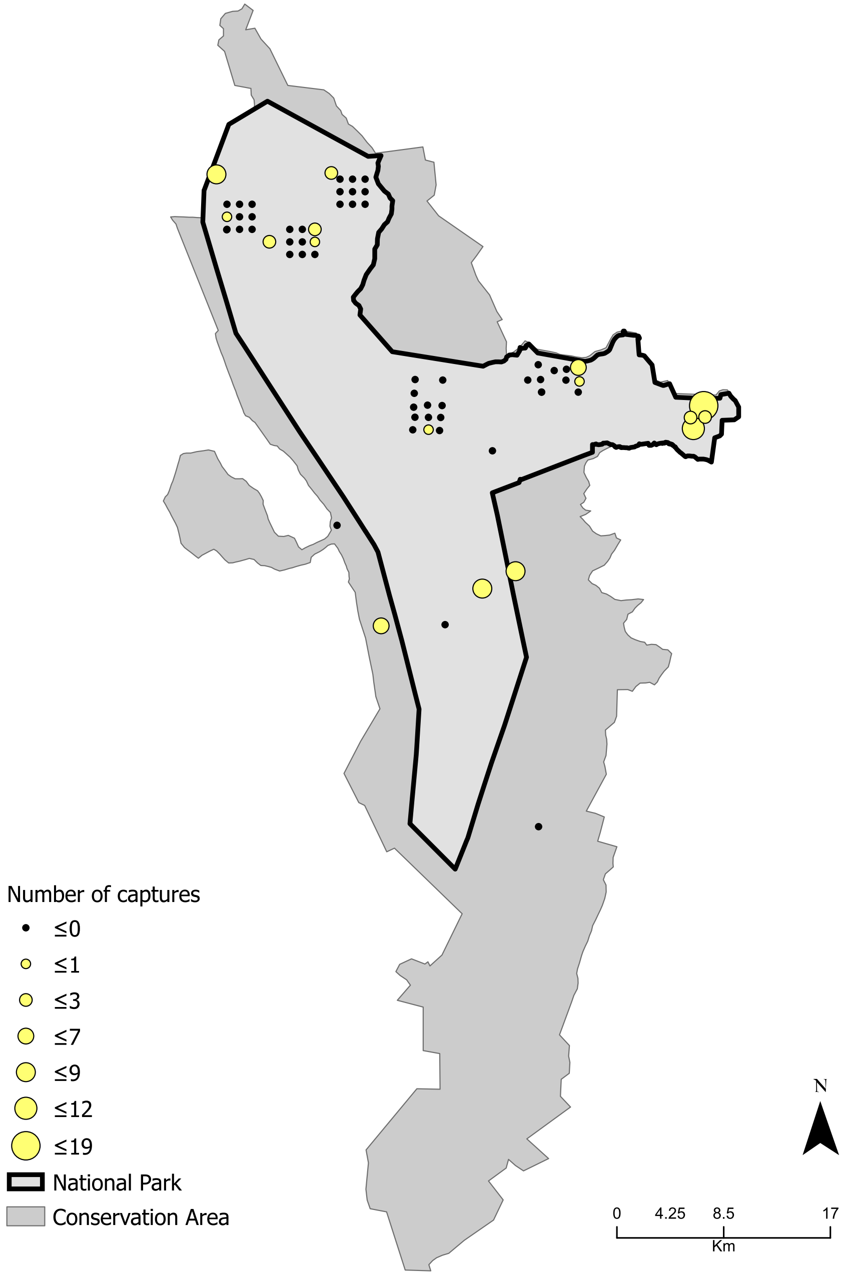

FIGURE 4 Proportional representation of the total number of African elephant images captured in the Aberdare Conservation Area, Kenya, 2015–2017, on each of the motion-sensitive cameras

productivity, a characteristic of the study site, has been identified as a driving factor influencing density (Duffy and Pettorelli 2012). The capacity of elephants in modifying landscapes has been documented, with the ACA exhibiting small-scale degradation (Morrison et al. 2018); the long-term sustainability of these density estimates in the study area are unknown.

Our findings clearly indicate the influence of vegetation type on elephant distribution. This concurs with evidence reported during a dung count survey conducted in the nearby Mount Kenya National Park (Vanleeuwe 2009), and is

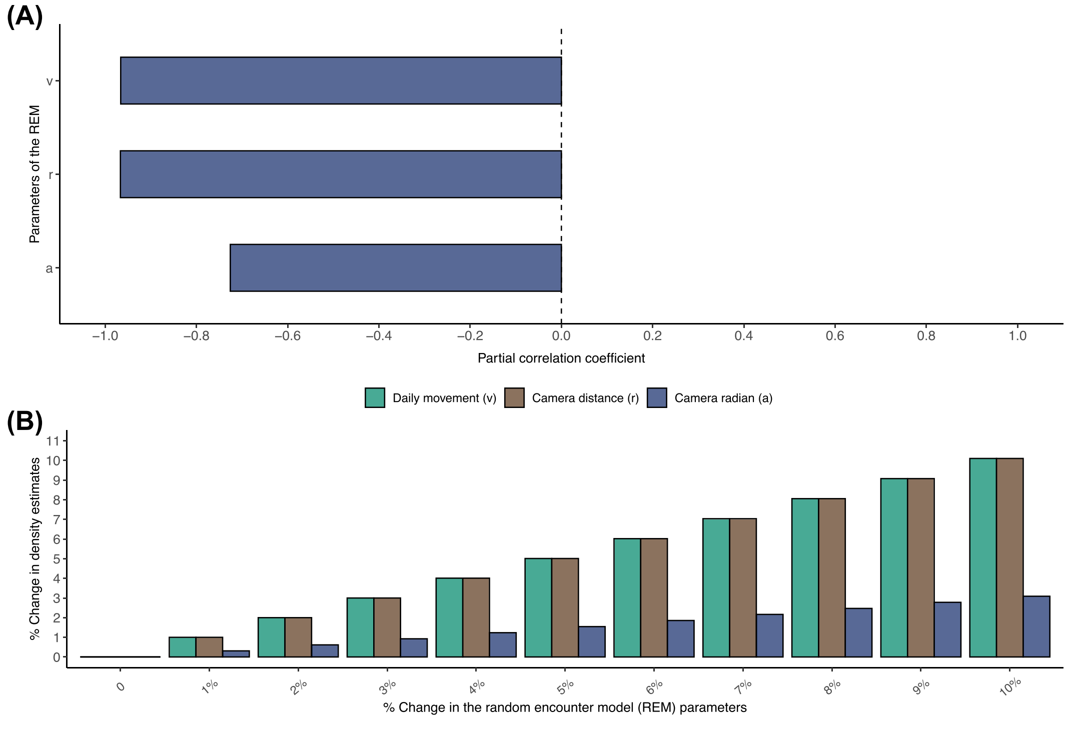

FIGURE 5 Sensitivity analysis on the African elephant density estimates in the Aberdare Conservation Area, Kenya, 2015–2017. A) Partial rank correlation coefficients for linear associations between each of the random encounter model (REM) parameters: daily animal movement (*v*), detection distance (*r*), and detection radians (a). B) Percentage of change in African elephant density estimates at varying percentages of changes in the parameters

likely attributed to the clumped distribution of elephants across the area. As with other wide-ranging species, elephants rely on spatially and temporally clustered resources, moving seasonally to areas where those resources are available, and favoring or avoiding certain characteristics (Loarie et al. 2009, Bohrer et al. 2014). Calculating an average density across an entire area would ignore the spatial variation in elephant distribution. Stratifying the site and accounting for heterogeneities in habitat use reduced bias and provided more reliable density estimates. For our study site, proportional representation for sampling was necessary for vegetation types at various altitudinal clines, and for the eastern area of the National Park, as this area has a high density of wildlife. Avoiding placing cameras in areas that elephants are frequently observed, would undoubtedly have under-estimated density. Likewise, placing too many cameras in high-density areas, would have artificially inflated estimates, and violated assumptions of independent movement (Rowcliffe et al. 2008, 2013).

Estimate reliability can be compromised in dung count surveys when decay and defecation rate parameters are either under- or over-estimated. Even small variations can result in considerable differences in density estimates (Vanleeuwe 2009). The REM is not without potential biases and also requires careful calibration. Our sensitivity analysis on the 3 REM parameters (*v*, *r*, and θ) measured the effect of each parameter on the final density estimate, identifying the parameters that require particular consideration during calibration. The speed of animal movement and camera detection distance parameters showed strong linear associations with density estimation (Figure 5). An error during the calibration of these parameters would result in the same perturbation of the density estimate (i.e., a 10% change in parameter calculation results in a 10% change in density estimates). Camera detection radians had a significantly lower influence on the final estimate; a 10% difference in parameter calculation resulted in a 3% change in density estimate. During the *ex situ* calibration of the camera detection zone (r, θ), we initially used human subjects approaching the camera. To improve the accuracy of the calibration, we later decided to perform the calibration with captive elephants. We recorded a substantial difference in the camera detection ability between the human and elephant trial, increasing from 8.4 m using human subjects, to 12 m using captive elephants. Miscalculating this parameter could potentially have altered the final density estimate by 43% and demonstrates the importance of a thorough calibration of this parameter to achieve high quality density estimates.

Detection distances were not always possible to determine at each camera location because of dense vegetation and physical obstructions in the field of view of the camera. During camera placement and setup, we recorded the distance to the closest obstruction of view, which subsequently altered the value of the r parameter for some cameras. Despite adjusting for these differences, and with the results from the sensitivity analysis, we suggest further modifications to increase estimation accuracy and reduce potential bias. For future surveys, we recommend calculating the detection distance of individual cameras using an overlaid grid setup during each camera placement using marking objects (such as bamboo canes) that can be superimposed onto each successful image taken (Caravaggi et al. 2016).

The animal movement parameter is an obvious source of potential error. Ideally, it is recommended that the daily distance traveled be calculated for each specific site (Rowcliffe et al. 2008). As with the challenges that transpire in calculating defecation and decay rates in dung count surveys, it is difficult to observe elephants within forests for any period of time. The GPS-collar data provides a solution; however, data may not always be available for specific sites. Fitting GPS-collars is expensive and presents difficulties with elephants in forests because of the risks of darting and sedating in dense vegetation and steep topography, it is therefore not practical to employ primarily for the calibration of the REM parameter. Data can be gathered from areas with comparable habitats, or from other studies; however, using existing collar data has its constraints because collar setup is restricted by other monitoring programs. For example, we were limited to the data setup for an existing, long-term monitoring program, with GPS fixes every 59 minutes. It is recommended to use short-interval GPS fixes where possible to reduce a potential under-estimation of the daily distance traveled by the focal animal (Rowcliffe et al. 2012). While we acknowledge the limitations of calculating our movement parameter (6.5 km/day) based on movement data from 1 individual male elephant, our data is comparable to more extensive studies documenting savanna and forest elephant movement in various vegetation types. Based on 17 individuals fitted with GPS-collars, daily distances traveled in a forest were calculated at 8 km/day, with no significant differences exhibited in movement rates between males and females (Mills et al. 2018). Similarly, movement data from 10 separate elephant herds in the wet season estimated mean daily speeds of 0.33 km/hour (7.9 km/day; Chamaillé-Jammes et al. 2013). The variance in daily distances traveled by our collared elephant were relatively large (1.9 km to 15 km), and although our mean estimates were recorded as 6.5 km/day, results from our sensitivity analysis determined that a 10% miscalculation of this parameter would result in a 10% difference in overall density estimates.

While careful calibration of parameter estimates is important for the REM and the dung count survey, the REM potentially offers an alternative, or complementary method to dung count surveys at a relatively low cost, and over a much shorter time period. When employing the REM, there is a recommended minimum of 10 independent photographs, or 20 when variance is high (Rowcliffe et al. 2008). The 84 elephants photographed during our survey exceeds these minimum requirements. Based on our encounter rates of 0.09 photographs/day, 20 independent photographs could have been achieved with a surveying effort of 224 days (i.e., deploying 16 cameras for 7 days at a time, relocated once). While this study focused on elephants, the REM offers the opportunity of conducting multi-species surveys at the same time, and in a range of land cover types, and only requires calibration of the REM parameters (v, r, θ) for each focal species. While the results from this study are promising, it would be beneficial to conduct further surveys using the REM and dung count method concurrently. Ideally, both surveys would be conducted in a population where the true population size is known, thereby providing a direct comparison of the accuracy of density estimates calculated.

MANAGEMENT IMPLICATIONS

This study has addressed the paucity of information on the suitability of using motion-sensitive cameras to estimate the density of elephants in forests. The REM potentially offers a viable alternative or complementary method to elephant dung count surveys that are commonly employed within forest environments. Compared to dung counts, the REM approach does not require extensive training or the employment of additional staff. Despite the initial start-up cost of the REM (~$4,050 for 12 cameras and memory cards), resource costs remain relatively low and the analysis uses open-source software. In addition, motion-sensitive cameras can be used in subsequent surveys, and with density estimates obtained in a relatively short time-frame, offers the potential of conducting a number of surveys per annum (accounting for deployment of equipment and maintenance). We recommend careful calibration of the model input parameters for estimation accuracy, particularly the daily animal movement and camera detection distance parameters, which should be calibrated using the focal species when possible. Secondly, our results clearly indicate variations in elephant density, dependent on habitat characteristics. Proportional representation of the habitat via stratification is necessary to account for heterogeneities in habitat use, reduce bias, and improve the accuracy of density estimates.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

This research was conducted under permit NACOSTI/P/16/30673/11 from National Council for Science and Technology of the Republic of Kenya.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study is openly available in figshare at 10.6084/m9.figshare.16826122. Data and code are additionally provided in a format suitable to model occupancy and is available in figshare at https://doi.org/10.6084/m9.figshare.16826140. The GPS locations have been omitted to protect vulnerable species subject to anti-poaching controls.

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