
Understanding the effect of landscape fragmentation and vegetation productivity on elephant habitat utilization in Amboseli ecosystem, Kenya

Tawanda W. Gara^{1,2*}, Tiejun Wang¹, Andrew K. Skidmore¹, Fadzai M. Zengeya², Shadrack M. Ngene³, Amon Murwira² and Henry Ndaimani²

¹Faculty of Geo-Information Science and Earth Observation (ITC), University of Twente, Hengelosestraat 99, PO Box 6, 7500 AA, Enschede, The Netherlands, ²University of Zimbabwe, Department of Geography and Environmental Science, P.O. Box, MP167, Mount Pleasant, Harare, Zimbabwe and ³Kenya Wildlife Service, PO Box 40241, 00100 Nairobi, Kenya

Abstract

Understanding factors affecting the distribution of the African elephant is important for its conservation in increasingly human-dominated savannah landscapes. However, understanding how landscape fragmentation and vegetation productivity affect elephant habitat utilization remains poorly understood. In this study, we tested whether landscape fragmentation and vegetation productivity explain elephant habitat utilization in the Amboseli ecosystem in Kenya. We used GPS (Global Positioning System) telemetry data from five elephants to quantify elephant habitat utilization. Habitat utilization was determined by calculating the time elephants spent within a unit area. We then used generalized additive models (GAMs) to model the relationship between time density and landscape fragmentation, as well as vegetation productivity. Results show that landscape fragmentation and vegetation productivity significantly ($P < 0.05$) explain elephant habitat utilization. A significant ($P < 0.05$) unimodal relationship between vegetation productivity and habitat utilization was observed. Results suggest that elephants spend much of their time in less fragmented landscapes of intermediate productivity.

Key words: dry matter productivity, effective mesh size, fragmentation, habitat utilization, time density

Résumé

Bien comprendre les facteurs qui affectent la distribution de l'éléphant d'Afrique est important pour sa conservation

dans des paysages de savane de plus en plus dominés par les hommes. Pourtant, on ne comprend pas encore très bien comment la fragmentation des paysages et la productivité de la végétation affectent la fréquentation du paysage par les éléphants. Dans cette étude, nous avons voulu savoir si la fragmentation du paysage et la productivité de la végétation expliquent la fréquentation de l'habitat par les éléphants dans l'écosystème d'Amboseli, au Kenya. Nous avons utilisé des données télémétriques GPS de cinq éléphants pour quantifier cette fréquentation de l'habitat. Celle-ci était déterminée en calculant le temps que les éléphants passent dans une unité de surface. Nous avons ensuite utilisé des Modèles Additifs Généralisés (MAG) pour modéliser la relation entre la densité de temps et la fragmentation du paysage, ainsi que la productivité de la végétation. Les résultats montrent que la fragmentation du paysage et la productivité de la végétation expliquent de manière significative ($P < 0.05$) la fréquentation de l'habitat par les éléphants. Nous avons observé une relation unimodale significative ($P < 0.05$) entre la productivité de la végétation et l'utilisation de l'habitat. Nos résultats suggèrent que les éléphants passent une grande partie du temps dans des paysages moins fragmentés où la productivité est intermédiaire.

Introduction

Understanding factors affecting the distribution and habitat use of the African elephant (*Loxodonta africana*) is key to its conservation in increasingly human-dominated savannah landscapes (Murwira & Skidmore, 2005; Evans & Adams, 2016). Although foraging resources have been

*Correspondence: E-mail address: t.w.gara@utwente.nl

widely hypothesized to be the major factor influencing elephant movement (Loarie, van Aarde & Pimm, 2009; Birkett *et al.*, 2012; Chiyo *et al.*, 2014), human-induced landscape fragmentation is also considered important (Blake *et al.*, 2008; de Boer *et al.*, 2013). Thus, selection of foraging areas by elephants has to take into account both foraging resources and landscape fragmentation. In this regard, understanding the combined effect of forage resources and landscape fragmentation on elephant movement is critical for predicting and managing species response to natural and anthropogenic changes in the landscape (Buij *et al.*, 2007).

The selection of foraging resources by large herbivores is primarily influenced by plant phenology which is closely linked to the nutritional quality/digestibility of the forage (Fryxell, 1991). Forage quality is known to decline with plant growth, and as the plant matures, there is also a reduction in forage digestibility due to changes in cell wall composition over time (Hebblewhite, Merrill & McDermid, 2008). Moreover, intake declines in low forage areas because of low net energy intake. In this regard, herbivores are known to prefer areas of intermediate forage productivity as they face forage quality–quantity trade-offs (Fryxell, 1991; Wilmshurst, Fryxell & Hudsonb, 1995; Hebblewhite, Merrill & McDermid, 2008). Intermediate forage productivity landscapes are vegetation communities that are on the transition from open grasslands (low forage biomass m^{-2} – low intake rates) to woodlands or thicker vegetation (high forage biomass m^{-2} poor forage quality) (Hebblewhite, Merrill & McDermid, 2008). Elephants being bulk feeders are less likely to be influenced by forage quality (Owen-Smith & Chafota, 2012). Instead, elephants maximize their energy intake by making a trade-off between scarce high-quality forage and abundant low-quality forage (Bergman *et al.*, 2001). It is therefore not known whether elephants respond to vegetation productivity in a similar manner to other herbivores.

Herbivores do respond not only to the variability in forage resources but also to the patchiness of forage resources (Murwira & Skidmore, 2005). It therefore becomes important to understand the response of herbivores to forage resources and habitat fragmentation (Groom & Western, 2013). The existence of human infrastructure termed ‘fragmentation geometries’ such as roads, settlements and agricultural fields not only impede animal movement but also fragment their habitats (Burnsilver, Worden & Boone, 2008; Western, Groom & Worden, 2009). However, studies on large herbivores

particularly elephant movement and habitat utilization have often considered different fragmentation geometries in isolation (Barnes *et al.*, 1991; Blake *et al.*, 2008). Habitat fragmentation is assumed to negatively influence elephant habitat utilization (Leimgruber *et al.*, 2003). We therefore expect elephants to spend more time in less fragmented habitats compared to fragmented habitats. Thus, any meaningful prediction of animal movement in response to fragmentation geometries should consider their combined effect. It therefore becomes important to understand not only animal response to spatial and temporal changes in forage resources but also their response to landscape fragmentation. Hence, objective quantification of these factors becomes important in providing improved insights into elephant distribution and habitat utilization. Remote sensing could thus provide a meaningful approach to objectively quantify landscape fragmentation as well as forage resources due to its ability to provide a synoptic view of the landscape.

The advancement of satellite remote sensing has allowed for the quantification of forage resources at large spatial extents and at high temporal resolution. To this end, spectral transform and derivatives such as vegetation indices have been developed that correlate with vegetation productivity and quality. For example, the satellite-derived normalized difference vegetation index (NDVI) has been used as a surrogate for forage greenness or abundance in explaining elephant movement (Loarie, van Aarde & Pimm, 2009; Matawa, Murwira & Schmidt, 2012). Although vegetation indices are useful as proxies of productivity, they are not able to account for short-term variations in productivity resulting from, for example changes in meteorological conditions (Monteith, 1972; Pachavo & Murwira, 2014). In this regard, there is need for the development of measures of forage resources that are sensitive to changes in meteorological conditions, that is temperature and humidity. The recent development of remotely sensed dry matter productivity (DMP) has allowed direct and precise estimates of productivity (Xu *et al.*, 2012). DMP is proportional to net primary productivity and measures the growth rate of vegetation (dry mass increase) (Copernicus, 2013). The use of DMP as a direct measure of productivity could therefore improve understanding the link between vegetation productivity and animal movement (Xu *et al.*, 2012). However, the application of DMP to wildlife studies has received limited attention despite its ability to provide a more direct measure of vegetation productivity.

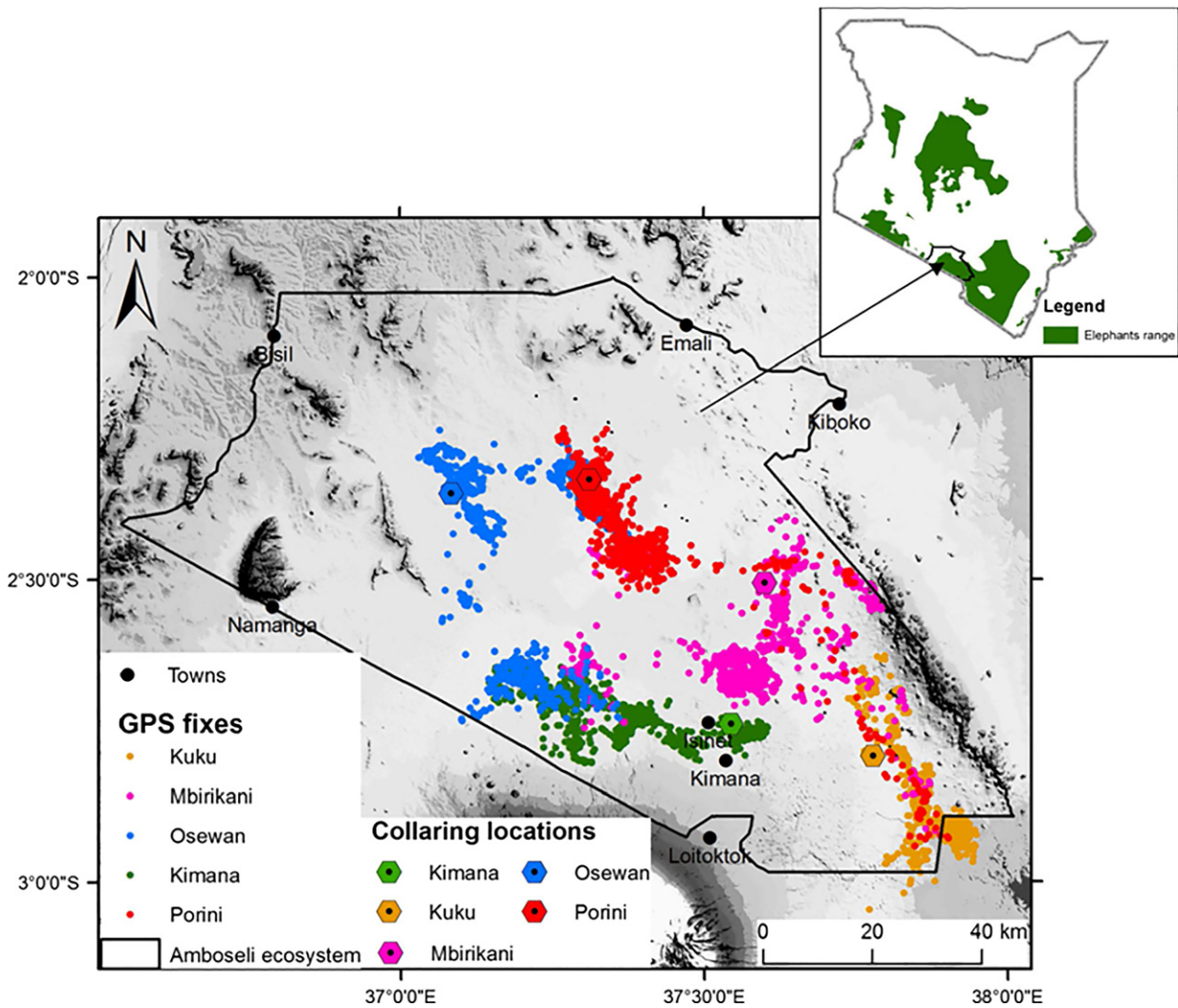


Fig 1 Spatial distribution of GPS fixes for each elephant group in the study area and elephant range in Kenya (Insert) [The colour version of this figure is available on Wiley Online Library]

In this study, we test whether and how seasonal habitat utilization of GPS collared African elephant is influenced by landscape fragmentation and remotely sensed DMP. We hypothesize that elephants would spend more time in habitats with intermediate vegetation productivity while utilizing habitats that are less fragmented.

Materials and methods

Study area

The Amboseli ecosystem is located in Kajiado District, Rift Valley Province, Kenya (Fig. 1). The ecosystem covers an

area ~ 8500 km² (Burnsilver, Worden & Boone, 2008). The area is classified as arid to semi-arid savannah with an average annual rainfall of 340 mm. Rainfall is bimodal with most rains being received from March to April and from November to December (Tuqa *et al.*, 2014). The area also experiences a dry period (June to September) and two transition periods (January–February and October–November) (Altmann *et al.*, 2002). The transition season is the period of change from wet to dry season or vice versa. During the transition period, the mean month rainfall is low but rising or declining. Temperature ranges between 20°C and 30°C, while elevation varies between 850 and 1350 m above mean sea level. The dominant

vegetation types include the broadleaf woodlands and dry tropical forests on the Kilimanjaro and Chyulu slopes, open grassland, riverine forest and scrubland in the Amboseli Basin as well as scattered *Commiphora* and *Acacia* woodlands (Western, 2007; Howe, Okello & Davis, 2013). The elephant population in Amboseli is estimated at about 1400 individuals (Chiyo *et al.*, 2011).

Elephant GPS tracking data

A total of five elephants were captured and fitted with GPS collars in Amboseli between 18th February and 15th March 2013 by Kenya Wildlife Service (KWS) and International Fund for Animal Welfare (IFAW). Of the five elephants, one was female and the rest were males and all the elephants belonged to different families (Table 1). The five GPS collared elephants represent five different elephant herds. Elephant herds can change numbers and composition, and examination of our tracking data indicated that these five collared animals belonged to distinct groups throughout the monitoring period. The fitted GPS collars were programmed to log the position of each individual after every 4 h for the period 20 February 2013 to 31 August 2013 resulting in a total of 4872 GPS fixes. The GPS collars had a relative error of 10 m which is marginal considering the minimal home range size of 10 km² an adult elephant requires to meet its daily requirements in African open savannahs (Douglas-Hamilton, Krink & Vollrath, 2005). The GPS collars had a success fix rate ranging between 93% and 96.8% which is within acceptable range to characterize wildlife movement patterns and make sound inference (Frair *et al.*, 2010). The GPS data were captured in geographic coordinates. The geographic coordinates were then reprojected in ArcGIS GIS 10.1 (ESRI, 2011) to Universal Transverse Mercator (UTM) Zone 37 based on WGS 84 Spheroid. Next, we split the GPS location data for each elephant into three seasons, that is wet season (March and April), dry

season (June to August) and transition season (February and May). This was based on the premise that seasonal variation in resources such as forage and water influences the distribution and movement patterns of the elephants differently.

Determining elephant habitat utilization

We determined habitat utilization within elephant home ranges by calculating the time that each elephant spent within a particular grid using the 'Time density tool' extension (Wall *et al.*, 2013) in ArcGIS GIS 10.1 (ESRI, 2011). Time density (T_G) determines the time (time occupancy) in hours that elephants spend per unit area of a landscape (space use) and is calculated as follows:

$$T_G = \sum_{k=1}^N \frac{d_k}{s_k} \quad (1)$$

where d_k is the length of track segment that intersects grid cell G , while N is the total number of track segments in the animal's trajectory. The symbol s_k represents the elephant speed over track segment k (Wall *et al.*, 2013). Time density for all the elephant tracking data was calculated per 9 km² grid cell. A grid cell of 9 km² was selected because it is the minimum home range area required by an elephant (Douglas-Hamilton, Krink & Vollrath, 2005). After determining the time density for each elephant, we summed the fractional linear path lengths for all the elephants between successive GPS tracks per grid cell (Wall *et al.*, 2013). We pooled the time density data for all the five elephants primarily due to the small sample size (de Boer *et al.*, 2013) which could not allow a mixed-model approach. In this study, we used the 'time density' function over other habitat utilization distributions such as probability habitat distribution because it provides an explicit amount of time an animal spends per unit area of landscape (Ngene *et al.*, 2012).

Table 1 Demographic data of the collared elephants

Name	Sex	Age (approx)	Herd size	Date of collaring	GPS fixes used	% of GPS fixes missing
Kimana	Male	26	5	19 February	1021	3.2
Osewan	Male	30	5	20 February	1004	4.2
Porini	Male	33	6	20 February	981	5.4
Kuku	Female	26	9	15 March	892	7.0
Mbirikani	Male	22	7	15 March	974	6.6

Estimating vegetation productivity from satellite remote sensing

We used 10-day DMP data with a spatial resolution of 1 km freely downloaded from the Flemish Institute for Technological Research (VITO) (www.vito.be) as a proxy of vegetation productivity. DMP is directly proportional to net primary production (NPP). DMP is derived from SPOT-VEGETATION sensor on board of SPOT-4/5 satellite. DMP is a proxy for dry matter biomass increase, that is vegetation growth rate expressed in kilograms of dry matter per hectare per day ($\text{kg DM}^{-1} \text{ha}^{-1} \text{day}^{-1}$) (Copernicus, 2013). It is directly proportional to net primary production (NPP), thus a measure of forage available for elephants. The DMP is derived by combining satellite data with meteorological data (solar radiation and temperature) following the classical Monteith approach (Monteith, 1972). The DMP data covered the period February 2013 to August 2013. We calculated the mean DMP for the three seasons based on the dekadal data using ENVI IDL (ITT Visual Information Solutions, 2009). Next, we extracted the mean DMP for each grid that coincided with an elephant GPS location using the average of a 3×3 km window. A 3×3 km window was selected because it is the minimum home range size required by an adult elephant (Douglas-Hamilton, Krink & Vollrath, 2005). Mean DMP was used in this study because it demonstrated to be highly correlated to elephant time density.

Quantifying landscape fragmentation

To quantify landscape fragmentation, we first identified human infrastructure that leads to the subdivision and isolation of elephant habitat (Jaeger, 2000; Girvetz *et al.*, 2008). Infrastructure considered were roads, agricultural fields, towns and human settlements. Data on human settlements were extracted from the Kenyan Wildlife Services (KWS) database. We verified the accuracy of KWS settlement geodatabase by overlaying the settlements on Google Earth (www.googleearth.com), and missing settlements were also digitized. The agricultural field layer was classified from MOD13Q1 MODIS NDVI (250 m) data set. The 16-day MODIS NDVI images for the period from August 2010 to August 2013 were downloaded from the USGS EROS Data Center (<http://lpdaac.usgs.gov/>). The NDVI data were then reprojected from the sinusoidal projection to UTM zone 37 based on WGS 84 Spheroid in ENVI 4.7 (ITT Visual Information Solutions, 2009). Prior to classification, we reduced noise in the NDVI images caused by remnants of

clouds using a Savitzky–Golay filter (Jonsson & Eklundh, 2004) using the TIMESAT package. We used the maximum-likelihood classification method and 15 ground truth data to classify the NDVI images into three broad land cover types, that is agricultural fields, water and nonagriculture. The nonagriculture class was composed of bare ground, wooded grasslands, shrubland, woodland and riverine woodland. The overall classification accuracy using 42 test ground control points was 85% ($\text{kappa} = 0.68$).

Fragmentation geometries influence elephant behaviour within a certain distance. Thus, areas close to landscapes used by humans become unavailable for elephants. We thus created a buffer of 500 m for roads (Blake *et al.*, 2008) as well as settlements (Harris *et al.*, 2008), while for towns, a buffer of 4 km from the town centre was created (Harris *et al.*, 2008).

Next, we determined landscape fragmentation using the effective mesh size landscape metric (m_{eff}) extension in ArcGIS 10.1 (ESRI, 2011) (Girvetz *et al.*, 2008). The m_{eff} expresses the probability that any two locations in a landscape are connected (not separated by barriers such as roads, urban areas, agriculture fields and human settlements) (Girvetz *et al.*, 2008). The probability that the two locations are connected is then converted into the size of an area which becomes the effective mesh size. Increasing levels of fragmentation result in low effective mesh size. The m_{eff} is calculated as follows:

$$m_{\text{eff}} = \frac{1}{A_t} \sum_{i=1}^n A_i^2 \quad (2)$$

where n is the number of remaining patches, A_i = size of patch i , and A_t = the total area of the landscape under consideration which has been fragmented. Landscape fragmentation analysis was performed per 3×3 km grid cell to harmonize the data with the habitat utilization data.

Statistical analysis

Prior to testing whether time density was influenced by DMP and landscape fragmentation, we first randomly selected sample grid cells from the time density data layer in a GIS. Next, we tested the sampled data for spatial autocorrelation using Moran I (Tiefelsdorf, 2002) as a way to check for spatial independence. For all seasons, the time density data did not show any spatial independence ($P < 0.05$). The data were then randomly selected at increasing distance until spatial autocorrelation was no longer detected, that is at 6 km. Thus, for the dry season, a total of 60 grid cells were

randomly selected, while for the transition and wet season, 47 grid cells selected, respectively. We then extracted DMP values and effective mesh size values that spatially coincided with the randomly selected time density sample grids using overlay analysis in a GIS.

Next, we tested whether variation in time density could be explained by productivity and landscape fragmentation during different seasons. To achieve this, we used generalized additive models (GAMs) that allow for both linear and nonlinear responses (Venables & Ripley, 1999). GAMs are able to identify nonlinearities using flexible nonlinear modelling approaches that utilize spline smoothing (Venables & Ripley, 1999). Time density was treated as the response variable, while mean DMP and effective mesh size were covariates in the models. Thus, we considered seasonal models which included either productivity or effective mesh size as well as models that included both covariates. The models were fit using the *mgcv* package in R (R Development Core Team, 2012). Prior to model development, we checked for multicollinearity between the covariates using the variance inflation factor (VIF) (O'Brien, 2007; Dormann *et al.*, 2013). We included both covariates if $VIF < 10$. In all cases, the VIF between DMP and effective mesh size for also seasons was less than 10 indicating that collinearity did not exist between the explanatory variables. Selection of the best model was based on the corrected Akaike information criterion (AICc) adjusted for small sample size (Burnham & Andersen, 1998). We retained models with the lowest AICc score. Although our model combinations resulted in < 10 candidate models, we only report models that are within $\Delta AIC \leq 10$ as these have substantial support (Burnham & Anderson, 2002). Retention of competing models within 2 ΔAIC was based on the significance of the additional parameter/s (Arnold, 2010). In addition, we assessed the relative strength of each model by considering the Akaike weights (w_i) which measure the probability that model i is the best among the whole set of models (Burnham & Andersen, 1998). Models with w_i greater than 0.5 are normally considered as candidate models providing the best fit (Loveridge *et al.*, 2009).

Results

During the wet season, the most accurate model that explained elephant time density based on AICc included landscape fragmentation as the only covariate (Table 2). Elephant time density increased nonlinearly with a

Table 2 Candidate models for the wet, transition and dry season

Model and terms	AICc	df	ΔAIC	w_i
Wet season				
Effective mesh size	376.8	4	0.00	0.528
Mean DMP + effective mesh size	377.0	6	0.22	0.472
Transition season				
Mean DMP + effective mesh size	342.5	7	0.00	0.999
Dry season				
Mean DMP + effective mesh size	586.5	6	0.00	0.954
Effective mesh size	592.6	4	6.07	0.046

Model ranking is based on differences in the corrected Akaike's information criterion ($\Delta AICc$) and Akaike weights (w_i).

decrease in landscape fragmentation ($edf = 1.83$, $P < 0.001$) (Fig. 2; Table 3). However, the additive model with vegetation productivity and landscape fragmentation as covariates had a $\Delta AICc < 2$ showing that the model was also comparable in explaining elephant time density. However, we selected the model with effective mesh size ($w_i > 0.5$) as the inclusion of vegetation productivity in the model did not improve model performance ($edf = 2.239$, $P = 0.23$).

For the transition season, the most accurate model explaining time density of elephants based on AICc includes vegetation productivity and landscape fragmentation (Table 2). A nonlinear inverted U-shaped relationship is observed between time density and productivity ($edf = 3.13$, $P < 0.002$) during the transition season (Fig. 2), while time density increases nonlinearly with a decrease in fragmentation ($edf = 2.36$, $P < 0.001$) (Table 3). It is worthwhile to note that time density is relatively high at intermediate levels of productivity and at high effective mesh size (less fragmented landscape) (Fig. 3(a)).

For the dry season, the most accurate model that explained the time density of elephants includes both the effects of productivity and effective mesh size (Table 2). A nonlinear inverted U-shaped relationship was also observed between time density and productivity ($edf = 2$, $P < 0.007$) (Fig. 2), while time density increases nonlinearly with an increase in effective mesh size ($edf = 2.19$, $P < 0.001$) (Table 3). Time density is relatively high at intermediate levels of productivity and at high effective mesh size (Fig. 3(b)).

Discussion

Results from this study suggest that habitat utilization by elephants in human-dominated landscapes is most

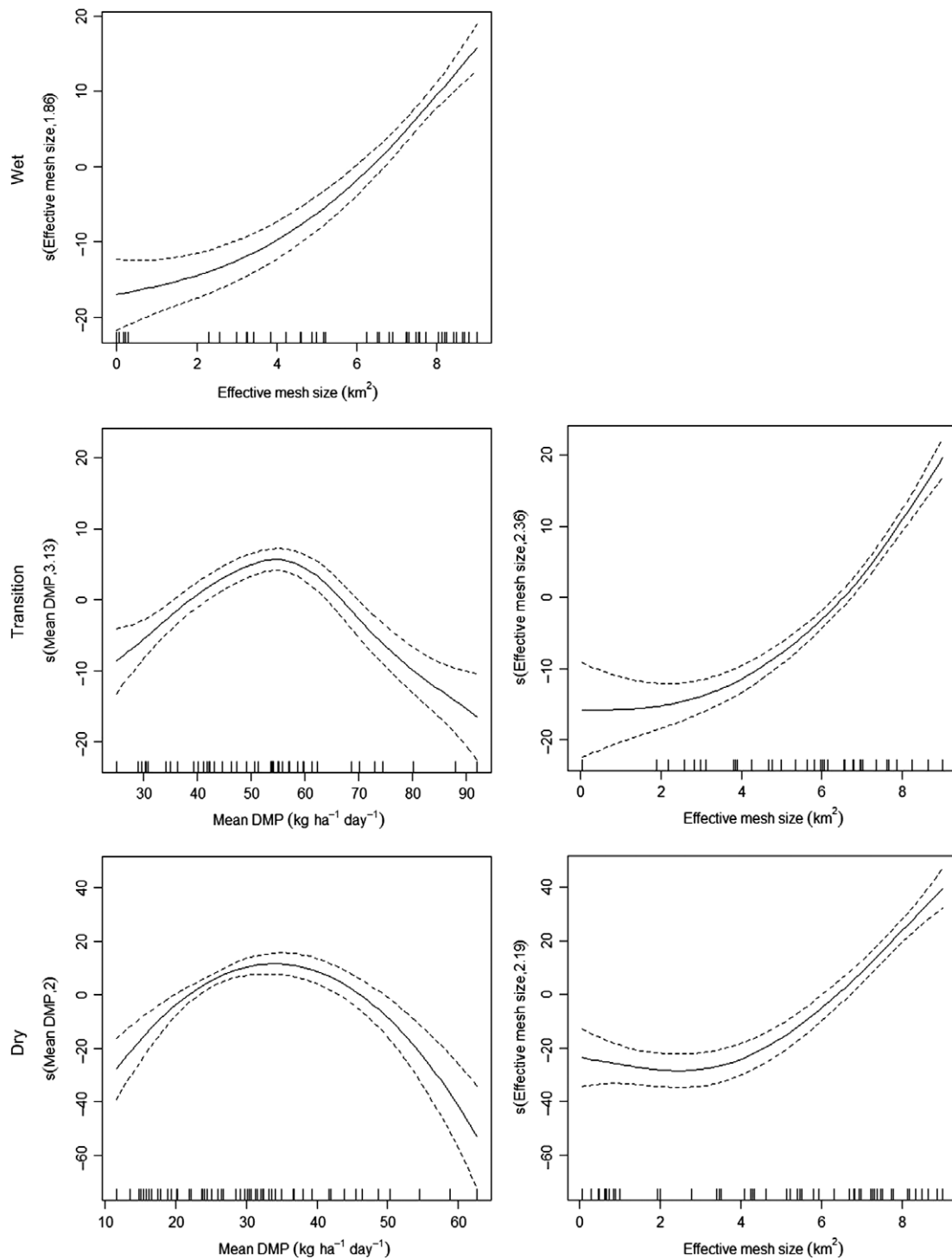


Fig 2 Effect of effective mesh size on time density during the wet season (upper panel) and productivity and effective mesh size during the transition season (middle panel) and dry season (lower panel). Estimates (solid lines) and point wise standard errors (dashed lines) are shown. Vertical lines on x-axis indicate the location of the observed sample values. s represents the fit of a smoothing spline for the continuous covariates, and the corresponding degrees of freedom are in brackets

Table 3 Estimated degrees of freedom (edf) and *F*-values for smooth-term predictors for the selected wet, transition and dry season models. Significance of predictors in the model is reflected by the *P*-value ($P < 0.05$)

Model	edf	<i>F</i>	<i>P</i>
Wet season			
Effective mesh size	1.86	14.870	<0.001
Transition season			
Mean DMP	3.13	5.114	0.002
Effective mesh size	2.36	21.916	<0.001
Dry season			
Mean DMP	2	5.425	0.007
Effective mesh size	2.19	13.259	<0.001

accurately explained by a combination of landscape fragmentation and vegetation productivity during the dry and transition seasons, than each of the factors alone (Table 2). However, during the wet season, fragmentation was the most important factor. The latter is not surprising as forage quality and availability are known to be high during the wet season, and thus, forage is limiting during the wet season (Birkett *et al.*, 2012; Zengeya & Murwira, 2014). This result is also consistent with observed behaviour of the African elephant in human-dominated landscapes where elephants often 'ensure' their safety from humans by spending more time in larger patches than in smaller patches (Barnes *et al.*, 1991; Graham *et al.*, 2009). In addition, this result is consistent with other studies (Fryxell, 1991; Drescher *et al.*, 2006; de Boer *et al.*, 2013) that have reported a preference by herbivores for areas with intermediate biomass/productivity. For example, McNaughton (1985) observed a high number of herbivores at intermediate levels of green biomass in the Serengeti ecosystem. We thus deduce a combination of

landscape fragmentation and productivity enhances our explanation of herbivore habitat utilization in human-dominated landscapes (Fig. 3). To the best of our knowledge, previous studies have not incorporated the combined effects of fragmentation and productivity in a single model to explain herbivore movement.

The positive relationship between elephant time density and effective mesh size is consistent with known elephant habitat preferences, that is that elephants 'prefer' to spend more time in larger unfragmented patches than smaller ones. For example, Buij *et al.* (2007) found a negative relationship between human infrastructure and elephant density. In this study, we used an innovative compound landscape fragmentation metric, that is the effective mesh size landscape metric to assess the effect of fragmentation on elephants, and the results showed consistency with what is ecologically expected of elephant response to fragmentation. Thus, we deduce that the effective mesh size landscape metric enables ecologically meaningful characterization of landscape fragmentation useful for predicting elephant movement.

The unimodal or inverted U-shaped relationship between DMP and time density of elephants found in this study has been reported for herbivores other than elephants. For example, de Boer *et al.* (2013) observed a unimodal relationship although focusing on the relationship between NDVI and elephant densities. These results imply that herbivores often make a trade-off between quality and quantity where areas of low productivity experience low habitat use (Western & Lindsay, 1984) as they may not offer sufficient forage quantity, while areas of high productivity are limited by plant chemical constituents and low forage quality (Fryxell, 1991; Mueller *et al.*, 2008). Bos, van de Koppel & Weissing (2004) also suggests that high

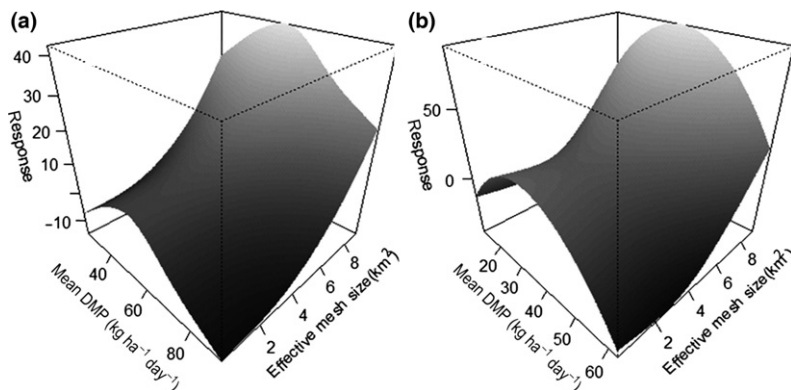


Fig 3 3D plots showing the relationship between time density (response) and the selected predictors, mean DMP (productivity) and effective mesh size during the (a) transition and (b) dry season. The response = time density on the z axis

productivity areas are less likely to be used due to increased costs of locomotion. This is also consistent with Loarie, van Aarde & Pimm (2009) who reported that elephants avoid densely vegetated areas (associated with high productivity values). Overall, the relationship observed between time density and productivity in this study amplifies the utility of DMP in understanding herbivore distribution. To the best of our knowledge, satellite remote sensing-derived DMP has not been previously used to understand wildlife habitat utilization.

Conclusion

The main objective of this study was to test whether landscape fragmentation and vegetation productivity explain habitat utilization of African elephants. Based on the results, we conclude that elephants spend much of their time in landscapes that are less fragmented and characterized by intermediate vegetation productivity. We also conclude that remotely sensed DMP can successfully be used to explain herbivore distribution. Results of this study imply that if the persistence of the African elephant is to be ensured, large undisturbed areas of intermediate vegetation productivity need to be conserved within savannah landscapes.

Acknowledgements

We are grateful to the Kenya Wildlife Services (KWS) for granting us permission to carry out this study in the Amboseli ecosystem and access to elephant GPS tracking data, fragmentation geometry data, and their assistance during fieldwork. We also acknowledge the International Fund for Animal Welfare (IFAW), for providing financial support for collaring elephants. We also thank the School for Field Studies (SFS) at Kimana and The Amboseli Trust for Elephants (ATE) for their support.

References

- ALTMANN, J., ALBERTS, S., ALTMANN, S. & ROY, S. (2002) Dramatic change in local climate patterns in the Amboseli basin, Kenya. *Afr. J. Ecol.* **40**, 248–251.
- ARNOLD, T.W. (2010) Uninformative parameters and model selection using Akaike's information criterion. *J. Wildl. Manage.* **74**, 1175–1178.
- BARNES, R.F.W., BARNES, K.L., ALERS, M.P.T. & BLOM, A. (1991) Man determines the distribution of elephants in the rain forests of northeastern Gabon. *Afr. J. Ecol.* **29**, 54–63.
- BERGMAN, C.M., FRYXELL, J.M., GATES, C.C. & FORTIN, D. (2001) Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* **70**, 289–300.
- BIRKETT, P.J., VANAK, A.T., MUGGEO, V.M.R., FERREIRA, S.M. & SLOTOW, R. (2012) Animal perception of seasonal thresholds: changes in elephant movement in relation to rainfall patterns. *PLoS One* **7**, e38363.
- BLAKE, S., DEEM, S.L., STRINDBERG, S., MAISELS, F., MOMONT, L., ISIA, I.-B., DOUGLAS-HAMILTON, I., KARESH, W.B. & KOCK, M.D. (2008) Roadless wilderness area determines forest elephant movements in the congo basin. *PLoS ONE* **3**, e3546.
- DE BOER, W.F., VAN LANGEVELDE, F., PRINS, H.H.T., DE RUITER, P.C., BLANC, J., VIS, M.J.P., GASTON, K.J. & HAMILTON, I.D. (2013) Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. *Biol. Conserv.* **159**, 468–476.
- BOS, D., VAN DE KOPPEL, J. & WEISSING, F.J. (2004) Dark-bellied brent geese aggregate to cope with increased levels of primary production. *Oikos* **107**, 485–496.
- BUIJ, R., MCSHEA, W.J., CAMPBELL, P., LEE, M.E., DALLMEIER, F., GUIMOND, S., MACKAGA, L., GUISSOU, N., MBOUMBA, S., HINES, J.E., NICHOLS, J.D. & ALONSO, A. (2007) Patch-occupancy models indicate human activity as major determinant of forest elephant *Loxodonta cyclotis* seasonal distribution in an industrial corridor in Gabon. *Biol. Conserv.* **135**, 189–201.
- BURNHAM, K.P. & ANDERSEN, D.R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- BURNHAM, K.P. & ANDERSON, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- BURNSILVER, S., WORDEN, J. & BOONE, R. (2008). Processes of Fragmentation in the Amboseli Ecosystem, Southern Kajiado District, Kenya. In: *Fragmentation in Semi-Arid and Arid Landscapes: Consequences for Human and Natural Systems* (Eds. K. A. GALVIN, R. S. REID, R. H. BEHNKE and N. T. HOBBS). Springer, Netherlands.
- CHIYO, P.I., LEE, P.C., MOSS, C.J., ARCHIE, E.A., HOLLISTER-SMITH, J.A. & ALBERTS, S.C. (2011) No risk, no gain: effects of crop raiding and genetic diversity on body size in male elephants. *Behav. Ecol.* **22**, 552–558.
- CHIYO, P.I., WILSON, J.W., ARCHIE, E.A., LEE, P.C., MOSS, C.J. & ALBERTS, S.C. (2014) The influence of forage, protected areas, and mating prospects on grouping patterns of male elephants. *Behav. Ecol.* **25**, 1494–1504.
- Copernicus. (2013). Dry Matter Productivity [Online]. Available: <http://land.copernicus.eu/global/products/dmp> [Accessed 10 October 2013].
- DORMANN, C.F., ELITH, J., BACHER, S., BUCHMANN, C., CARL, G., CARRÉ, G., MARQUÉZ, J.R.G., GRUBER, B., LAFOURCADE, B., LEITÃO, P.J., MÜNKEMÜLLER, T., MCCLEAN, C., OSBORNE, P.E., REINEKING, B., SCHRÖDER, B., SKIDMORE, A.K., ZURELL, D. & LAUTENBACH, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46.

- DOUGLAS-HAMILTON, I., KRINK, T. & VOLLRATH, F. (2005) Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* **92**, 158–163.
- DRESCHER, M., HEITKÖNIG, I.M.A., VAN DEN BRINK, P.J. & PRINS, H.H.T. (2006) Effects of sward structure on herbivore foraging behaviour in a South African savanna: an investigation of the forage maturation hypothesis. *Austral. Ecol.* **31**, 76–87.
- ESRI (2011) *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute, Redlands, CA.
- EVANS, L.A. & ADAMS, W.M. (2016) Fencing elephants: the hidden politics of wildlife fencing in Laikipia, Kenya. *Land Use Policy* **51**, 215–228.
- FRAIR, J.L., FIEBERG, J., HEBBLEWHITE, M., CAGNACCI, F., DECESARE, N.J. & PEDROTTI, L. (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2187–2200.
- FRYXELL, J.M. (1991) Forage Quality and Aggregation by Large Herbivores. *Am. Nat.* **138**, 478–498.
- GIRVETZ, E.H., THORNE, J.H., BERRY, A.M. & JAEGER, J.A.G. (2008) Integration of landscape fragmentation analysis into regional planning: a statewide multi-scale case study from California, USA. *Landscape Urban Plan* **86**, 205–218.
- GRAHAM, M.D., DOUGLAS-HAMILTON, I., ADAMS, W.M. & LEE, P.C. (2009) The movement of African elephants in a human-dominated land-use mosaic. *Anim. Conserv.* **12**, 445–455.
- GROOM, R.J. & WESTERN, D. (2013) Impact of Land Subdivision and Sedentarization on Wildlife in Kenya's Southern Rangelands. *Rangeland Ecol. Manag.* **66**, 1–9.
- HARRIS, G.M., RUSSELL, G.J., VAN AARDE, R.I. & PIMM, S.L. (2008) Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. *Oryx* **42**, 66–75.
- HEBBLEWHITE, M., MERRILL, E. & McDERMID, G. (2008) A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* **78**, 141–166.
- HOWE, M., OKELLO, M.M. & DAVIS, J.M. (2013) Interspecific Variation in the Distribution of Ungulates Relative to Human Infrastructure Surrounding Amboseli National Park. *Afr. Zool.* **48**, 159–166.
- ITT Visual Information Solutions (2009). *ENVI 4.9*. Colorado: ITT Industries Inc.
- JAEGER, J.G. (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecol.* **15**, 115–130.
- JONSSON, P. & EKLUNDH, L. (2004) TIMESAT - a program for analyzing time-series of satellite sensor data. *Comput. Geosci.* **30**, 833–845.
- LEIMGRUBER, P., GAGNON, J.B., WEMMER, C., KELLY, D.S., SONGER, M.A. & SELIG, E.R. (2003) Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. *Anim. Conserv.* **6**, 347–359.
- LOARIE, S.R., VAN AARDE, R.J. & PIMM, S.L. (2009) Elephant seasonal vegetation preferences across dry and wet savannas. *Biol. Conserv.* **142**, 3099–3107.
- LOVERIDGE, A.J., VALEIX, M., DAVIDSON, Z., MURINDAGOMO, F., FRITZ, H. & MACDONALD, D.W. (2009) Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. *Ecography* **32**, 953–962.
- MATAWA, F., MURWIRA, A. & SCHMIDT, K.S. (2012) Explaining elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*) spatial distribution in the Zambezi Valley using maximum entropy modelling. *Ecol. Model.* **242**, 189–197.
- McNAUGHTON, S.J. (1985) Ecology of a Grazing Ecosystem: the Serengeti. *Ecol. Monogr.* **55**, 260–294.
- MONTEITH, J.L. (1972) Solar radiation and productivity in tropical ecosystems. *J. Appl. Ecol.* **9**, 747–766.
- MUELLER, T., OLSON, K.A., FULLER, T.K., SCHALLER, G.B., MURRAY, M.G. & LEIMGRUBER, P. (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J. Appl. Ecol.* **45**, 649–658.
- MURWIRA, A. & SKIDMORE, A.K. (2005) The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. *Landscape Ecol.* **20**, 217–234.
- NGENE, S.M., SKIDMORE, A.K., GILS, V.H., WIEREN, V.S.E., PRINS, H.H.T., DOUGLAS-HAMILTON, I. & TOXOPEUS, A.G. (2012) *Intensity of elephant occupancy in Marsabit protected area, Kenya: effects of Biophysical and Anthropogenic Factors*. Elephants, Ecology, Behavior, and Conservation. Nova Scientific Publishers Inc, New York.
- O'BRIEN, R. (2007) A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Qual. Quant.* **41**, 673–690.
- OWEN-SMITH, N. & CHAFOTA, J. (2012) Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *J. Mammal.* **93**, 698–705.
- PACHAVO, G. & MURWIRA, A. (2014) Remote sensing net primary productivity (NPP) estimation with the aid of GIS modelled shortwave radiation (SWR) in a Southern African Savanna. *Int. J. Appl. Earth Obs. Geoinf.* **30**, 217–226.
- R Development Core Team (2012) *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- TIEFELSDORF, M. (2002) The Saddlepoint approximation of Moran's i 's and local Moran's I 's reference distributions and their numerical evaluation. *Geogr. Anal.* **34**, 187–206.
- TUQA, J.H., FUNSTON, P., MUSYOKI, C., OJWANG, G.O., GICHUKI, N.N., BAUER, H., TAMIS, W., DOLRENY, S. & VAN'T ZELFDE M., DE SNOO, G. R., DE IONGH, H. H. (2014) Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. *Glob. Ecol. Conserv.* **2**, 1–10.
- VENABLES, W.N. & DICHMONT, C.M. (2004) GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fish. Res.* **70**, 319–337.
- VENABLES, W.N. & RIPLEY, B.D. (1999) *Generalized Linear Models*. Modern Applied Statistics with S-PLUS. Springer, New York.
- WALL, J., WITTEMYER, G., KLINKENBERG, B., LEMAY, V. & DOUGLAS-HAMILTON, I. (2013) Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biol. Conserv.* **157**, 60–68.

- WESTERN, D. (2007) A half a century of habitat change in Amboseli National Park, Kenya. *Afr. J. Ecol.* **45**, 302–310.
- WESTERN, D., GROOM, R. & WORDEN, J. (2009) The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. *Biol. Conserv.* **142**, 2538–2546.
- WESTERN, D. & LINDSAY, W.K. (1984) Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.* **22**, 229–244.
- WILMSHURST, J.F., FRYXELL, J.M. & HUDSON, R.J. (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behav. Ecol.* **6**, 209–217.
- XU, C., LI, Y., HU, J., YANG, X., SHENG, S. & LIU, M. (2012) Evaluating the difference between the normalized difference vegetation index and net primary productivity as the indicators of vegetation vigor assessment at landscape scale. *Environ. Monit. Assess.* **184**, 1275–1286.
- ZENGEYA, F. M. & MURWIRA, A. (2014) Intraspecific variations in home range overlaps of a semi-free range herbivore are explained by remotely sensed productivity. *Int. J. Geogr. Inf. Sci.* **30**, 1–15.

(Manuscript accepted 30 May 2016)

doi: 10.1111/aje.12346