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RESEARCH ARTICLE

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Elephants move faster in small fragments of low productivity in Amboseli ecosystems: Kenya

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ABSTRACT
Understanding factors affecting the behaviour and movement patterns of the African elephant is important for wildlife conservation, especially in increasingly human-dominated savanna landscapes. Currently, knowledge on how landscape fragmentation and vegetation productivity affect elephant speed of movement remains poorly understood. In this study, we tested whether landscape fragmentation and vegetation productivity explains elephant speed of movement in the Amboseli ecosystem in Kenya. We used GPS collar data from five elephants to quantify elephant speed of movement for three seasons (wet, dry and transitional). We then used multiple regression to model the relationship between speed of movement and landscape fragmentation, as well as vegetation productivity for each season. Results of this study demonstrate that landscape fragmentation and vegetation productivity predicted elephant speed of movement poorly ($R^2 < 0.4$) when used as solitary covariates. However, a combination of the covariates significantly ($p < 0.05$) explained variance in elephant speed of movement with improved R^2 values of 0.69, 0.45, 0.47 for wet, transition and dry seasons, respectively.

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KEYWORDS
Fragmentation; dry matter productivity; speed of movement; effective mesh size

Introduction

Mega-herbivores, such as the African elephant (*Loxodonta africana* hereinafter elephant) traverse a mosaic of heterogeneous landscapes in search of resources such as forage and water. The distribution of these resources in most landscapes, especially in African savannas is spatially and temporally heterogeneous (de Beer & van Aarde 2008). Thus, elephants objectively roam the landscape guided by their own instincts in order to maximize on forage intake and water availability, as well as minimize human contact (Harris et al. 2008).

Understanding factors affecting the distribution and persistence of elephants is key to its conservation in increasingly human-dominated savanna landscapes (Murwira & Skidmore 2005). Although foraging resources have been widely hypothesized to be the major factor influencing elephant movement (Loarie et al. 2009; Birkett et al. 2012; Chiyo et al. 2014), human-induced landscape fragmentation

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is also considered important (Blake et al. 2008; de Boer et al. 2013). Thus, the movement pattern of elephants has to take into account both foraging resources, as well as landscape fragmentation. In this regard, understanding the combined effect of forage resources and landscape fragmentation on elephant movement patterns is critical for predicting and managing the species' response to natural and anthropogenic changes in the landscape (Buij et al. 2007).

Herbivores do not only respond to the variability in forage resources but also to the patchiness of forage resources (Murwira & Skidmore 2005). It is therefore important to understand the response of elephants to forage resources and habitat fragmentation (Groom & Western 2013). The existence of human infrastructure (hereinafter 'fragmentation geometries'), such as roads, settlements and agricultural fields not only impede animal movement but also fragment their habitats (BurnSilver et al. 2008; Western et al. 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). Fragmentation geometries are known to trigger behaviour change in elephants (Leimgruber et al. 2003). For example, Blake et al. (2008) observed that elephants increase their average daily speed 14-fold when crossing roads in the Congo Basin. Human-related fragmentation has also been linked to increasing elephant poaching levels and human wildlife conflict (Maingi et al. 2012; Ihwagi et al. 2015). In this regard, we hypothesize that elephants move faster in more fragmented habitats of low productivity compared to less fragmented habitats of high productivity. Thus, any meaningful prediction of animal movement in response to fragmentation geometries should consider their combined effect (Gara 2014). It is therefore 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 is critical in providing improved insights into elephant movement patterns.

The advent of remote sensing has allowed for the quantification of forage resources over large spatial extents at high temporal resolution. To this end, 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 et al. 2009; Matawa et al. 2012). Although vegetation indices are useful as proxies of productivity, they are not able to account for short-term variations in productivity resulting from, e.g. changes in meteorological conditions (Monteith 1972). In this regard, there is need for the development of measures of forage resources that are sensitive to changes in meteorological conditions i.e. 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.

In this study, we test whether and how seasonal speed of movement of GPS-collared elephant is influenced by landscape fragmentation and remotely sensed DMP. We hypothesize that elephants would move faster in more fragmented habitats of low productivity compared to less fragmented habitats of high productivity.

Materials and methods

Study area

The Amboseli ecosystem (Figure 1) is located in Kajiado District, Rift Valley Province, Kenya. The ecosystem covers an area ~8500 km^2 (BurnSilver et al. 2008). The area is classified as arid to semi-arid savanna with annual rainfall ranging from 250 to 600 mm. Rainfall is seasonal with most rains being received from March to April and from November to December. The area also experiences a

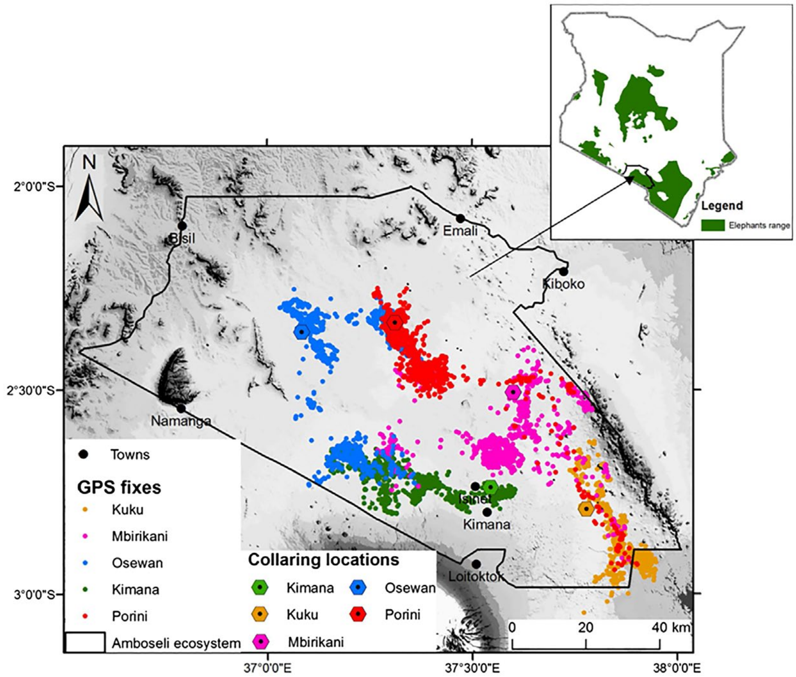

Figure 1. Spatial distribution of GPS fixes for each elephant group in the study area and elephant range in Kenya (Insert).

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

dry period (June–September) and two transition periods (January–February and October–November) (Altmann et al. 2002). Temperature ranges between 20 and 30 °C, while elevation varies between 850 and 1350 m above mean sea level. The dominant vegetation types include the broad-leaf 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 et al. 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 18 February and 15 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 belonged to different families (Table 1). The five GPS-collared elephants represent five different elephant herds. Elephant herds can change numbers and composition; examination of our tracking data indicated that these five collared animals belonged to distinct groups throughout the monitoring period. GPS collars were fitted on each elephant and were programmed to log the position of each individual after every 4 h for the period 20 February 2013–31 August 2013 resulting in a total of 4872 GPS fixes. The GPS collars had a relative error of 10 m. 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 re-projected 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–August) and transition season (February and May). This was based on the premise that the spatial and temporal variation in resources such as forage and water influence the distribution of the elephants in space and time.

Elephant speed of movement

The speed of movement (km/hr) was computed from the GPS fixes by dividing the distance between two consecutive GPS fixes by time lapse between the fixes (Galanti et al. 2006). After computing speed of movement of each elephant, the data were checked for consistency with known knowledge on elephant speed of movement. The known maximum speed of movement of an African elephant is approximately 13 km/hr (Wall et al. 2013), thus any speed of movement beyond the maximum threshold was removed from the data-set before analysis. Only one track was removed from the data-set. The abnormal speed of the removed track was a result of missing of consecutive fixes due to GPS malfunction. After computing the speed for each elephant, the data were merged and a velocity grid tool in Movement Ecology Tools for ArcGIS (ArcMET) (Wall 2013) was used to summarize the mean speed of movement per 9 km^2 grid for each of the three seasons. The velocity grid tool computes the mean speed of all tracks intersecting a user-specified grid, in this case a 9 km^2 grid was used. A grid cell of 9 km^2 was selected because the minimum home range area required by a elephant is 10 km^2 (Douglas-Hamilton et al. 2005).

Estimating forage abundance based on dry matter productivity

We used 10-day DMP satellite-derived data with a spatial resolution of 1 km freely (www.vito.be) to estimate forage abundance available for elephants. DMP is a measure of vegetation productivity that 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 i.e. vegetation growth rate expressed in kilogrammes of dry matter per hectare per day (kg DM/ha/day) (Copernicus 2013). Considering that an elephant is a bulky feeder (Maloiy & Clemens 1991; Cumming et al. 1997), we conceptualized that higher DMP would imply more forage resources 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–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. The mean of 3 × 3 pixels were used so as to harmonize the DMP data (1 km resolution) to the elephant speed of movement data-set (3 km resolution) and landscape fragmentation data (3 km resolution).

Quantifying landscape fragmentation

In order to quantify landscape fragmentation, we first identified human infrastructure that lead 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 also verified the settlement data by overlaying the settlements on Google Earth (www.googleearth.com) and also included missing settlements by digitizing them. 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 Centre (http://lpdaac.usgs.gov/). The NDVI data were then re-projected 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 (Jönsson & Eklundh 2004) in the TIMESAT package. We used the maximum likelihood classification method and 15 ground truth data to classify the NDVI images into three broad landcover types, i.e. agricultural fields, water and non-agriculture. The non-agriculture 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% ($\kappa = 0.68$).

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 (Girvetz et al. 2008; ESRI 2011). 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

$$m_{\text{eff}} = \frac{1}{At} \sum_{i=1}^{n} Ai^2. \tag{1}$$

where n is the number of remaining patches, Ai = size of patch i, and At = 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 elephant speed of movement was influenced by DMP and landscape fragmentation, we first randomly selected sample grid cells from the speed of movement data layer in a GIS. Next, we tested the sampled data for spatial auto-correlation using *Moran's I* (Tiefelsdorf 2002) as a way to check for spatial independence. For all seasons the speed of movement data was significantly spatially auto-correlated. The data were then randomly selected at increasing distance until spatial auto-correlation was no longer detected, i.e. at 6 km. The total number of sample grid cells for the dry season was 71, transition was 52 and wet season was 63. 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 speed of movement could be explained by productivity and landscape fragmentation during different seasons. In order to achieve this, we used regression analysis. Speed of movement 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. 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 all 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 & Anderson 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 ΔAIC ≤ 10 as these have substantial support (Burnham & Anderson 2002). Retention of competing models within 2 ΔAIC was based on the significance of

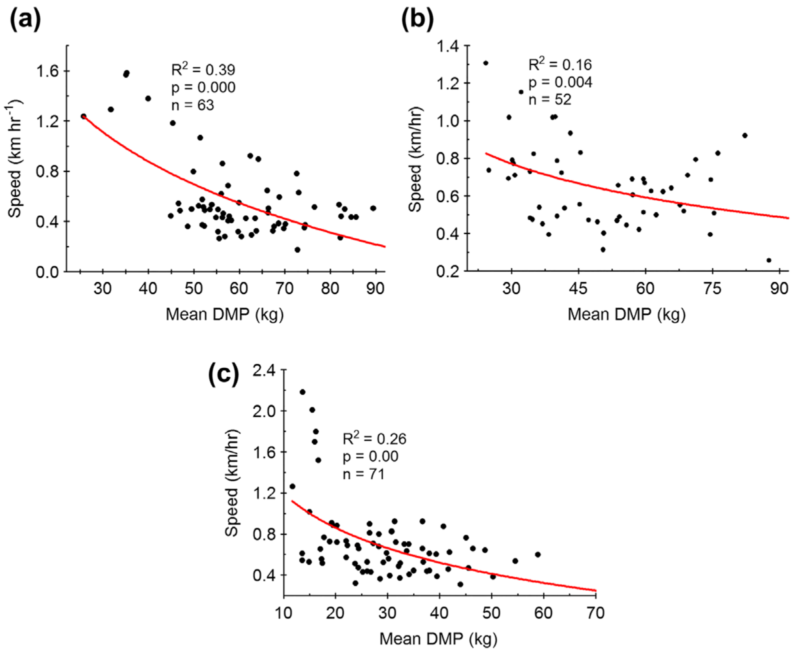

Figure 2. Relationships between forage abundance and speed of movement for (a) wet season (b) transition season and (c) dry season.

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 & Anderson 1998). Models with w_i greater than 0.5 are normally considered as candidate models providing the best fit (Loveridge et al. 2009).

Results

The relationship between landscape fragmentation and elephant speed of movement for all the three seasons are best described by non-linear regression models (Figures 2 and 3). An increase in level of landscape fragmentation resulted in an increase in speed of movement. This implies that elephants move faster in more fragmented landscapes and generally reduce speed in less fragmented landscapes. A significant ($p < 0.05$) negative relationship was observed between forage amounts and speed of movement throughout the three seasons. Elephants moved faster in landscapes characterized by low forage resources.

Based on model evaluations for the three seasons, we observed that the top models i.e. with the lowest AICc and relatively higher Akaike weights (w_i) explaining elephant speed of movement included the effect of both fragmentation and DMP (Table 2). For the wet and dry seasons a model with DMP and effective mesh size as solitary variables had no weights at all. For the transition season, the weights for effective mesh size and DMP are all less than 0.5 indicating little support to explain elephant speed of movement as solitary variables. It is worthwhile to note that the interaction effect of landscape fragmentation and DMP explained speed of elephant movement with the lowest AICc, more weights (Table 2) and high R^2 (Figure 4) across all the three seasons. Elephants move faster in landscapes that are highly fragmented and contain very low forage across the three seasons in Amboseli (Figure 3).

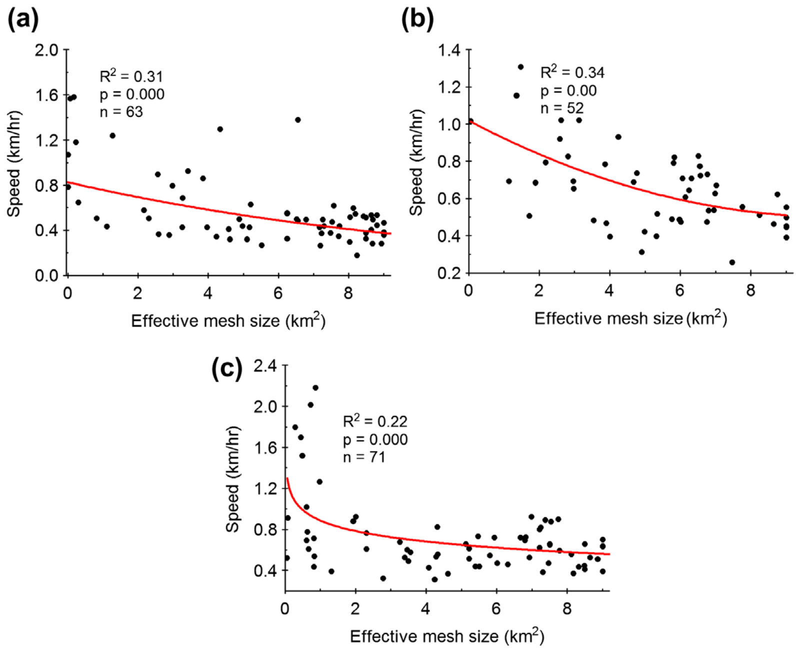

Figure 3. Relationships between speed of movement and landscape fragmentation for (a) wet season (b) transition season and (c) dry season.

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

Season	Model and terms	AICc	df	ΔAIC	w_i
Wet	Mean DMP + effective mesh size	−27.65	7	0	1
Transition	Mean DMP + effective mesh size	−27.53	7	0.00	0.86
	Effective mesh size	−23.75	5	3.78	0.13
	Mean DMP	−18.13	5	9.39	0.01
Dry	Mean DMP + effective mesh size	29.09	5	0	1

Model ranking is based on differences in the corrected Akaike's Information Criterion (ΔAICc) and Akaike weights (w_i).

Discussion

Results from this study suggest that the speed of movement of elephants in human-dominated landscapes is better explained by a combination of landscape fragmentation and vegetation productivity across all seasons, than each of the explanatory alone. Although previous studies have attempted to link elephant movement patterns with fragmentation geometries such as agriculture fields (Hoare 1999), roads (Barnes et al. 1991; Blake et al. 2008) and human settlements, the effect of these fragmentation geometries have often been analysed in isolation. In this regard, understanding the combined effects of fragmentation geometries that influence elephant movement is critical for conservation. Such kind of approach helps wildlife managers and landuse planners to make informed decisions that balance wildlife conservation and human need for space.

The relationship between elephant speed of movement, productivity and fragmentation observed in this study is consistent with known elephant behaviour, i.e. that elephants move faster in more fragmented patches of low productivity. For example, Graham et al. (2009) observed that elephants in Laikipia, central Kenya moved faster in pastoral and smallholder landuse types where human presence and activities are high compared to forests and large-scale ranches landuse where human presence and activities are low. Moreover, elephants are known to increase their speed of movement when for

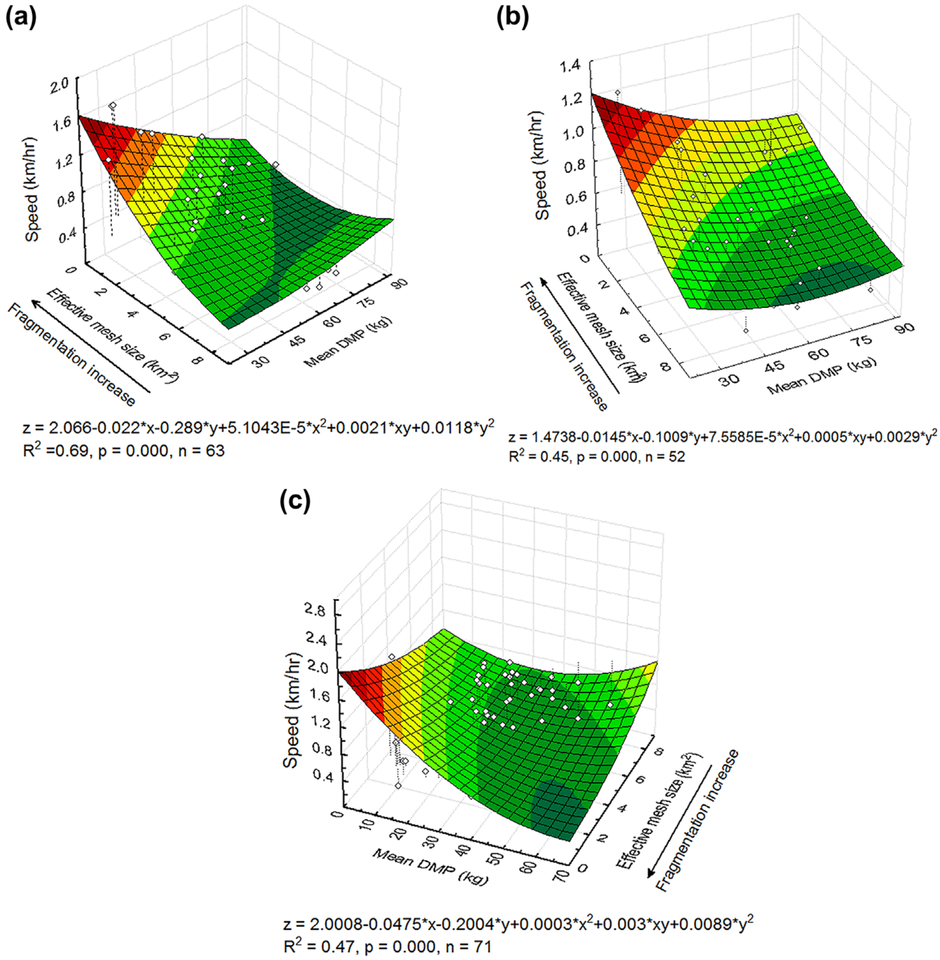

Figure 4. Relationships between landscape fragmentation level, forage abundance and speed of movement. Speed increase from dark green (low speed) to dark red (high speed). (a) Wet season, (b) transition season (c) dry season.
Note: White dots represent points used to compute the model.

example crossing roads. In another study, Blake et al. (2008) found out that elephants increase their average daily speed 14-fold when crossing roads in the Congo Basin. A number of studies have also demonstrated that poaching is correlated with distance from roads (Barnes et al. 1991; Blake et al. 2008; Maingi et al. 2012). Douglas-Hamilton et al. (2005) observed that elephants significantly move faster along unprotected corridors than inside protected zones, suggesting awareness of hunting pressure in human-dominated landscapes. These studies support the notion observed in this study that landscape fragmentation triggers behaviour change in elephants by moving faster in human-dominated landscape. In this study, we used an innovative compound landscape fragmentation metric, i.e. 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.

Elephants are known to move faster in landscapes characterized by low foraging resources due to low forage intake. In the Amboseli ecosystem, a shift from extensive nomadic pastoralism and transhumance to intensive sedentary agro-pastoralism has resulted in limited mobility of pastoral herds and establishment of permanent settlements. The transition from nomadic pastoralism to sedentarization of the Maasai tribesman has presented a twofold challenge to elephant movement patterns. Firstly, exclusion of prime habitats due to an increase in permanent settlements and expanding agriculture. Worden (2007) observed low wildlife densities in Eselenkei (part of Amboseli ecosystem) where permanent settlements and high livestock concentration are known to exist. Secondly, the sedentarization of the Maasai tribesman has resulted in low net productivity and subsequently low foraging resources in landscapes around settlements as a result of increased livestock grazing (Groom & Western 2013). These two challenges potentially trigger behaviour change in elephants by moving faster and spending less time in these human-dominated landscapes.

Although this study successfully demonstrated the effect of landscape fragmentation and productivity based on 4-h interval GPS fixes. There is need for future studies to ascertain whether high temporal resolution GPS fixes of probably 1 h or less can improve results shown in this study.

Conclusion

The main objective of this study was to test whether landscape fragmentation and vegetation productivity explain speed of movement of African elephants. Based on the results we conclude that elephants move faster in landscapes that are more fragmented and characterized by low vegetation productivity. We also conclude that remotely sensed DMP can successfully be used to explain herbivore movement patterns. Results of this study imply that if the persistence of the African elephant is to be ensured, large undisturbed areas of relatively moderate to high vegetation productivity need to be conserved within savanna landscapes.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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