Geospatial patterns and behavioural responses of elephants to cattle and mortality risk in a pastoralist Maasai Mara landscape, Kenya

ABSTRACT

The unprecedented pace and scale of anthropogenic changes to environments and direct species harvesting are causing substantial wildlife species declines globally. For many species, behavioural plasticity forms the first line of response to exploitation and environments altered by humans. Although behavioural plasticity can enhance survival in altered environments, maladaptive behavioral scenarios or "evolutionary traps" can threaten the persistence of some species from anthropogenic alteration. In elephants, poaching bias towards older individuals. Altered social structures and habitats may impact decision making of elephant social groups in anthropogenic landscapes creating maladaptive responses that can amplify conflict. In this study, we examined geospatial patterns of elephant mortality risk, cattle distribution, Normalized Difference Vegetation Index (NDVI) and habitat protection status on elephant distribution and group-sizes at the Maasai Mara National Reserve (MMNR), Community Wildlife Conservancies (CWC) and surrounding Community Grazing Lands (CGL) in the Maasai Mara ecosystem. We also investigated how social group type, group-size, age of the oldest individual in a group and habitat openness influence elephant response to experimental cowbells. Using kernel density analyses from ten years of georeferenced clinical reports pertaining to elephant injuries and elephant mortality due to poaching, we show that elephant injuries and mortalities were highest in CWC and CGL compared to MMNR. Our study showed a positive relationship between elephant group-size with NDVI, and the risk of elephant mortality or injury. Concealed cowbells played to elephants revealed that elephant aggression towards cowbells was not influenced by matriarch age, group-size, habitat type or status of habitat protection. However, defensive bunching was positively related to the matriarch's age, group-size and social group type. These results suggest sensitivity of older matriarchs to poaching risk and that elephants use group defense or avoidance behavioural strategies irrespective of vegetation cover.

Keywords: Evolutionary Traps, Human–Elephant Conflict, Mortality Hotspots

1. INTRODUCTION

Humans are causing unprecedented changes to environments from environmental degradation to over-harvesting of wildlife populations [1, 2]. These anthropogenic impacts are causing substantial species declines globally, but less attention is given to behavioural changes caused by the loss of ecological knowledge and habitat alteration. Given the rapid pace and the global scale of human-induced environmental changes, it is vital to understand how organisms cope with increasing anthropogenic disturbances. For many species, changes in behaviour or behavioural plasticity forms the first line of response to anthropogenic exploitation and altered environments [3], and this may moderate impacts of environmental change on species survival. Although behavioural plasticity can buffer some species against environmental changes [3], maladaptive behavioural scenarios, called "evolutionary traps", can threaten the persistence of some species. Moreover, some behavioral changes may be due to loss of specific individuals with ecological knowledge on how to respond to dynamic ecological and social environments due to animal harvesting. Evolutionary traps occur when behaviours that evolved for survival in the original environment change, resulting in lowered fitness in altered contemporary environments. Understanding geospatial patterns and behavioral responses of wildlife species to harvesting and anthropogenic environments is vital in contemporary conservation as this information is needed to effectively mitigate or eliminate evolutionary traps. Such information also enables wildlife managers understand why some species thrive in anthropogenic landscapes while other species do not, and it is critical in predicting the influence of anthropogenic disturbance on different wildlife species.

Several studies show that elephants (*Loxodonta africana africana*, Blumenbach) can facultatively alter their behavior to avoid risk of human encounter. In human-dominated landscapes, elephants spend a high proportion of night hours close to human settlements and nearly all daylight hours in protected areas [4]. Elephants also move swiftly in areas dominated by humans compared to their movement in protected areas [5,6,7] and can completely avoid to use areas with conspicuous human presence [8,9]. Where hunting is the main cause of mortality, animals may assume anti-predator behavior in the presence of humans, such as increase in group size, amplified vigilance and flight response or increased aggression towards humans [10,11]. Many animals, particularly ungulates, bunch together in a defensive and protective formation in the presence of predators [12,13]. Large groups of ungulates are more effective at defending themselves than are solitary animals because they can join up and form defensive formations with their vulnerable rumps protected by other members of the group [14,15]. Elephants form large temporary aggregations or large group sizes in human dominated habitats such as when foraging on farms or in communal grazing lands versus when foraging in protected areas or refuge habitats [16,17]. Elephants also form a characteristic defensive bunching posture against predators such as lions or humans to protect their vulnerable young from predation risk. The infants and juveniles are held in the inner circle surrounded by a concentric circle of adults lead by a matriarch [18].

In long-lived species, where knowledge and experience are likely to be an important behavioral trait for coping with temporally- and spatially-variable environments, harvesting of older animals reduces the resilience of species to environmental perturbations [19, 20]. Loss of these sources of social and ecological knowledge leads to increase in maladaptive behaviors, such as aggression which in turn precipitates species declines via retaliatory killing especially when this aggression is directed towards humans. For example, in South Africa, translocated young male elephants developed aggressive behavior towards rhinos but this behavior was controlled after the introduction of older male elephants [21]. Aggression and formation of large groups, as an antipredator behavior in many large herbivores, can be maladaptive in human-dominated landscapes where humans are the primary predator. Aggression and formation of large groups towards humans wielding automatic rifles for hunting are not effective because entire herds or populations can easily be decimated by hunters. Elephants typically respond to predatory and competitive threats by bunching to protect the defenceless calves followed by scrutiny of the threat and attack by the matriarch [19]. Elephant poaching can potentially amplify conflict with humans [22] because poaching targets older elephants with larger tusks [23]. In African elephants, poaching for ivory has led to the decimation of older males and females [23]. In African elephants, the ability to make ecologically pertinent decisions crucial to survival such as reacting to predatory and competitive threats is influenced by age of the matriarch [24, 25]. It is important to understand how elephants respond to anthropogenic risk, to characterize patterns of risk and to understand how age impacts on decision making to anthropogenic risk factors.

In this study, we first characterized spatial patterns in mortality and injury in relation to landscape variables, such as major towns, roads, rivers, and status of habitat protection. Secondly, we examined how geospatial variation in risk, along with other relevant variables, such as habitat protection status and primary production determined from remotely sensed vegetation reflectance influence elephant distribution and group sizes. Thirdly, we investigated whether elephants and livestock display spatial avoidance or attraction. And lastly, we examined the behavioral response of elephant groups to cowbells and how it is influenced by social group category, group size, habitat and age of the matriarch or oldest animal in the group.

2. MATERIALS AND METHODS

2.1 Study Area

This study was conducted in the Maasai Mara Ecosystem (MME) which encompasses the Maasai Mara National Reserve (MMNR), several Community Wildlife Conservancies (CWC) (e.g. Siana, Olaro, Olkinyei, Naboisho and Koiyaki) and surrounding Community Grazing Lands (CGL), cultivated lands and settlements (Fig.1). The MME is located in Narok County, southwestern Kenya along the Kenya-Tanzania border. It lies between 1°13' and 1°45'S and 34°45'and 35°25'E. MMNR covers 1,510 km² and forms the northernmost extension of Serengeti-Mara Ecosystem covering approximately 25,000 km² [26]. Mean annual rainfall at MMNR varies from 500 mm in the southeast to 1200 mm in the northwest. Rainfall is bimodal, with a main dry period from mid of June to mid of October and January to February constituting a shorter dry season [27]. Average maximum daily temperature is 28.3°C (range = 25.1 to 32.3°C) and average minimum daily temperature is 13.8°C (range = 12.2 to14.9°C). MMNR has four major vegetation types which include bushed and wooded grasslands, semi-evergreen thickest and grasslands [28]. *Vachellia gerrardii* woodland occurs as stands and *Croton dichogamus* is the dominant species in the thickets while *Balanites aegyptiaca* occur in the western parts of Mara [26]. The expansive grasslands are dominated by *Themeda triandra*. Woody vegetation is in decline because of fire and browsing pressure from a high-density of elephants [29, 30]. Woody vegetation is limited to locations along the Mara River, and consists of *Croton dichogamus bushland* on hill slopes and *Vachellia* woodland along some drainage lines. MMNR has one of the highest mammal-diversity in Kenya and it is famous for the so-called “Big Five” including the Cape buffalo (*Syncerus caffer caffer*), elephant (*Loxodonta africana*), leopard (*Panthera pardus*), lion (*Panthera leo*) and black rhinoceros (*Diceros bicornis*). It is especially famous for its concentration of migratory herbivores, including zebras (*Equus quagga*), wildebeest (*Connochaetes taurinus*), Thomson’s gazelles (*Eudorcas thomsonii*) and associated carnivores such as lion, cheetah and hyaena [31, 32].

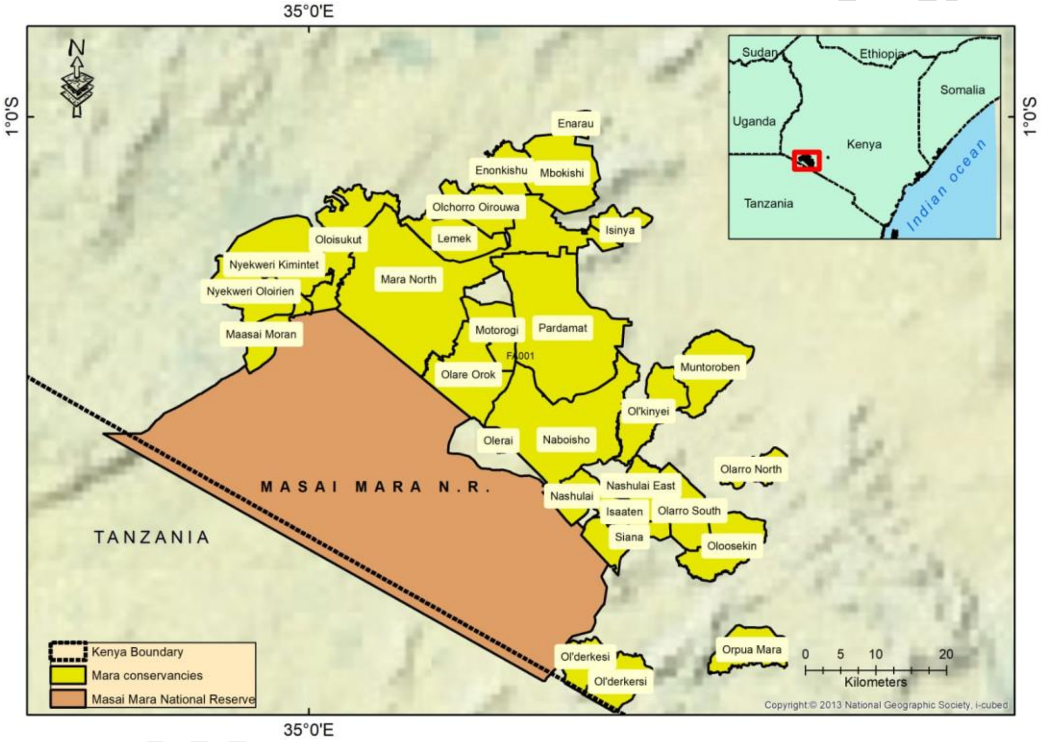

Fig. 1. The Maasai Mara Ecosystem (MME) study area

2.2 Elephant Injuries and Mortality

Elephant mortality was obtained for the years 2006 to 2015 from the Kenya Wildlife Service (KWS) elephant mortality records while the elephant injury data were obtained from the Maasai Mara Wildlife Mobile Veterinary Unit clinical reports for the years 2008 to 2015 time periods. Approximately 129 elephant mortality cases and 91 injuries were analysed. However, 28 mortality cases were recorded outside the study area and were thus excluded from further analyses. For each sighting of an injured or dead elephant, the sex, type of injury (arrow, bullet spear, etc.) or suspected cause of death, and GPS location were recorded. . The Mara vet team provided the injury cases attended.

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2.3 Elephant Distribution and Grouping Patterns

The distribution and group sizes of elephants in the MME were determined from total aerial counts following [33]. The counts were conducted in blocks of 900 km^2 using a fixed wing Cessna 182 from 7th to 11th of June 2010 and again from 28th May to 1st of June 2014. A total of 42 census blocks, 3 straddling the Kenya-Tanzania border. Systematic aerial surveillance of each block was conducted with aircraft flying at an altitude of 350 to 400 ft. and an average speed of 120 to 180 km/hour. The survey was conducted using transects spaced at 0.6, 1.0, 1.2 and 2 km depending on vegetation thickness and habitat type. The group sizes of elephant herds were recorded. Large elephant herds (>10 animals) were circled to enable a complete and accurate count of all individuals in the group. In addition, digital photographs were taken to aid in the validation of animals counts. During flight, observed events, tracks and flight lines were captured as GPS waypoints and downloaded using DNR Garmin® software and Garmin Basecamp© Version 4.3.1. Digital cameras were used to photograph large herds which were later used to validate visual observations.

2.4 Elephant Behaviour and Experimental Responses to Cowbells

To assess the influence of a matriarch's age, group size and habitat type on elephant reaction to cowbells, 63 experiments were recorded (17 in CWCs, and 46 in MMNR). No experiments were undertaken in CGL because elephants were rarely sighted in these areas during the day. Of the experiments conducted at MMNR and CWCs, half of the experiments were conducted in the open grasslands and the other half in the wooded grasslands. The experiments involved observing the behaviour of the groups and allowing elephants to get used to the vehicle (*ca.* 15 minutes). The age, sex and number of individuals in each group observed were georeferenced. Following [24] and [36], cowbells were played and elephant reaction documented (e.g., listening, sniffing, aggression, defense and retreat). Before the experiments, 15 to 30 minutes were spent to acclimatize our presence to elephants. The experiments involved playing concealed cowbells for 10 to 15 minutes near an elephant group 20 to 30 meters away from the concealed bells. Elephant responses to cowbell sounds were observed with binoculars and video recording obtained using a SONY (HD) HANDYCAM video camera. Consequently, a comprehensive list of postures and movements indicating any of the five key behaviours including listening, sniffing, aggression, defense and retreat were recorded. The presence or absence of each of the key behaviours as a response to cowbell sounds were used in subsequent analyses.

2.5 Age and Sex Determination of Live Elephants

Age of elephants was determined from growth and developmental features like relative body size and morphological attributes such shape of the head and the body, temporal depression, status of the mammary gland and size and shape of tusks. This method has been used extensively in field ageing of elephants by several researchers [37, 38], and has been further validated using the appearance of known age elephants from long-term monitoring of individually known animals [39]. Males and females were distinguished based on genitalia, presence of breasts and shape of the forehead [39].

2.6 Satellite Image Data and NDVI Extraction

Satellite images from Landsat 8 that uses the Operational Land Imager and Thermal Infrared Sensors were retrieved from the Libra development seed website for 2014 image and USGS (United States Geological Survey) website for 2010 image. In addition, the satellite images were of 30-meter resolution from the 2nd June 2014 and 9th July 2010. The downloaded satellite images were pre-processed using QGIS to remove both radiometric and geometric errors. The corrected images were used to generate the Normalized Difference Vegetation Index (NDVI) for a 1 square km around a GPS location which was calculated using equation (1).

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED}) \qquad (1)$$

Where, NIR represent the near infrared electromagnetic reflectance and RED is visible red reflectance. NDVI is a measure of vegetation greenness or plant phenology and it is often employed as an indicator of primary productivity, plant growth vigor, plant biomass and forage quality as green vegetation absorbs very well near infrared and red-light spectra [34,35]. It is used to determine the density of green vegetation in locations where elephants were found in this study. Results obtained are mostly between -1 and +1. Where negative values show water and values close to 0 show bare soils. Between 0.1 and

0.5 show low to medium vegetation cover density while 0.5 to +1 show high vegetation density. The NDVI was generated using the raster calculator tool in QGIS (3.0). In addition, 235 random points were generated within the study area, where the NDVI values for each random point were extracted for 2010 and 2014. The generated NDVI values for the random points were compared with the sampled actual elephant location for period 2010 and 2014 within the Mara Serengeti ecosystem.

2.6 Proximity and Home Range Kernel Density GIS Analysis

Analysis on elephants' proximity to roads, rivers and townships (centers) was carried out using ArcGIS Version 10.3. The points were extracted using the Euclidean distance to the closest source employing spatial analysis tool and layers on elephant mortality, injuries and sightings (bells) were generated (appendix 1). The ArcGIS 10.3 Spatial Analyst tool was also employed to create distance surfaces from the buffer zone to permanent rivers, seasonal rivers, roads and town centers. Elephant mortality point data was added onto Euclidean distance surfaces. Subsequently, the distance of injured elephants or elephant carcasses to rivers, roads and towns were extracted as described by [40] using ArcGIS 10.3 extraction of distance to a point tool with a spatial analyst tool. This produced an attribute table with distances of all elephant mortality, injury and sightings locations from the geophysical attributes and human infrastructure. This was eventually used to model areas of high risk in terms of injuries and mortalities in the study area.

Video recordings on elephant responses to cowbells were analysed and compared with elephant injuries and mortality data to describe the spatial-temporal patterns observed. To determine elephant mortality in high, medium and low risk areas, spatial analyses were carried out using ArcGIS 10.3 with an additional software for home range analysis (HRT 2.0). The HRT includes both fixed and adaptive kernel methods. The kernel probability density function used in the HRT was the standard bivariate normal (i.e., Gaussian) curve as described by [41]. Ecological factors and human disturbance were examined to assess their influence on elephant poaching levels. These factors included distances to (a) permanent rivers (b) town centres and (c) roads. Live elephant distribution data at the MME were obtained from aerial censuses undertaken in 2010 and 2014 by KWS, Tanzania National Parks (TANAPA) and Tanzania Wildlife Research Institute (TAWIRI). Euclidean distances were created using spatial analyst tool (ArcGIS 10.3) and values were extracted to point features (rivers, roads and towns) in relation to elephant mortalities and injuries. Maps on the same were generated and the analyses done. To identify areas with high and low mortality and injury risk, kernel density analyses were performed using ArcGIS tools.

2.7 Statistical Analyses

A Student's *t*-test was used to test whether average distances of injured elephants and elephant carcasses were significantly different from distances expected from a random distribution with respect to human settlements, roads and rivers, with injuries and deaths as factors, and distances as dependent variables. Equal and unequal variances were assumed when sample sizes were similar and unequal, respectively. To test for whether the risk of elephant injury or mortality varied with conservation status of their location, Chi-square test was used. To test for the influence of NDVI, conservation status and level of risk on elephant grouping patterns, zero truncated Poisson Models were employed, with NDVI, conservation status and level of risk as predictor variables, and group size as the dependent variable. The most parsimonious model was selected using Bayesian Information criteria. Cochran–Mantel–Haenszel (C-M-H) test was used to examine whether matriarchs performed defensive bunching prior to retreat when cowbells were played. The Cochran-Mantel-Haenszel test discovers if there is a relationship between two categorical variables (bunching verses retreat) after blocking across a third classification (conservation status) [42]. C-M-H test can inform whether there is a consistent difference in proportions across the repeats. Secondly, we tested the hypothesis that matriarch age and group size were important predictors of defensive behaviour in mixed or all female elephant groups using generalized linear models (GLMs) with binomial error structure and a logit link function. The chi-square test was used to test for the influence of habitat and protection status on elephant reaction to cowbells. However, the alternative Fishers test was used when assumptions of the chi-square tests were not met due to small sample size. All means are presented ±SD. These analyses were carried out using R statistical software (R version 4.0.0) with a probability threshold of $P = 0.05$ as a cut off for statistical significance.

3. RESULTS

3.1 Patterns of Elephant Injury and Mortality

Ninety elephants were treated from injuries between 2007 and 2015. Injured elephants were located close to rivers (t_{84} = 6.44; $P < 0.001$) but were farthest from settlements (t_{140}= -4.68; $P < 0.0001$) than expected from a random distribution of injury locations (Table 1). There was however no significant difference between the distribution of injured elephants with respect to roads from a distribution based on a random expectation (t_{139} = 0.22; $P = 0.825$). One hundred and ninety-three elephant mortality cases were recorded between 2006 and 2015. Like in elephant injury locations, elephant mortalities occurred close to rivers (t = 4.219, df = 100.39, p < 0.0001) and farthest from human settlements (t = -4.035, df = 139.72, p < 0.0001) compared to a distribution based on a random expectation. Again, roads had no influence on the distribution of dead elephants (t_{223} = -1.76; $P = 0.080$).

Table 1. The average (mean and median) distances of elephant injuries and mortalities from human settlements, roads and rivers when compared with distances generated assuming a random distribution

	n	mean	SD	Median	Median absolute deviation	Minimum	Maximum
Injuries							
Roads	91	3.89	3.3	3.12	2.55	0	15.16
Rivers	91	8.53	8.09	6.18	5.82	0.01	51.58
Towns	91	18.03	6.26	18.48	7.93	5.65	31.84
Mortalities							
Roads	193	5.2	6.9	3.43	3.69	0.01	31.83
Rivers	193	14.22	16.95	8.83	6.72	0.05	71.87
Towns	193	17.16	8.05	17.82	8.89	0	33.15
Random locations							
Roads	71	4.02	3.8	2.56	3.27	0	12.57
Rivers	71	26.66	22.61	20.7	26.68	0	63.63
Towns	71	13.01	7.14	12.12	6.67	1.89	32.99

Elephant injuries were highest in Community Wildlife Conservancies (Mean ± SD) compared to either Community Grazing Lands (Mean ± SD) or within MMNR (Mean ± SD) even after adjusting for the expectation based on elephant distribution patterns in the MME ($\chi^2_{(2,\ n\ =\ 284)}$ = 191.25 $P < 0.0001$). Elephant mortalities were also higher than expected based on elephant distribution in the Community Wildlife Conservancies (Mean ± SD) and Community Grazing Lands (Mean ± SD) compared to the MMNR (Mean ± SD) (Fig. 2). There was a statistically strong association between the spatial distribution of the type of risk and protection status ($\chi^2_{(2,\ n\ =\ 284)}$ = 28.76; $P < 0.0001$). Specifically, there was greater mortality than injury risk in Community Grazing Land (88% mortality and 12% Injury risk) and the converse was true for the MMNR (32% mortality and 68% Injury risk) (Table 2., Figs. 3 & 4).

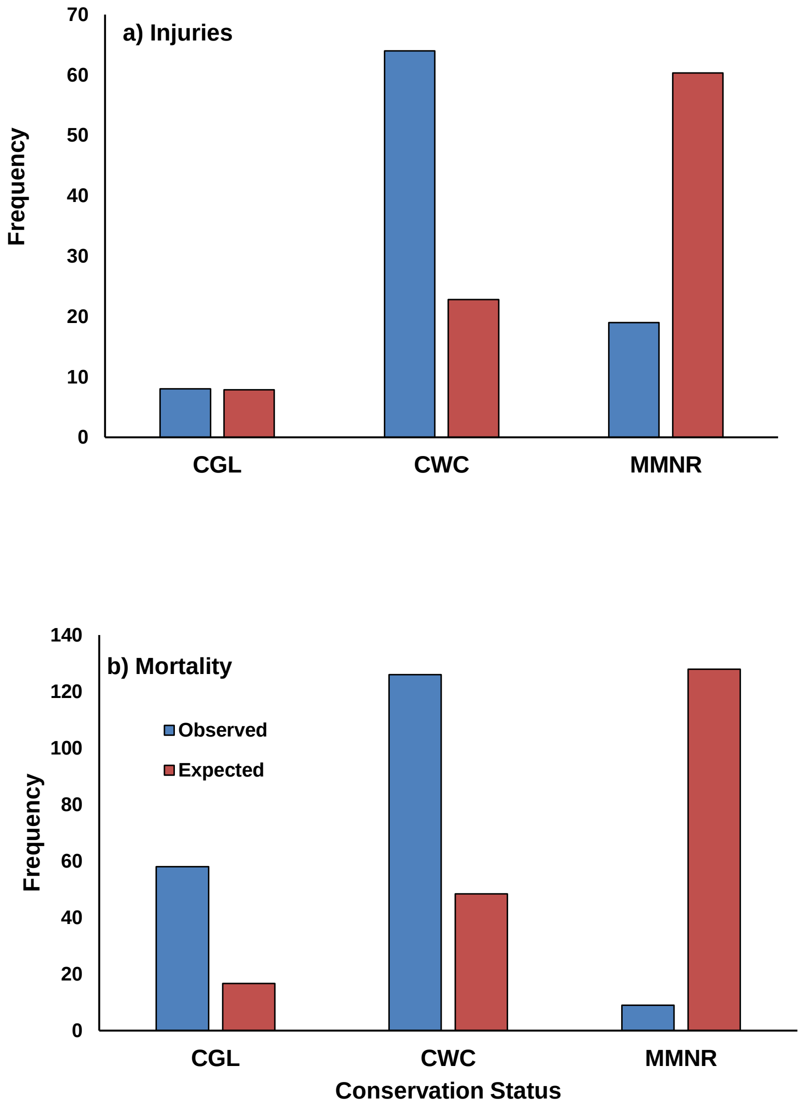

Fig. 2. **The distribution of elephant a) injury and b) mortality at Community Grazing Land (CGL), Community Wildlife Conservancies (CWC) and Maasai Mara National Reserve (MMNR)**

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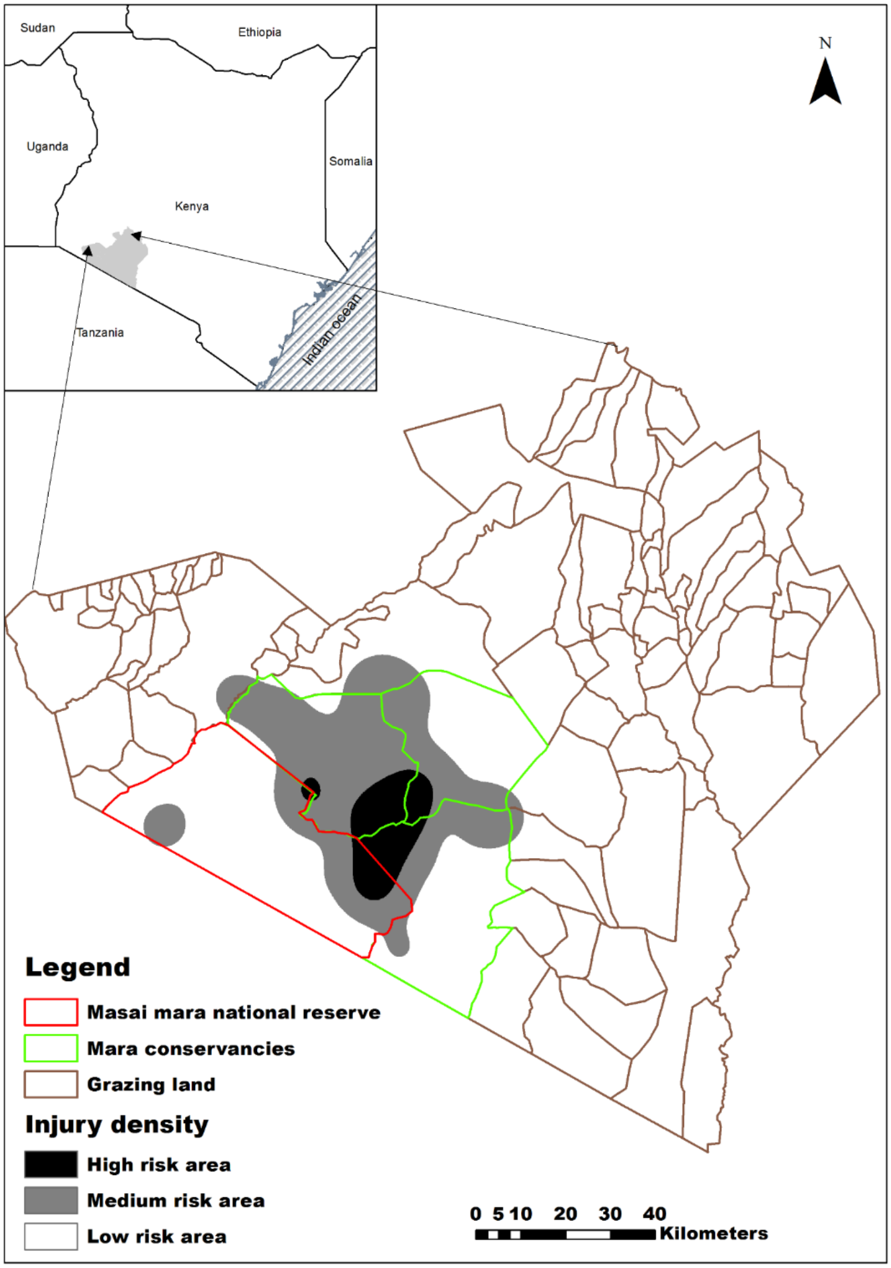

Fig. 3. Injury risk classification in relation to protection status of the locales within the Maasai Mara Ecosystem

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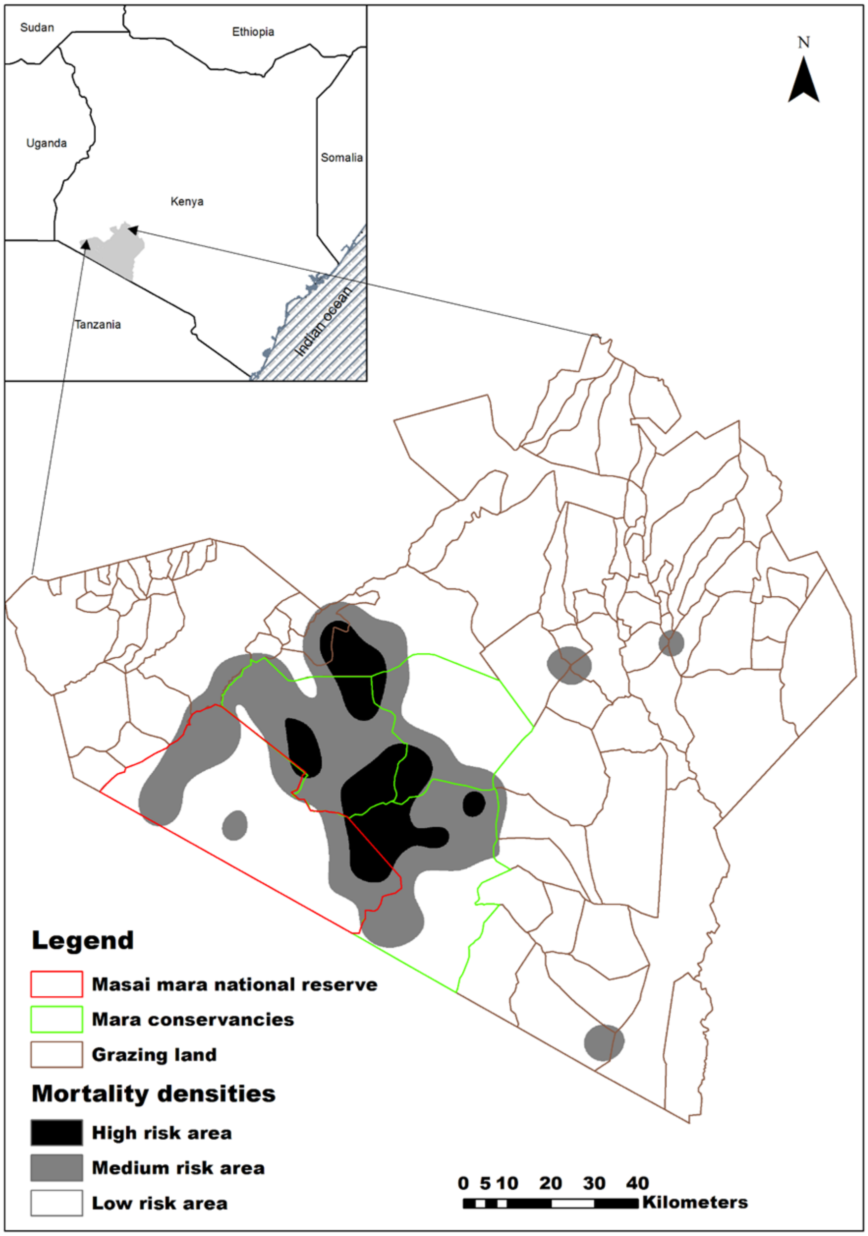

Fig. 4. Spatial variation in mortality in the Maasai Mara Ecosystem (2010-2015) as an index of risk

Table 2. Frequency distribution of injured and dead elephants between 2006 and 2015 based on the protection status in the MME, Kenya

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	Risk Type		
Protection Status	Injury	Mortality	Total
Community grazing lands (CGL)	8	58	66
Community Wildlife Conservancies (CWC)	64	126	190
Maasai Mara National Reserve (MMNR)	19	9	28
Total	91	193	**284**

More males than females suffered from injury and mortality compared to the expectation based on sex ratio (74% male, 26% female; $\chi^2_{(1,\ n\ =\ 269)} = 33.90$, $P < 0.0001$). In addition, there was a modest association between the type of risk (injury versus mortality) and elephant sex ($\chi^2_{(1,\ n\ =\ 269)} = 4.69$, $P = 0.030$). Specifically, 77% ($n = 58$) females suffered from mortality compared to 63% ($n = 125$) of males, whereas a greater proportion of males than females suffered from injuries (37% for males and 23% for females). There was no significant association between age and type of risk (mortality of injury) ($\chi^2_{(2,\ n\ =\ 209)} = 1.52$; $P = 0.468$). Adult elephants suffered the most from injuries and mortalities than juveniles or sub-adult elephants ($\chi^2_{(2,\ n\ =\ 209)} = 253.90$; $P < 0.0001$). Eighty five percent ($n = 178$) of elephants incurring injury or mortality were adults, 11% ($n = 22$) sub-adults and 4% ($n = 9$) were juveniles/infants.

3.2 Elephant Grouping Patterns, NDVI, and Spatial Variation in Mortality/Injury

Based on aerial counts conducted in 2010 and 2014, 394 elephant groups were recorded with about 235 sightings in 2010 and 159 sightings in 2014. The average group size in 2010 was 13.07 ± 20.08 whereas in 2014 the group size was 9.58 ± 9.34. The elephant distribution during these censuses in relation to the protection status of these locations is shown in Fig. 5.

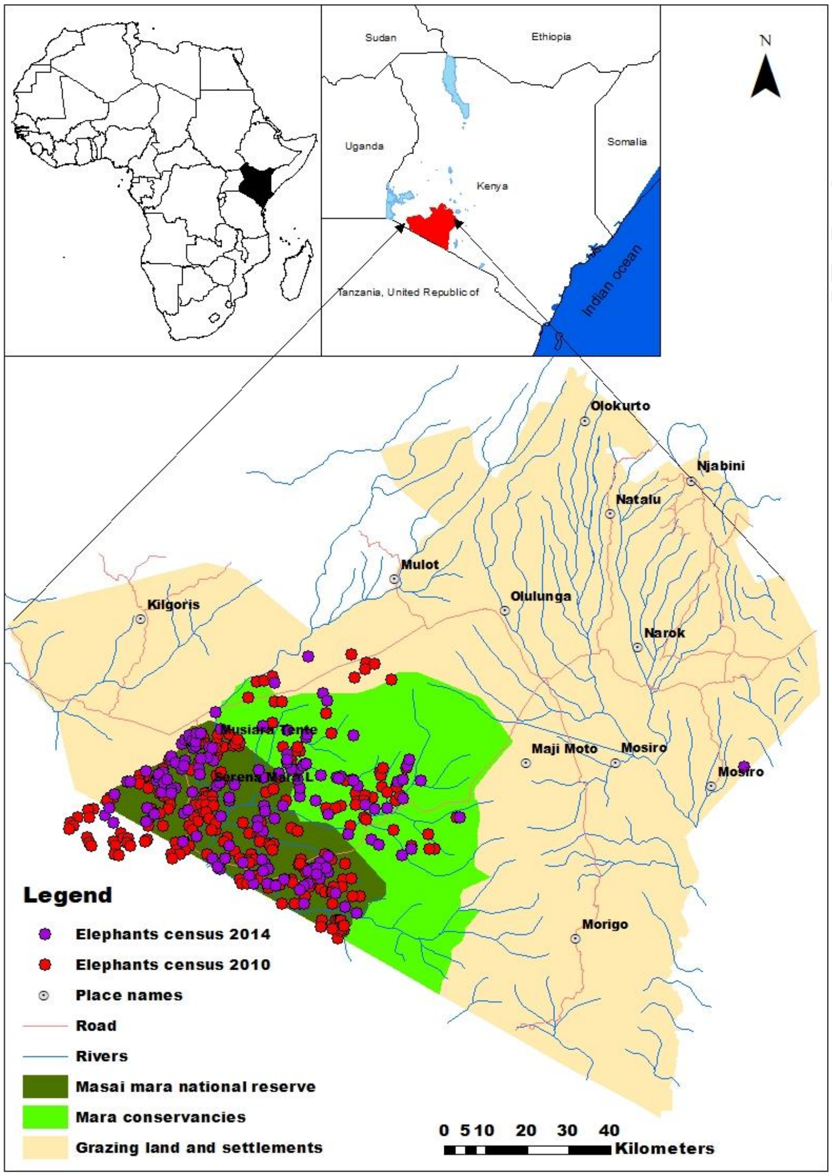

Fig. 5. Distribution of elephants in the MME, Kenya during the 2010 and 2014 aerial censuses

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Communal grazing lands had fewer elephants than expected, but Community Wildlife Conservancies and the MMNR had higher densities of elephants. More elephants were sighted at MMNR (66%) compared to either Community Wildlife

Conservancies (25%) or Community grazing lands (9%). Generally, where elephants were less sighted, the group sizes tended to be larger compared to areas where elephants were frequently sighted (Table 3).

Table 3. Group sizes of elephants as a function of protection status and mortality and injury risk level in the MME, in 2010 and 2014

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	n	mean	Standard deviation	median	median absolute deviation
Protection Status					
CGL	31	19.29	20.02	15	19.27
CWC	90	14.73	19.50	9.5	9.64
MMNR	238	8.54	8.67	6	5.93
Risk Level					
Low risk locations	329	10.92	14.08	7	7.41
High risk locations	30	12.07	10.94	9.5	9.64
All	359	11.02	13.83	7	7.41

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A truncated zero Poisson mixed model revealed a strong positive relationship between elephant group size with NDVI, increased risk of mortality and injury (Table 4). Moreover, elephant group size was responsive to protection status controlling for NDVI and risk, with MMNR and Community Wildlife Conservancies having lower group sizes than Community grazing areas.

Table 4. A model showing the influence of NDVI, injury or mortality risk and conservation status on elephant group sizes

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Covariate	Coefficient Estimate	Std. Error	z value	Probability value
Intercept	2.027	0.202	10.03	< 0.001
NDVI	3.146	0.282	11.16	< 0.001
Risk Level	0.193	0.057	3.37	< 0.001
CWCs compared to CGL	-0.198	0.051	-3.90	<0.0001
MMNR compared to CGL	-0.746	0.047	-15.77	< 0.001

3.3 Behavioural Response of Elephants To Cowbells: Effects of Group-Size and habitat

Cochran–Mantel–Haenszel analyses revealed that there was a strong association between defensive bunching and retreat behaviour (Mantel-Haenszel $\chi^2_{(1,\, n\,=\,46)} = 10.04$, $P = 0.002$). The association was consistent across protection status of locations where bells where played (Woolf's test, $\chi^2_{(2,\, n\,=\,46)} = 1.12$, $P = 0.571$). Defensive bunching was not observed in all-male groups but was more common among matriarchal groups ($\chi^2_{(1,\, n\,=\,60)} = 22.531$, $P < 0.001$). Among matriarchal groups, defensive bunching increased in correspondence to the age of the matriarch ($\beta = 0.11$, $Z_{(44)} = 2.059$, $P = 0.0395$). In addition, the occurrence of defensive bunching increased in correspondence with groups size ($\beta=0.892$, $Z_{(44)} = 2.502$, $P = 0.012$), but there was a strong positive correlation between elephant group size and age estimate of the oldest female or matriarch (Rs = 0.56, $S_{(45)} = 7073.6$, $P < 0.001$). Defensive bunching was not associated with either habitat type – wooded grassland versus open grassland– ($\chi^2_{(1,\, n\,=\,46)} = 0.013$, $P = 0.909$) or conservation status – Community Wildlife Conservancies versus MMNR ($\chi^2_{(1,\, \text{n=46})} = 0.09$, $P = 0.762$). Elephant aggression was not influenced by how old the matriarch was ($\beta = -0.02$, $Z_{(44)} = -0.40$, $P = 0.692$), group size ($\beta = -0.02$, $Z_{(44)} = -0.24$, $P=0.810$), habitat type ($\chi^2_{(1,\, \text{n=46})} = 0.33$, $P = 0.566$) or conservation status of the experimental location ($\chi^2_{(1,\, n\,=\,46)} = 0.09$, $P = 0.770$).

4. DISCUSSION

4.1 Patterns of Elephant Injury and Mortality

Long-term data on mortality and injury of elephants from the Maasai Mara Ecosystem, indicated that injured and dead elephants were located close to rivers but were farthest from settlements than expected from a random distribution. These findings are consistent with long-term studies from the Tsavo Ecosystem, Kenya, where the distribution of illegally killed elephants occurred close to rivers and surface water [43]. Similarly, a study in the Zambezi valley, Zimbabwe, found that poaching activities occurred in areas with high forage and close to waterholes [44]. Water is an important resource for elephants; driving their spatial distribution as they drink water and mud-bathe on a daily basis [45,46]. In habitats that strongly experience illegal killing of elephants, water bodies present a high risk area for elephants, especially during the dry spell [47]. Water bodies also influence the movement patterns and spatial distribution of elephants [48, 46]. Other studies have noted further that, elephants are attracted to water bodies, and riverine habitats with huge concentrations of elephants occurring in locations where water and forage can be accessed easily [49]. In contrast with previous studies in the Maasai Mara and the Tsavo Ecosystems which found a correlation between the location of injured elephants and roads [43, 47], this study found that roads were not a factor in influencing both injuries and mortalities of elephants arising from poaching. Roads may provide poachers access to remote areas with high elephant densities where poaching would be easier [50]. However, in areas where there is poaching or risk of mortality and injury, elephants are known to avoid roads and villages [51, 52, 53]. Our findings, thus, suggest that elephants avoided roads because of the risks they pose. The contradictory effects of roads on elephant mortality suggest elephant response to roads is temporally sensitive. Initially, when poaching is initiated, elephants will be naïve to risks roads pose and more mortality may be recorded on roads. As poaching persists however, elephants may avoid roads all together and mortality cases will occur at random with respect to roads and settlements or farthest. An alternative explanation is that poachers may find elephants in remote locations far from security apparatus easy targets as illegal killings are likely to remain undetected. This scenario can create a positive relationship between the degree of elephant mortalities with distance from roads.

This study revealed that the occurrence of injured elephants was highest at Community Wildlife Conservancies (CWCs) compared to either Community grazing lands (CGLs) or at MMNR. A similar trend was observed for elephant mortality rates, with CWCs and CWLs recording higher mortalities than MMNR (Figs. 3 & 4). These findings are in agreement with a study in northern Kenya where they found higher elephant poaching levels occurred in Community Wildlife Conservancies than in privately-owned land or the National Parks or Reserves [54]. Similarly, at Tsavo Conservation Area, some of elephant poaching hotspots occurred in Community ranches [55]. The high proportion of individual elephants injured or dying at CGLs and CWCs in this study could be attributed to herders spearing elephants as they graze their livestock and the absence of security in these areas. In contrast, MMNR recorded low elephant mortality cases probably because of improved security there. Middle men use herders to get access to illegally kept ivory or use young men to kill elephants for ivory [56]. This has generally escalated elephant mortalities and injuries associated with this illegal business and has contributed immensely to behavioural change in elephants observed in human dominated landscapes [57]. Our study showed that more males than females accounted for injuries and mortalities compared to the expectation based on sex ratio (74% male, and 26% female). This observation is comparable to what was documented by [58] in Sri Lanka and [59] at Amboseli National Park (Kenya), where male elephants were observed to take risks in search of forage to enhance reproductive benefits [60] in their countrywide study in Kenya also documented that adult males were predominantly injured compared to females. They further noted that high prevalence of human-inflicted injuries may correlate with incidences of the human–elephant conflicts (HEC) where males raid crops frequently as compared to females as has been widely observed [16,61,62]. The high prevalence of injuries to male elephants compared to female concurs with what [63], [64] and [65] documented in their studies and which can be related to a high preponderance of male elephants involvement in HEC as reported in both Africa and Asia. The optimal foraging theory proposed by [64] and supported by [59] explains why bull elephants take risks in human dominated landscapes, and have higher contact or interaction rates with humans, culminating in either injuries or mortalities. This observation is also supported by studies on crop-raiding Asian elephants in the South East Dry Zone (SEDZ) of Sri Lanka [58].

In this study, there was no association between mortality or injury risk with the age class but there was a weak association between being male or female and the type of risk incurred. Females had a relatively higher mortality rate compared to males while injury reports were relatively higher in males consistent with research on injury and mortality patterns [66]. The lack of association between risk type with age but the presence of variation in risk type inflicted on each sex suggest that the male high risk and high gain reproductive strategy may expose males irrespective of age to killing attempts which leads to more injuries. Moreover, females are exposed less to such risks but when they do, they are more likely to succumb to death from injuries caused by similar weapons because of their smaller size relative to males.

4.2 Elephant groups, NDVI, Protection Status and Spatial Patterns of Elephant Injury and Mortality

Our study revealed a strong positive relationship between elephant group size with NDVI and increased risk of injury or mortality. This finding is in agreement with studies on many social mammalian species, where group living has been shown to play a crucial role in individual survival, including reduction in predation risk through group defense, risk dilution, predator confusion and increased predator detection [67]. Because group living has other benefits including provision of opportunities for play, mates and information acquisition, the major factor limiting formation of large groups is competition for food. When food resources are in plenty, indicated by increased greenness as determined using NDVI, large mammalian aggregations can form. Results from several studies support this. For example, [17] found larger groups of male elephants to be positively correlated with NDVI and risky locations (farther away from the safety of protected areas). A study of khur (*Equus hemionus khur*), an endangered equid in India, also revealed that group sizes increased in correspondence with higher primary productivity and rainfall [68]. The higher values of NDVI associated with higher greenness and increased plant growth in the MME, suggest that the lush grass attracts big concentration of elephants. The MMNR and Community Wildlife Conservancies had lower group sizes than CGL. This could be attributed to spatial variation in apparent risk of mortality and injury. Elephants and many other mammal species react to increased risk of predation by forming large groups as a mechanism of reducing predation risk. In this study, more elephants were sighted at the MMNR (66%) compared to either the CWCs (25%) or CGL (9%) suggesting that risk of injury and mortality may influence elephant distribution patterns. Elephants in the MME may have avoided human disturbance by staying at the MMNR during the day and probably moving to other areas at night when herders invade the reserve with their livestock. Anthropogenic activities at MMNR have a direct relation on elephant distribution. Elephants tend to avoid livestock grazing areas during the day and congregate in the Reserve and that explains the pattern that was observed during the aerial surveys where large concentrations of elephants were sighted in the Reserve as compared to areas outside the reserve. This pattern of livestock avoidance by elephants has been observed elsewhere [69].

4.3 Behavioural Response of Elephants to Cowbells: The Influence of Group Size and Habitat

Our study showed that among matriarchal groups, defensive bunching towards sounds of cowbells increased in correspondence with matriarch age and group size. There was, however, a strong positive correlation between matriarch age and group size, with older matriarchs associated with larger group sizes and vice versa. This result agrees with [19] who demonstrated using experimental playback of lion roars, that age affects the ability of matriarchs to assess predatory threat to African elephants. Specifically, they found out that the sensitivity to the level of predation threat was more heightened in social groups with the oldest matriarchs. They concluded that older matriarchs have accumulated the most experience indicating that their presence in elephant social groups is essential for crucial decision making in the face of a predation [19].

Livestock grazing in elephant occupied areas, can lead to direct interactions which can be fatal resulting in injuries or even deaths to livestock, elephants and sometimes humans. Elephants in the MME have learnt with time to associate cowbells with danger or human presence. Herders (and farmers) are known to throw spears or pointed sticks at elephants while chasing them away from the crop fields or cattle foraging areas to create room for their livestock to graze [70]. This act sometimes leads to serious encounters and has partly contributed to elephants associating injury or pain with the presence of livestock. These behavioural responses to changes in the environment caused by humans have profound effects on the distribution of animals like elephants. Elephants in the MME have learned to avoid conflict by foraging within MMNR during the day and probably moving out during the night to avoid unnecessary confrontation with herders who invade the park at night and vacate the grazing fields on first light to escape apprehension from security personnel.

Defensive bunching in response to experimental cowbells was surprisingly not associated with either habitat type –wooded grassland versus open grassland – or protection status –Community Wildlife Conservancy versus Maasai Mara National Reserve. Our findings suggest that elephants may not use concealment as an antipredator or anti-poaching strategy when confronted with an immediate predation/poaching threat but instead use group defense or risk avoidance behavioural strategies. This is in contrast to many other mammalian species (e.g. buffalos, wildebeest, zebra and gazelles) where large aggregations are associated with more open habitats [71, 72, 73] while small groups are associated with more closed habitats where visibility may be low [74,75,76,77]. For such species, formation of large groups in open habitats enhances predator detection, group defense and attack, and vigilance. Conversely, in closed habitats, reduction in group sizes, freezing and concealment are the most common antipredation strategies [78, 79]. Elephant defensive bunching was not observed in all-male groups but was more common among matriarchal groups, suggesting that bunching is not a common antipredation strategy in males. Indeed, our study revealed a positive relationship between defensive bunching and group size in matriarchal groups suggesting that males, with often smaller group sizes, may not form adequate group sizes to allow group defense.

Our study revealed that elephant aggression was surprisingly not influenced by matriarch age, group size, and habitat type or habitat protection status of the experimental location. The lack of association between defensive aggression with matriarch's age could be because this study did not investigate parental care and investment, where aggressive defense is considered a part [80]. In several mammal species, aggressive defense is considered as aspect of parental care and investment. The degree of aggression is thought to be elevated for groups with many offspring, the age and sex of offspring, and the maternal age [80, 81, 82, 83]. The amount of parental effort should be determined by the degree of risk to future reproductive potential, the value of present offspring compared with the parent's expected future contribution, and the expected increase in offspring welfare resulting from such a parental expenditure [80].

5. CONCLUSION

In conclusion, the exploration of how geospatial patterns and behavioural responses influence elephants in pastoralist landscapes highlights the urgent need for informed conservation initiatives. The complexities of these interactions demonstrate that effective management must account for the dual pressures of cattle grazing and mortality risk. By deepening our understanding of these dynamics, we can develop targeted strategies that mitigate human - elephant conflict and promote sustainable coexistence. Future research should continue to investigate the nuances of elephant behaviour in response to pastoralist practices, focusing on innovative approaches that reconcile wildlife conservation with agricultural and pastoralist needs. This study serves as a foundation for further inquiry into the spatial ecology of elephants, ultimately contributing to the broader goal of preserving both wildlife and human livelihoods in shared landscapes.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Authors hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during writing or editing of manuscripts.

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