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HUMAN AND LANDSCAPE FACTORS INFLUENCING LION MORTALITIES IN THE MAASAI STEPPE ECOSYSTEM, NORTHERN TANZANIA

***G. Soka, and J. Lyimo**

Department of Wildlife Management,
College of Forestry, Wildlife and Tourism
Sokoine University of Agriculture, Morogoro, Tanzania

****Corresponding author**: gsoka@sua.ac.tz*

ABSTRACT

The demography of the African lion is increasingly shaped by interactions with humans. Habitat fragmentation and persecution by humans are both linked to the decline in lions in most of their historical ranges such that current populations are largely restricted to isolated protected areas. This study examined the spatial and temporal patterns of lion killings in the Maasai steppe ecosystem. We used eighty-two lion mortality records for the last 13 years (2005 - 2017). Distances from the roads, river, lake, settlements, and the Normalized difference vegetation index value extracted for each lion killing location were the key landscape variables used to map the lion anthropogenic mortalities. There was a significant difference ($p<0.05$) between female and male lions killed from 127 mortality records. The anthropogenic retaliatory killing caused 77.9% of female and 22.1% of male mortalities. About 58% of the lions killed were adults, 39.1% were sub-adults and only 2.9% were cubs. The majority of lion killings incidences took place during the wet season around the Maasai homestead. The lion killings incidences were rampant in the eastern side but slightly clustered in the northern part. Vegetation cover in the actual lion killings areas influenced lion killings incidences. Distances from the public roads, rivers, and human settlements significantly ($p<0.05$) contributed to lion anthropogenic mortalities. It is anticipated that retaliatory killings of lions could intensify due to growing cattle herds in the ecosystem. To promote coexistence between humans and lions, conservation authorities should invest more in awareness and sensitization programs on the conservation of lions.

Keywords: African lion, anthropogenic mortality, retaliatory killing, conservation, Maasai Steppe.

INTRODUCTION

Globally, human populations are increasing at the edges of protected areas (Wittemyer *et al.* 2008, Abade *et al.* 2018). Wide-ranging species that roam outside protected areas, as is typical of large predators, are particularly vulnerable to different sources of anthropogenic mortality (Loveridge *et al.* 2017). Projected human population increases of 400 percent in sub-Saharan Africa over the next century (United Nations, 2015) suggest that lions and other large African species will become increasingly space limited as available habitats are converted into agricultural lands (Nzunda *et al.* 2013, Soka and Ritchie 2016, Loveridge *et al.* 2017). The associated loss in natural habitat and intensification of human activities and human-wildlife interactions increase the isolation of protected areas and ultimately threaten the wildlife populations living inside them (Woodroffe and Ginsberg 1998, Wittemyer *et al.* 2008, Newmark 2008). In human-populated areas at the edge of protected areas, different sources of wildlife mortality exist, ranging from the legal hunting of animals (Packer *et al.* 2011) to illegal killing (Liberg *et al.* 2012) and human sources of anthropogenic mortality (Loveridge *et al.* 2017, Treves and Karanth 2003).

The African lion (*Panthera leo*) is a generalist hypercarnivore and is considered to be both an apex and keystone predator due to its wide prey spectrum (Frank 1998, Loarie *et al.* 2013). Lions are social carnivores living in territorial groups and can capture prey twice their size (Schramm *et al.* 1994, Kissui 2008). Lions can survive on a broad range of prey species that vary between habitats (Hayward and Kerley 2005, Borrego *et al.* 2018, van Hooft *et al.* 2018). Its prey consists mainly of mammals particularly ungulates weighing 190-550 kg with a preference for wildebeest (*Connochaetes taurinus*), plains zebra (*Equus burchelli*), and African buffalo (*Syncerus caffer*) (Mills and Shenk 1992, Funston *et al*. 2001, Kissui and Packer 2004), and warthog (Scheel and Packer 1991, Hayward and Kerley 2005). Although lions are most active at night, they frequently hunt during the day (Schaller 1972). Many African lion populations are declining, and the geographic range has declined by 75 percent in the last 500 years (Barnett *et al.* 2006). Anthropogenic edge effects are particularly detrimental to lion populations, impacting population density, population structure as well as elevating adult mortality and causing declines in juvenile and dispersing sub-adult survival (Riggio *et al.* 2013, Loveridge *et al.* 2010, Elliot *et al.* 2014, Green *et al.* 2018). It is now known that the most urgent threats to lions include human population growth, and the associated impacts from habitat degradation, extirpation, and disease (Weber and Rabinowitz 1996, Nowell and Jackson 1996, Kissui and Packer 2004 Kissui 2008). Habitat fragmentation and persecution by humans are both linked to the decline in lions in most of their historical ranges such that current populations are largely restricted to isolated protected areas (Woodroffe 2001, Ogada *et al.* 2003, Packer *et al.* 2005).

Lions are regularly killed in retaliation of livestock depredation, a pressure that is expected to rise with Africa's growing cattle herds (IUCN 2006, Hazzah *et al.* 2014). Kissui (2008) reported that conflicts caused by livestock predation lead to retaliatory killing of large carnivores including lions in Tanzania. Lions have been reported to utilize adjacent dispersal areas for supplementary food (Woodroffe and Frank 2005) leading to conflict-related mortalities (Woodroffe and Ginsberg 1998, Kolowski and Holekamp 2006). Widespread illegal bushmeat hunting is responsible for decimating prey populations across Africa, thus reducing habitat suitability for lions (Lindsey *et al.* 2013) as well as impacting lions directly through mortalities as by-catch in wire snares set for prey species (Becker *et al.* 2013). Understanding how large predator populations are affected by anthropogenic mortality in the landscapes they inhabit, particularly on the periphery of protected areas, is critical in designing conservation management strategies for these species in an African savanna environment that is far from secure.

The Maasai rangelands of East Africa are home to several of the largest remaining lion populations on the continent (Ikanda and Parker 2008). Many parts of Maasai land are unfenced and lions frequently kill Maasai cattle in adjacent rangelands (Kolowski and Holekamp 2006, Kissui 2008). Ikanda and Parker (2008) predicted that lion's retaliatory killings in the Maasai steppe may intensify as the human population continues to increase. This paper contributes to an understanding of how lion populations are affected by anthropogenic mortality in the Maasai steppe ecosystem. It is critical in designing focused and cost-effective lion conservation and management strategies.

METHODS

Study Area Description

The Maasai steppe is mainly centered in two districts namely Monduli (Latitude 3° 17'S, Longitude 36° 27' E) and Simanjiro (Latitude 4° 26' S, Longitude 37° 7'E). The Maasai steppe is a vibrant and important ecological stronghold for wildlife and people in northern Tanzania (Figure 1). This magnificent ecosystem encompasses approximately 40,000 km^2 or nearly 10 million acres of woodlands, bushland, and open grasslands. Tarangire (2,800 km^2) and Manyara (330 km^2) National Parks are the core protected areas within the Maasai steppe (Borner 1985, Prins 1987). Most of this critical ecosystem is designated Maasai village lands where livestock husbandry represents the primary livelihood (Mkonyi *et al.* 2017). It is home to rare wildlife species such as the African wild dog (*Lycaon pictus*), the fringe-eared oryx (*Oryx beisa callotis*), the most threatened African lion population (Lamprey 1964). The Maasai steppe is rich with diverse plant species in East Africa. The steppe is also well known for its migration of wildebeests (*Connochaetes taurinus*), zebras (*Equus burchelli*), and elephants (*Loxodonta africana*) (Lamprey 1964). The predominant vegetation type is comprised of riverine forest with species that include *Ficus sycomorus* and *Acacia siberiana*. Swamps are dominated by *Cyperus* species and elephant grasses; the woodland vegetation is dominated by *A. tortilis*, *A. commiphora*, *A. mellifera*, *Terminalia brownie*, and *Adansonia digitata*, forming extensive mixed woodland (Miller and Doyle 2014). The Maasai Steppe is classified as arid rangeland forming part of the Somali-Maasai bio-geographical region (Townshend *et al.* 1986). The Maasai steppe ecosystem is characterized by dry and wet seasons with an average annual rainfall of 800-1000 mm (Prins and Loth 1988). The wild animals move seasonally between the National Parks and the adjacent dispersal areas during the dry season (June - November), the migratory species remain inside protected areas but move into dispersal areas outside protected areas (in communal village lands) for most of the wet season (November - May) (Lamprey 1964, Kahurananga and Silkiluwasha 1997, TMCP 2000, Kissui 2008, Mponzi *et al.* 2014).

Figure 1: Map of Maasai steppe ecosystem showing the core protected areas (Tarangire and Manyara National Parks) and the surrounding villages.

Field data collection

Lion Global Positioning System (GPS) mortality data were collected from all the sites where lion killings took place in the Maasai steppe ecosystem. We used eighty-two incidences of lion killings for the last 13 years (January 2005 to December 2017) from the Tarangire Lion Project (TLP). The cause of mortality was assessed by the field team when mortalities were found or reported from January 2005 to December 2017. The lion killings dataset obtained from the TLP contained the number of lions killed, the cause of killings, age groups and sex of the lions killed, village name, date, location of the killings, time of the killings, the season of the year, and GPS coordinates. The lion killings dates were translated into seasonal categories based on rainfall distribution in the Maasai steppe ecosystem.

The landscape variables including distance from the road, distance from the river, distance from the lake, distance from the settlements, aspect value, and the Normalized difference vegetation index (NDVI) were extracted for each location where lions had been killed. Shuttle Radar Topographic Mission Digital Elevation Model Image (SRTM-DEM) of 30-meter spatial resolution on global coverage product obtained from the United States Geological Survey website (www.earthexplorer.usgs.gov) was mosaicked to cover the Maasai steppe ecosystem. The spatial data (shapefile layers) for the landscape variables including roads, lakes, rivers, and settlements were digitized from existing topographical maps of the Maasai steppe ecosystem. The NDVI values were extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard NASA's Terra satellite of 250-meter spatial resolution. Random locations were generated with the 'Generate Random Points' option of Hawth's tools in ArcGIS 10.3 within the same mosaicked DEM to make an equal number of random points as actual points to achieve 1:1 locations. In each point, the distance (km) to the closest river, the distance (km) to the closest village center, the distance (km) to the closest lake, and the distance (km) to the nearby road, aspect value, and the NDVI value were extracted.

Data analysis

We pooled the 127 mortality events from both sexes and all age classes and developed logistic regression models to identify the variables associated with each anthropogenic mortality source. Demographic characteristics of the killed lions were analyzed using descriptive statistics. We used the chi-square test to compare the number of female and male lions killed for 13 years. Pearson's chi-squared test was used to determine whether there is a statistically significant difference between the numbers of lions killed in different sex, age groups, seasons, and time of the day. Lion killings coordinates were converted to layers and added to the Maasai steppe boundary layer. Lion's killings incidences were grouped based on the seasons of the year, locations of the incidences, and the time of the incidences. Lion's killings sites were then coded as presence and absence. The presence/actual locations were denoted by the value one and the value zero for the absence/random location. The locations of anthropogenic mortalities (presence) ($n = 82$, dependent variable = 1) were compared to randomly generated locations in the core area (absence) ($n = 82$, dependent variable = 0) as response variables while the landscape variables i.e., aspect, NDVI, distance to the road, distance to the river, distance to the lake, and distance to the settlements were used as explanatory variables when running spatial logistic regression (MINITAB software version 18.0). We used the function 'Map Algebra' of ARCGIS 10.3 'Spatial Analyst' extension to generate the lion anthropogenic mortality hotspots map for the Maasai steppe ecosystem.

RESULTS

Demographic characteristics of the killed lions in the Maasai steppe ecosystem

This study estimated that there were eighty-two (82) lion killings incidences with more than one lion carcasses recorded, bringing a total of 127 lions killed between 2005 and 2017. There was a significant difference between female and male lions killed for the 13 years, $\chi^2_{(1,\ 123)} = 45.732$, $p < 0.0001$. Female lions killed accounted for about 77.9 percent while male lions accounted for 18.6 percent. The proportion of unknown sex was 3.5 percent of the total lions killed. Unfortunately, identification was impossible since their carcasses were decomposed beyond recognition. Between 2005 and 2017, there were significant differences in the numbers of lions killed in different age groups, $\chi^2_{(2,\ 127)} = 56.537$, $p < 0.0001$. About 58 percent, 39.1 percent, and 2.9 percent of the lions killed were adults, sub-adults, and cubs respectively (Figure 1). There was a significant difference in the numbers of lions killed in different seasons, $\chi^2_{(1,\ 127)} = 59.598$, $p < 0.0001$.

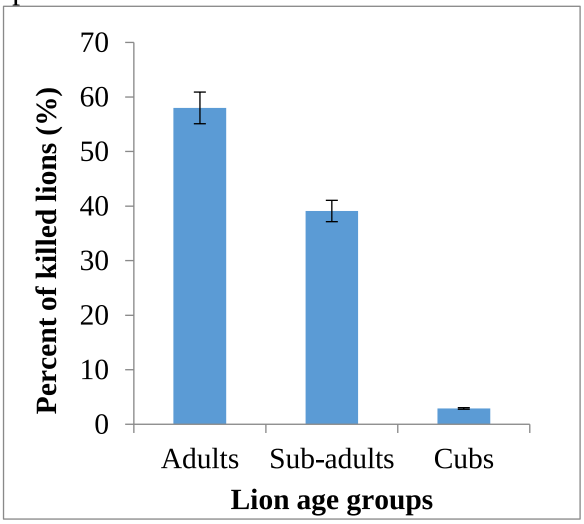

Figure 1: The percentage of killed lions by age groups in the Maasai steppe.

The majority (84.2%, n = 106) of lion killings incidences took place during the wet season (November to April) and 15.8% (n = 21) happened in the dry season (June to October) (Figure 2).

Temporal distribution of lion anthropogenic mortalities

Furthermore, there was a significant difference in the numbers of lions killed at different times of the day, $\chi^2_{(1,\ 127)} = 35.346$, $p < 0.0001$. Most (76%, n = 97) of the lion killings took place during darkness (night) around the Maasai homestead (bomas), while few cases (24%, n = 30) took place during the day in the grazing areas. The lion killings were found to be clustered in grazing areas between Tarangire and Manyara National Parks (Figure 3). The lion killings incidences were rampant in the eastern side but slightly clustered in the northern part (Figure 3). In addition, it was observed that as the frequency of livestock predation increases in a given area it also elevated the number of lions killed in a given locality. Between 2005 and 2017, Esilalei, Loborsoit, and Oltukaihad villages experienced both the highest frequencies of lion anthropogenic mortalities as well as the highest numbers of lions killed compared to other villages in the study area (Table 1). Two villages, Emboret and Losirwa located furthest from the two parks experienced the lowest frequency of lion anthropogenic mortalities.

There was no lion anthropogenic mortality recorded in the year 2007 in the Maasai steppe, however, the maximum frequencies of the lion killings took place in 2009, 2011, and 2015 (Figure 4). As shown in figure 5, most lion anthropogenic mortalities took place in village lands located between the two parks in the Maasai steppe. It was learned that habitat loss and conflicts with humans were the greatest causes for concern.

Relationships between landscape variables and lion anthropogenic mortalities

The spatial logistic regression model consisted of six predictor variables which explained about 66.7% of the observed variations among landscape variables that influence lion anthropogenic mortalities in the Maasai steppe (Table 2).

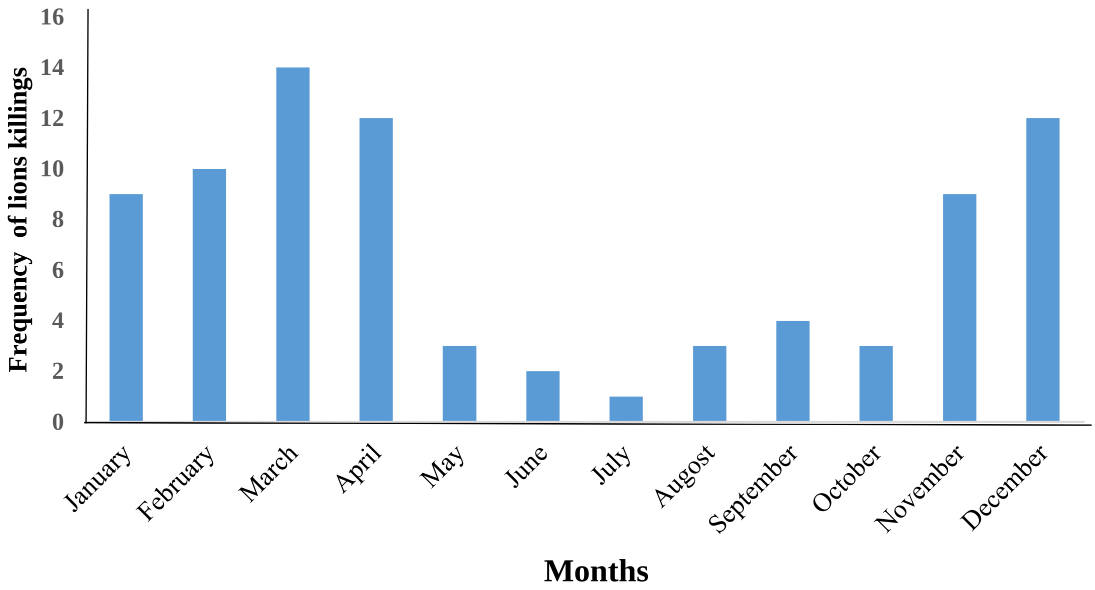

Figure 2: Monthly distribution of the lion anthropogenic mortalities in the Maasai steppe.

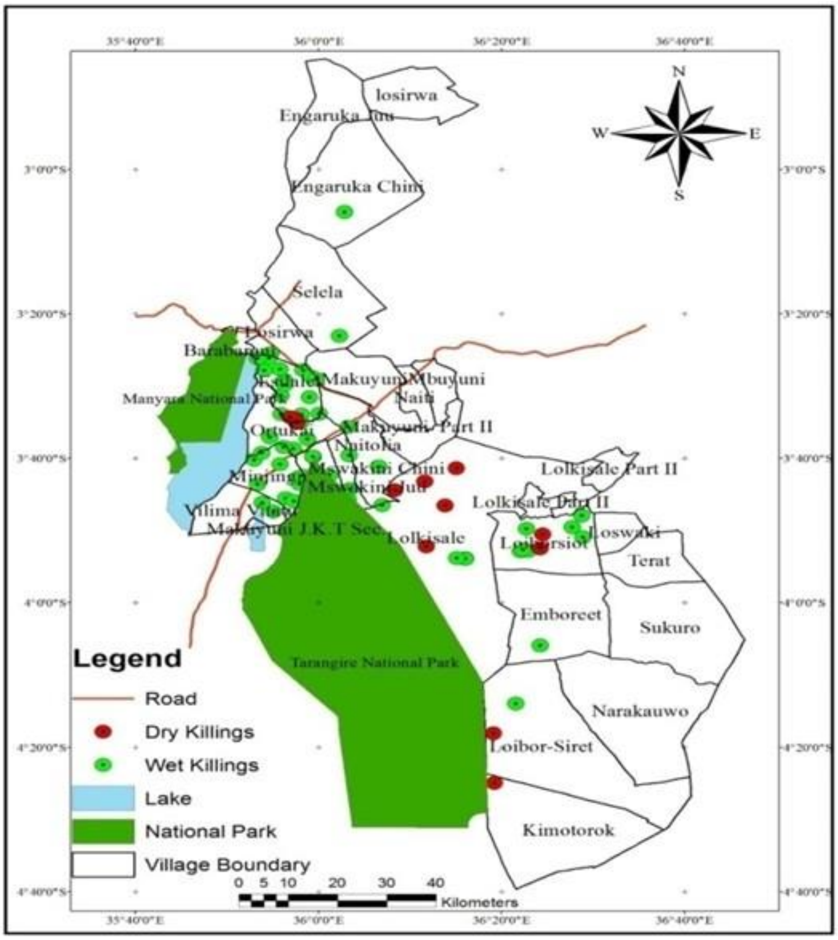

Figure 3: Seasonal distribution of the lion anthropogenic mortalities in the Maasai steppe.

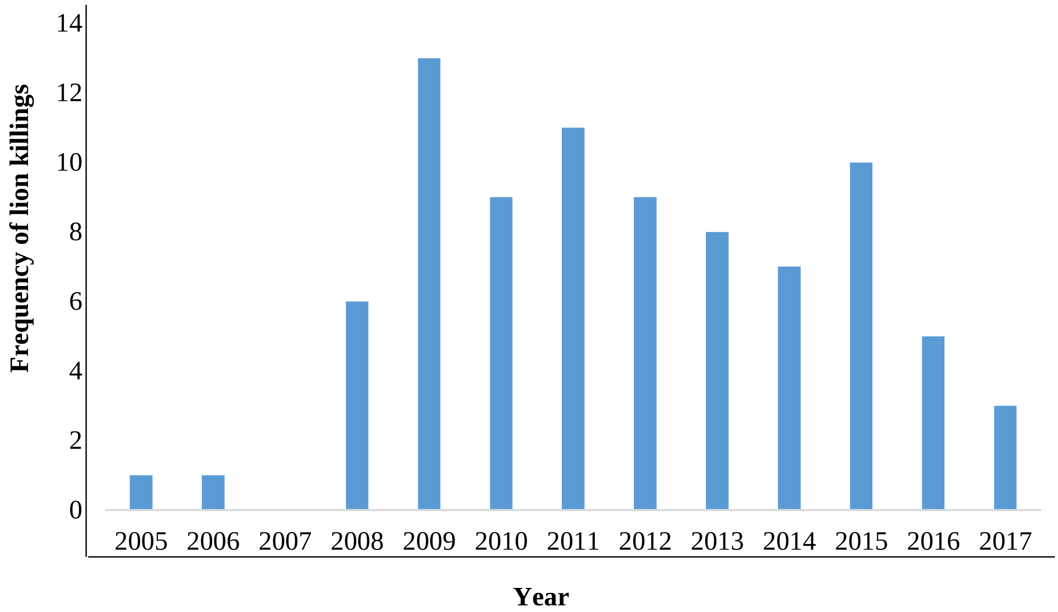

Figure 4: The annual trends of lion anthropogenic mortalities between 2005 and 2017.

Table 1: Distribution of lion killings incidences in villages in the Maasai steppe

Village name	Lions killing frequencies	Number of lions killed
Esilalei	16	31
Loiborsoit	12	22
Oltukai	11	12
Minjingu	6	7
Mswakinijuu	5	5
Vilimavitatu	5	5
Kakaoi	4	4
Makuyuni	4	4
Olasiti	3	10
Lobosiret	3	2
Mswakinichini	2	6
Manyara ranch	2	5
Naitolia	2	3
Lolkisale	2	2
Engaruka	2	2
Kimotorok	1	5
Emboret	1	1
Losirwa	1	1
Total	**82**	**127**

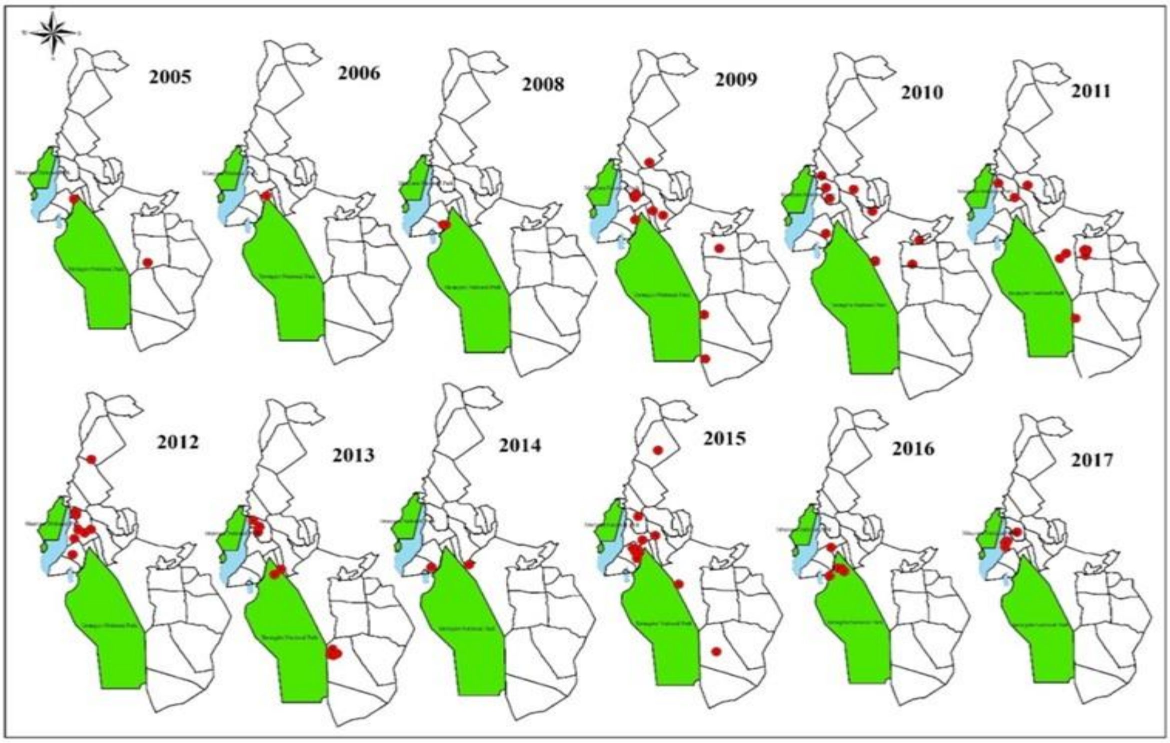

Figure 5: The annual spatial distribution of the lion anthropogenic mortalities in village lands (2005 - 2017) in the Maasai steppe.

Table 2: Summary of spatial logistic regression of landscape variables

Term	***β***	**EXP(*β*)**	**95% CI**		***p-value***
			Lower	Upper	
Constant	2.203	0.052	0.0015	1.776	0.001*
Vegetation cover (NDVI)	-2.96	0.104	0.016	0.662	0.094
Distance to the lake	-1.123	1.024	1.014	1.034	0.089
Distance to the road	-2.267	30.319	5.717	160.793	0.025*
Distance to the river	3.412	0.325	0.086	1.224	0.001*
Topography (Aspect value)	0.024	1.081	1.050	1.112	0.001*
Distance to settlements	0.078	0.077	0.015	1.207	0.001*

An asterisk (*) signifies a significant difference at $p < 0.05$.

Among the landscape variables, vegetation cover insignificantly but negatively (β= -2.96, p = 0.094) influenced lion killing incidences in the study area. The Odds ratio indicates that a unit decrease in NDVI value increases the likelihood of lion killing incidences in the actual locations by a factor of 0.052 than in randomly selected locations. Furthermore, it was observed that vegetation cover in the actual lion killing areas influenced lion killings incidences. For example, areas with the lowest NDVI values had the highest killing of lions in the Maasai steppe between 2005 and2017. The distance from the lake influenced lions' killings incidences negatively and it was statistically insignificant (β = -1.123, p = 0.089). The Odds ratio indicates that a unit decreases in distance towards the lake the higher the likelihood of a lion being killed by a factor of 1.024 than is the case in randomly selected locations. The distance from the nearby roads influenced lion killing incidences negatively and significantly (β = -2.267, p = 0.025). The negative sign implies that as the distance from the road decreases, the chance of a lion being killed increases. The Odds ratio indicates that a unit decrease in distance from the road increases the likelihood of a lion being killed in the actual locations by a factor of 30.32 as opposed to randomly selected locations.

The distance to the nearby river was significantly and positively correlated with the actual location of the incidences of lion killings (β = 3.412, p = 0.001). The Odds ratio indicates that a unit increase in the distance away from the river, the likelihood of a lion being killed increases by a factor of 0.35 as opposed to randomly selected locations. Additionally, our study found that the lion anthropogenic mortalities were positively correlated and significantly influenced by topography in the Maasai steppe (β = 0.023, p = 0.001). The Odds ratio indicates that a unit increase in the elevation increases the likelihood of a lion being killed by a factor of 1.081 as opposed to randomly selected locations. The distance to human settlements was significantly and positively correlated with the actual location of the incidences of lion killings (β = 0.078, p = 0.001). The Odds ratio indicates that a unit increase in the distance away from the river the likelihood of a lion being killed increases by a factor of 0.077 as opposed to randomly selected locations (Table 2).

Point pattern and hotspot detection of lion anthropogenic mortalities

Both the nearest neighbor and the point density analyses showed that the killings of lions were not dispersed but rather clustered. The clustering of the incidences of lion killings was also revealed by the kernel density analysis when detecting the hotspots. In both seasons, Ripley's K-function analysis showed that lion killings in the Maasai steppe ecosystem were significantly clustered. The incidences of lion killings were clustered at all distances examined up to 45 km. The analysis of lion killing scenes using ArcGIS's incremental spatial auto-correlation tool showed that the maximum clustering occurred at a distance of 41 km. The kernel density analysis also revealed the variation in the number and size of lion killings hotspots between 2005 and 2017 (Figure 6).

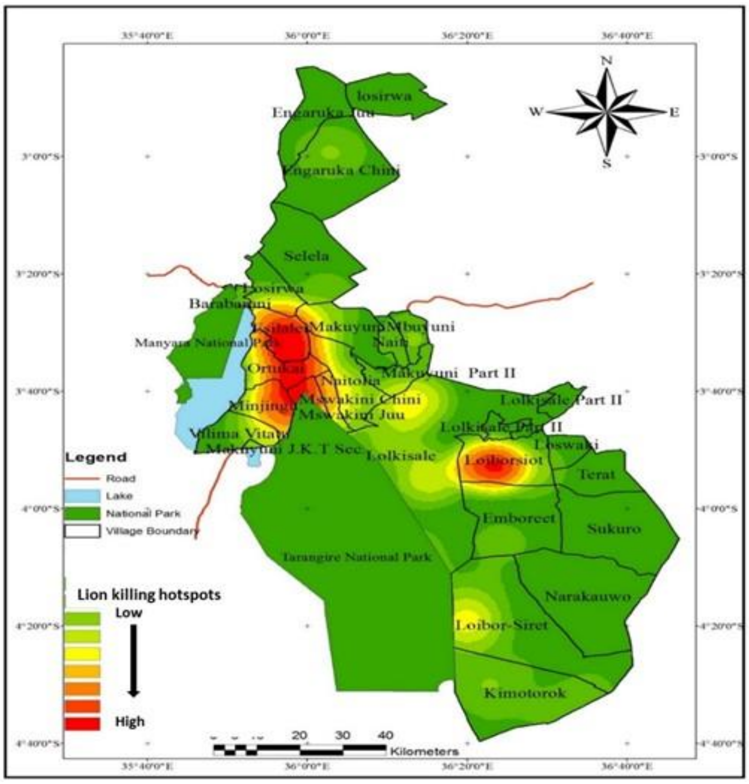

Figure 6: The lion anthropogenic mortalities hotspots: red colour represents areas with the highest frequencies of the lion killings incidences between 2005 and 2017 in the Maasai steppe.

DISCUSSION

Lion attacks on domestic animals are more frequent in the savannah and grasslands where pastoralism remains the main source of livelihood for many people. The highest lion killings incidences with more than one lion carcass were recorded in the Maasai steppe between 2005 and 2017. Significant lion killings incidences took place during the wet season (November to April) compared to the dry season (June to October). The high rate of lion killings may be due to the seasonal shift of prey species from the park to the village lands during the wet season which exerts pressure on large carnivores to follow them to the village land and end up being killed by humans once they attack livestock. Grazing areas between Tarangire and Manyara National Parks had the highest frequencies of the lions' killings. The three villages, Esilalei, Loborsoit, and Oltukai had experienced both the highest frequencies of lion anthropogenic mortalities as well as the highest numbers of lions killed compared to other villages in the study area. It was learned that livestock keepers retaliate by kill lions once they attack livestock in the village land. An increase in livestock attacks and cases of large carnivores being killed occur when they move to the village land (Woodroffe and Frank 2005, Kolowski and Holekamp 2006, Kissui 2008, Gebresenbet *et al.* 2018). Eyebe *et al.* (2012) found that where human-lion conflicts regularly occurred in six villages provoking the killing of lions and led to a 70% reduction in the lion population in Waza National Park. Cultural practices remain an important motivation for lion-killing (Ikanda and Parker 2008) Furthermore, adherence to traditional cultural beliefs still motivates lion hunting by Maasai youth even though ritual lion hunting was banned in the 1970s (Thompson 1997); secrecy surrounding these rituals generally makes it impossible for wildlife managers to enforce the ban (Spencer 1988). By killing a lion, a warrior (*Morani*) demonstrates his courage and strength (Spear and Waller 1993). The *Alamayo* may be a purely cultural act or in retaliation against a livestock attack.

Our study results showed that the vegetation cover in actual lion killings areas influenced lion killings incidences. For example, areas with the lowest NDVI values had the highest killing of lions in the Maasai steppe. We noted that as the vegetation cover of an area decreases the chances of lion killing incidences increase. Lions were likely to be killed in open grassland and small shrubs than in dense areas. Similar to our findings, Fischhoff *et al.* (2007) reported the highest lion killings in open grasslands.

Water bodies have much influence on lion appearance in the Maasai steppe landscape. The distance from the lake influenced lion killing incidences negatively. Our study results revealed that the shorter the distance from the lake the more the killings in the Maasai Steppe. Veilex *et al.* (2010) found that water holes normally alter key habitat features that determine the dispersion of prey, which in turn influence the spatial ecology and movement patterns of terrestrial predators such as lions. A similar observation was made by other scholars (e.g. Mosser and Packer 2009, Loveridge *et al.* 2009) who found that the indulgence of water holes across the landscape determines habitat selection and the potential lion territories.

Furthermore, distance from the nearby roads influenced lion killings incidences. We found that as the distance from the road decreases, the chance of a lion being killed increases. Spatially, it was observed that most of the lion killings occurred mainly near tarmac road across the Kwakuchinja Wildlife corridor, which bisects Tarangire and Manyara National Parks. The nearby roads are in the villages' centers, which are characterized by different human activities mainly livestock keeping. Consequently, when lions and large ungulates start their seasonal movement, lions could normally face fierce retaliatory attacks at this juncture due to livestock predation. Furthermore, it was learned that seasonal movements of the large ungulates to the village lands in the Maasai steppe ecosystem force them to share water resources with livestock which automatically triggers large carnivores attacking livestock. Similarly, de Boer *et al.* (2011) found that water was one of the dependent factors that determinate spatial distribution of lion prey, since the availability of prey is higher closer to water sources. Elsewhere, it has been reported that conflicts intensify as the incidences of human-lion interactions increase with human population growth and encroachment into lion habitats, eventually resulting in lion killings range contractions and decreasing numbers of lions (Woodroffe 2000). Poor animal husbandry practices create further opportunities for livestock depredation as humans move into or close to protected areas in search of resources (Patterson *et al.* 2004) and lions disperse to adjacent areas in search of prey (Woodroffe and Frank 2005). Predators, such as lions, may represent actual or perceived threats to humans or livestock (Gebresenbet *et al.* 2018). Additionally, our study found that the lion anthropogenic mortalities were influenced by topography in the Maasai steppe. This suggests that as the elevation of an area increases it would increase the chances of a lion being killed. It has been shown elsewhere that landscape features such as erosion gullies and the availability of kopjes can increase the risk of predation from lions (Hopcraft *et al.* 2005).

Distance to human settlements significantly and positively correlated with the actual location of the incidences of lion killings. We noted that as distance to human settlements increases the likelihood of a lion being killed also increases. We predicted that infrastructure development could increase the competition for limited land resources and thus escalate the situation. Conflicts will continue to escalate as the frequency of human-lion interactions increase with human population growth and encroachment into lion habitats. In addition, poor animal husbandry practices will create further opportunities for livestock depredation as humans move into or close to the parks in search of resources and lions disperse to adjacent areas in search of prey.

CONCLUSIONS AND RECOMMENDATION

The location of the hotspots suggests that human-lion conflicts and social practices in the area may be contributing to the killing of lions. The identified lion-killing hotpots could be used as starting points by the Tanzania wildlife authorities in taking measures to ensure that the local communities provide their support to the conservation of lions. Non-Governmental Organizations and the Tanzania Wildlife Management authority should conduct a joint operation in dealing with lion killing practices in the Maasai steppe ecosystem. Since anthropogenic mortalities were found to threaten the existence of lion populations in the Maasai Steppe, there is a need for wildlife management authorities to pay attention to the determinants of lion killings. Emphasis should focus on educating people about the value of wildlife and their habitats, the consequences of habitat destruction, and ways of mitigating the problem.

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