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Human-wildlife conflicts and their correlates in Narok County, Kenya

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A B S T R A C T

Human-wildlife conflicts (HWC) are often caused by human population increase, high livestock and wildlife population densities and changing land use and climate. These conflicts are typically most intense in human-dominated systems where people, livestock and wildlife share the same landscapes and during severe droughts. Consequently, HWC are common in developing countries where wildlife still roam outside protected areas, such as in parts of Africa. We analyze how HWC vary across multiple wildlife species, seasons, years, and regions to quantify their extent, causes and consequences using data collected by the Kenya Wildlife Service (KWS) in Narok County of Kenya during 2001–2017. Wildlife species contributed differentially to HWC such that only six species plus non-human primates contributed 90% of all the conflict incidents ($n = 13{,}848$) in the 17-year period. Specifically, the elephant (46.2%), buffalo (10.6%), Burchell's zebra (7.6%), leopard (7.3%), spotted hyena (5.8%) and lion (3.3%), collectively contributed 80.8%, whereas non-human primates contributed 11.7% of all the conflicts. The three most common conflict types were crop raiding (50.0%), attacks on humans (27.3%) and livestock depredation (17.6%). Crop raiding was most acute where cereals (wheat and maize) are grown on large scales. Carnivores were more likely to attack livestock species with body sizes comparable to their own. Thus, the leopard (44.0%, $n = 3{,}368$) and spotted hyena (37.9%, $n = 2{,}903$) killed most sheep and goats whereas the lion (63.1%, $n = 531$) and spotted hyenas (14.5%, $n = 122$) killed most cattle. HWC showed evident seasonal and inter-annual fluctuations, reflecting underlying rainfall variation. Accordingly, HWC were highest in 2008–2009 when rainfall was lowest in Narok County. Similarly, crop raiding peaked in the late wet season when crops mature whereas livestock depredation was higher in the wet season when natural prey density is lowest. Land conversion to agriculture and increase in human and livestock numbers were all positively associated with increase in HWC. Effective strategies for reducing HWC should be multi-faceted and integrate variation in the intensity and type of HWC between species, regions, seasons and years. Such strategies should discourage habitat conversion but encourage regulating livestock density. Further, they should promote land use zoning to minimize contacts between people, livestock and wildlife; effective livestock herding methods and predator-proof livestock corrals to minimize livestock depredation and fencing farms at greater risk of crop destruction.

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1. Introduction

Human-wildlife conflicts (HWC) are increasing in many human-dominated landscapes, with significant implications for biodiversity conservation worldwide (Ruyle, 2013; Redpath et al., 2013; Acharya et al., 2016; Anand and Radhakrishna, 2017). HWC can be defined as the negative interactions between humans and wildlife (Messmer, 2009). They are caused primarily by human population expansion, climate change and variability, land use change and the associated habitat degradation, fragmentation and loss and their impacts on livestock and wildlife populations (Hoare, 1999; Woodroffe et al., 2005a; Distefano, 2005). These processes alter resources for humans, livestock and wildlife, intensifying competition for space, forage and water. The conditions causing HWC are particularly pronounced in developing countries (Smith and Kasiki, 2000; Birch and Grahn, 2007; Seoraj-Pillai and Pillay, 2016). As with other developing countries, Kenya has experienced exponential human population growth in recent decades, from about 8 million people in 1960 to 49 million people in 2018 (https://data.worldbank.org/country/kenya). This growing human population requires more land for settlements, cultivation and other developments (Lamprey and Reid, 2004; Mukeka et al., 2018a). The impacts of land use developments on HWC are amplified by climate change and its widening variability (Kanga et al., 2012).

HWC incidents should be especially high in Kenya because over 65% of Kenya's wildlife are found on private and communal lands outside protected areas (Western et al., 2009). Similarly, HWC should be particularly high in Narok County of Kenya because it supports about 30% of all Kenya's wildlife (Ogutu et al., 2016), most of which occur on private and communal lands and wildlife conservancies outside the state protected Maasai Mara National Reserve (MMNR; Ogutu et al., 2008; Ogutu et al., 2014). Conflicts between humans, livestock and wildlife in Narok County are accentuated by the expansion of human and livestock populations, cultivation, infrastructure, fences and settlements that reduce the space and other resources for wildlife. These changes transform and truncate wildlife habitats (Waithaka, 2004) and compress wildlife into the MMNR and the adjoining conservancies (Veldhuis et al., 2019). Although pastoralism is the major form of land use in large parts of Narok and is more compatible with wildlife conservation than most other land use types (Western, 1982), changing economic opportunities, culture and human immigration (Omondi, 1994; Lamprey and Reid, 2004), have led to substantial changes in the lifestyles of the Maasai, the main inhabitants of Narok County.

Even though habitat degradation, climatic variation, human and livestock population sizes are the primary drivers of HWC, surprisingly few studies have related long-term changes in HWC to changes in these variables. In Narok County, human population expansion, increasing livestock numbers and climate change jointly exacerbate human-wildlife conflicts. Narok County has experienced a striking human population growth from 110,100 people in 1962 through 470,000 in 1999 to 720,000 in 2009 (Ogutu et al., 2016) and the number is expected to increase to about one million by 2019 (Mukeka et al., 2018a). This is putting considerable pressure on available land as the demand for settlements and food rises, reducing wildlife habitat and increasing competition between livestock and wildlife for resources. Livestock numbers have also been increasing in Narok County (Ogutu et al., 2016), further reducing the available resources and increasing HWC. A similar increase in livestock numbers was also associated with an increase in HWC in India (Mishra, 1997). Climate change and widening climatic variability affect HWC through their effects on the food and water supply for wildlife (Shen and Ma, 2014). In particular, recurrent droughts and rising temperatures (Ogutu et al., 2008; Bartzke et al., 2018) cause frequent food and water shortages for herbivores, resulting in greater movements and likelihood of contacts between wildlife and people and livestock.

Understanding how changing land use, climatic variation and human and livestock population sizes drive HWC can therefore yield crucial insights for developing effective HWC mitigation and biodiversity conservation strategies. Although they can reveal seasonal and inter-annual dynamics, extent, severity and consequences of HWC for both wildlife and human communities, analyses of long-term patterns in HWC for multiple species are rare because of data scarcity. Moreover, many HWC studies rely on survey questionnaires (Omondi, 1994; Holmern et al., 2007; Yirga et al., 2013) that are prone to bias, for example, because livestock owners tend to exaggerate livestock losses to large carnivore depredation (Siex and Struhsaker, 1999), than actually reported HWC incidents.

Here, we analyze how human-wildlife conflicts vary across species, regions, species and years using HWC data collected by the Kenya Wildlife Service (KWS) in Narok County during 2001–2017. Our analysis extends, expands upon and updates earlier studies of HWC that focused on single species (Sitati et al., 2003; Mijele et al., 2013; Smith and Kasiki, 2000; Kanga et al., 2013), or multiple species (Omondi, 1994; Mukeka et al., 2018a) by considering long-term monitoring HWC data for multiple wildlife species and their environmental and anthropogenic correlates.

Our analyses of HWC patterns for Narok County cover the 17 years spanning from 2001 to 2017 and address the following four questions by testing predictions of nine hypotheses (Table 1). (1) What are the long-term temporal trends in HWC for each of the 18 common wildlife species in each of the four contrasting regions of Narok County? (2) What are the crop type preferences of the herbivore species based on the type of crops they damage? (3) How many people are injured or killed? (4) How many individuals of the different livestock species are killed by particular large carnivore species and when? (5) How do HWC vary with land use change, specifically land conversion to agriculture, seasonal and inter-annual variation in rainfall, temperature, human and livestock population size?

Table 1
Hypotheses, their predictions and rationale concerning human-wildlife conflicts in Narok County 2001–2017.

Hypotheses and Predictions	Rationale
Objective 1	
H1: Frequency of HWC incidents should differ among species, reflecting inter-specific distinctions in population abundance, distribution, resource requirements, and use	Inter-specific contrasts in resource requirements and use should lead to differences in species' contributions to HWC (Mukeka et al., 2018).
H2: If HWC incidents do not reflect spatial habitat differences then their frequency should be proportional to the areal size of a region	Larger regions should have more human-wildlife conflicts than smaller ones simply because of their size. However, heterogeneity in resource distribution across landscapes and inter-specific differences in species' use of these resources should lead to uneven distribution of conflicts across landscapes (Sitati et al., 2003)
H3: HWC incidents should show evident seasonal and inter-annual variation. In particular, HWC should peak in the late wet season and during severe drought years.	HWC should vary seasonally because rainfall is strongly seasonal and controls the quantity and quality of food and water for herbivores as well as seasonal herbivore dispersal and migration in savannas (Boutton et al., 1988a, b; Deshmukh, 1984). Inter-annual rainfall variation therefore also governs inter-annual variation in food and water availability and quality for herbivores (Ogutu and Owen-Smith, 2005; Bartzke et al., 2018).
Objective 2 **H4:** HWC incidents involving crop raiding should (**H4.1**) peak in the late wet season and vary with the (**H4.2**) crop type, (**H4.3**) foraging behavior (resident, migratory, or wide ranging) and (**H4.4**) feeding style (grazer, browser or mixed feeder) of wild herbivores	Crop raiding should peak in the late wet season because grazers and mixed feeders should predominate HWC involving raiding of cereals (e.g. maize and wheat), browsers should dominate HWC involving raiding of legumes whereas nonhuman primates should dominate HWC involving roots and tubers (Thouless and Sakwa, 1995; Hill, 2000; Conover, 2001; Mackenzie and Ahabyona, 2012; Meinecke et al., 2018)
Objective 3 **H5:** HWC incidents involving livestock depredation should (**H5.1**) increase with increasing livestock density (**H5.2**) peak in the wet season and (**H5.3**) reflect the body size of carnivore species relative to livestock species. (**H5.4**) Livestock depredation should also be higher in the conservancy and Narok North with higher predator densities in the wet season	Livestock attacks by carnivores should increase with increasing livestock density (Sangay and Vernes, 2008). Livestock depredation should also be higher in the wet season when migratory ungulates are absent from Narok. Lion (*Panthera leo*), spotted hyena (*Crocuta*) and leopard (*Panthera pardus*) should be the leading carnivores killing livestock in Narok. Lions should kill more cattle (*Bos taurus)* because of their larger body size, whereas hyenas and leopards should kill more sheep (*Ovis aries)* and goats (*Capra aegagrus hircus)*, calves and dogs (*Canis lupus familiaris)* for the same reason. Carnivore attacks on livestock should be more common closer to wildlife protected areas, such as the Maasai Mara National Reserve and the adjoining wildlife conservancies, expected to have higher large carnivore densities (Kolowski and Holekamp, 2006; Patterson et al., 2004)
Objective 4 **H6:** HWC incidents should increase with the proportion of the land area converted into uses incompatible with wildlife use (e.g., agriculture and settlements)	Land conversion to uses incompatible with wildlife, such as agriculture and settlement, degrade, fragment and reduce suitable wildlife habitats (Veldhuis et al., 2019). This increases competition between livestock and wildlife for food, water and space and subsequently increases the probability of conflicts between humans and wildlife (Sitati and Walpole, 2006; Okello, 2005; Ogutu et al., 2009; Acharya et al., 2017)
H7: HWC incidents should increase with increasing rainfall and temperature	Rainfall peaks in Narok County in the wet season months of November–June. Wildlife abundance is lowest in Narok in the wet season because the migratory wildebeest and zebra are in Serengeti National Park in Tanzania at this time. Food and water for herbivores are more abundant and widely distributed in the wet season leading to better body condition, more dispersed distributions and reduced susceptibility to predation. Consequently, livestock depredation should increase with increasing rainfall in Narok (Pennycuick, 1975; Kolowski and Holekamp, 2006). Rising temperature increases habitat desiccation (Ogutu et al., 2008) and can increase HWC by elevating water scarcity and herbivore movements in search of water and high-quality food
H8: HWC incidents, especially attacks on humans, should increase with increasing human population density	Human population size has increased 10-fold in Narok County from 1962 to 2017 (Fig. S 1). This increases competition for limiting resources and the likelihood of contacts between humans and wildlife (Woodroffe et al., 2005b; Ogutu et al., 2016)
H9: HWC incidents, especially livestock attacks, should increase with increasing livestock numbers	Livestock numbers, especially of sheep and goats, increased by 124.5–648.1% in Narok County from 1977 to 2016 (Ogutu et al., 2016). Contemporaneously, wildlife numbers decreased dramatically (Ogutu et al., 2016, Fig. S 2). The high livestock density accentuates competition between livestock and wild herbivores for food, water, and space and depresses wild herbivore abundance (Ogutu et al., 2011). The depressed prey abundance increases the probability of carnivore depredation on livestock (Sangay and Vernes, 2008). Competition with wild herbivores should peak in the dry season when food and water are most scarce and migrants are present in Narok but livestock depredation should peak in the wet season when migratory ungulates are absent from Narok County (Sinclair et al., 2000; Ogutu et al., 2009).

2. Methods

2.1. Study area

Narok County (17,944 km^2) is situated between longitudes 34° 34′ E – 36° 23′ E and latitudes 0° 27′ S - 2° 7′ S in southwestern Kenya. It borders the Serengeti National Park and the Loliondo Game Controlled Area in Tanzania to the south (Fig. 1). Southern Narok is the northern-most section of the Greater Mara-Serengeti Ecosystem (GMSE) (Mukeka et al., 2018a).

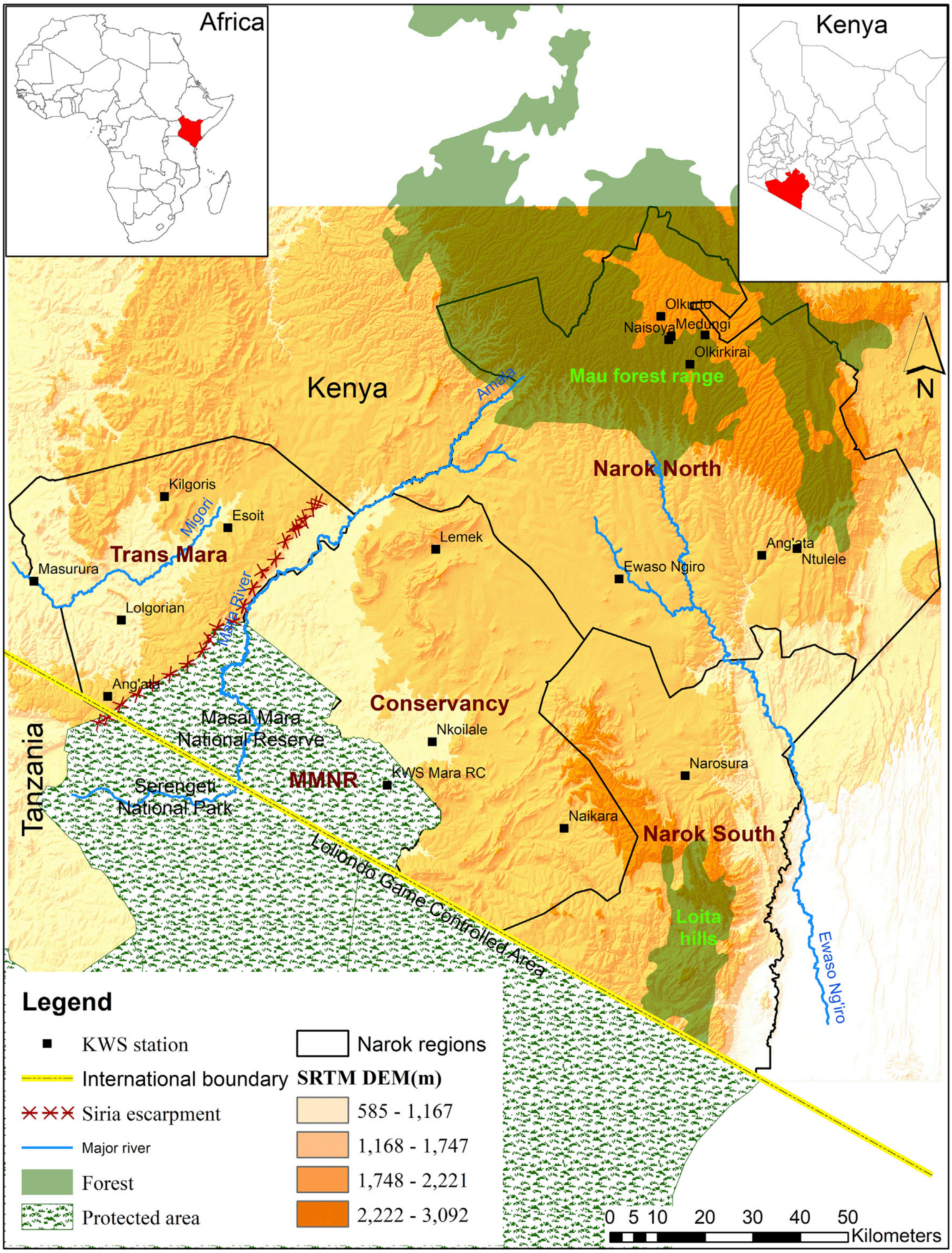

Fig. 1. Map showing the study area. The Narok County adjoins the Serengeti NP to the south and Loliondo Game Controlled Area in Tanzania to the southeast. KWS stations that respond to and keep records on HWC are distributed across the County. SRTM DEM means Shuttle Radar Topography Mission - Digital Elevation Model.

Maasai Mara National Reserve (MMNR), famous for its rich biodiversity, including the great wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) migration from the Serengeti in Tanzania to Maasai Mara in Narok County in Kenya (Ogutu et al., 2008). Rainfall in Narok is bimodal, with the wet season spanning November–June and the dry season covering July–October. The annual rainfall in the County is strongly determined by topographic relief and Lake Victoria and increases from south to north, east to west and southeast to northwest, and ranges between 500 mm in the Loita Plains to the east to about 1400 mm in the high altitude Mau ranges in the north (Campbell and Hofer, 1995; Norton-Griffiths et al., 1975; Fig. S 3). As well, temperatures range from a low of 7.3 °C to a high of 28.5 °C. Both the minimum and maximum temperature components increased throughout Narok County by an average of 2.5 °C between 1965 and 2015 (Fig. S 4). However, a trend of decreasing annual rainfall (Bartzke et al., 2018) and rising temperatures (Ogutu et al. 2008, 2016) in the region have been associated with recurrent severe droughts and flush floods.

A rich diversity and abundance of large mammalian herbivores are found within the MMNR, wildlife conservancies and community areas in Narok County (Broten and Said, 1995; Ottichilo et al., 2000). The common resident large herbivores include the African elephant (*Loxodonta africana*), the Maasai giraffe (*Giraffa cameleopardalis*), the cape buffalo (*Syncerus caffe*r) and hippo (*Hippotamus amphibius*). Furthermore, the migratory wildebeest, Thomson's gazelle (*Gazella thomsoni*), Burchell's zebra and the eland (*Tragelaphus oryx*) are common in Narok. The spotted hyena, lion, leopard and cheetah (*Acinonyx jubatus*) constitute the common large carnivores in Narok. Further details on large mammals found in Narok can be found elsewhere (e.g., Broten and Said, 1995; Bhola et al., 2012).

Vegetation in Narok County comprises mostly grasslands in the MMNR, wildlife conservancies and community areas in southern Narok and on the Loita Plains in Narok North (Fig. 1). Woodlands dominate Narok South while forests dominate the northern part of Narok North, which encompasses the Mau Forest range. Riverine vegetation fringes the major rivers and drainage lines in the region. Elephants and human-induced fires are the key drivers of vegetation dynamics in the region (Dublin, 1995; Guldemond and Van Aarde, 2008).

We partitioned Narok County into five regions using major land use, land management and physical landforms (Fig. 1). The first region, the MMNR is a protected area within which all human activities except wildlife conservation and tourism are prohibited. The second region is the area falling within a 50 km radius of the MMNR boundary to the north and east, which we designate as a conservancy because it is predominantly occupied by wildlife conservancies. These conservancies were set aside for wildlife conservation and tourism from 2005 onwards after land subdivision and privatization of land tenure in former Maasai group ranches (Lamprey and Reid, 2004; Norton-Griffiths et al., 2008). The wildlife conservancies support many wildlife species and also serve as important dispersal areas for the MMNR. Pastoralism, agro-pastoralism and human settlements are the major land uses on community areas bordering the conservancies (Bedelian and Ogutu, 2017).

The third region, Trans Mara, is separated from the rest of Narok County by the Siria escarpment and the Mara river. Intensive agriculture, pastoralism, settlements and wildlife conservation in a few wildlife conservancies are the major land uses in Trans Mara. The fourth region, Narok South, includes the Loita Hills, which is covered with forests and woodlands. The last region, Narok North, is characterized by small and large-scale wheat and maize farming, and dense settlement around urban and markets centers. Narok North encompasses the Mau forest range, which is severely threatened by human encroachment, charcoal burning, logging, and general habitat destruction. The Mau forest range is also an important wildlife habitat. The high rainfall in the Mau uplands makes it the major water catchment and source of water for wildlife in the low lands of the MMNR and the Serengeti National Park in Tanzania (Table 2). Also, the Conservancy and Narok North regions are cooler than the other three regions of Narok County (Table 2, Fig. S4). Narok County is still undergoing land privatization and associated land subdivision and fencing.

Drainage in Narok County is by two major rivers; the Mara and Southern Ewaso Ng'iro. The Mara river drains into Lake Victoria through the MMNR and the Serengeti National Park whereas the Ewaso Ng'iro drains into Lake Magadi in the adjoining Kajiado County of Kenya to the east.

2.2. Processing human-wildlife conflict and other data sets

KWS oversees the conservation of all wildlife in Kenya, inside and outside of protected areas since 1989. KWS has a network of wildlife incident reporting stations distributed throughout the whole country that collects data on HWC, poaching, and visitor security-related information (Mukeka et al., 2018a). We obtained HWC data captured in daily occurrence books from the Mara Research Center (MRC) and all the KWS community or security outposts in Narok County for 2001–2017 to ascertain that all incidents reported were captured. We verified the data during field visits to remove duplicity and by cross checking between records. The information collected on HWC includes the date (day, month and year) and place of incident, the local or common name of the wildlife species involved and conflict type (crop damage, human death, injury or threat, livestock killed or injured, property damage (water pipes, grain stores and houses)). Further, names of the crops damaged and livestock species killed during an attack are also recorded. We identified four main human-wildlife conflict types: 1) attack on humans, 2) livestock attack, 3) crop raiding, 4) property damage, and 5) 'other' – all the other conflict types. Also, we organized the 35 wildlife species involved in HWC into 13 individual species plus five groups of species (Appendix I, Table A.I and A.2). HWC data for 2001–2017 are provided in S1 Data in the supplementary materials.

Crop raiding is a major HWC type (Kumar et al., 2017). Because the type of crop destroyed reflects their foraging habits, we used crop type to infer crop preferences of crop raiding wildlife species. We grouped the crops damaged during crop raiding incidents into six broad categories. 1) Cereals, denoting where wheat (*Triticum aestivum*) and maize (*Zea mays*) were

Table 2
Summary description of the four study regions constituting the study area. The area of the regions (in km^2) are in parentheses. Average maximum and minimum temperatures are provided below the average annual rainfall, respectively.

Region (Area in km^2)	Average (1966–2017) annual rainfall (mm), maximum and minimum temperatures (°C) ± 1 SD	Average (1962–2017) human population density (number/km^2) and annual growth rate (1962–2017)	Average (1977–2016) livestock density (number/km^2)	Habitat characteristics	Predominant land use
Conservancy (4002)	869.2 ± 174.5 24.9 ± 0.7 10.2 ± 0.6	10 ± 6 (range 4–23) people 3.45%	35 cattle 45 sheep and goats 1 donkey	In good condition, dense fences in settled (community) areas	Wildlife conservation, ecotourism
Narok South (3593)	769.4 ± 1565 27.32 ± 0.66 13.42 ± 0.61	9 ± 5 (range 3–21) people 3.26%	25 cattle 29 sheep and goats 1 donkey	Mostly intact, water deficient region, Low fencing	Wildlife conservation, forests, livestock, limited small-scale agriculture, sisal plantations, settlements
Narok North (6425)	791.5 ± 145.5 22.52 ± 0.67 8.45 ± 0.62	32 ± 18 (range 7–73) people 4.17%	29 cattle 43 sheep and goats 1 donkey	Highly fragmented and degraded, dense fence	Large scale wheat and maize farming. Horticulture and small scale cultivation. Limited wildlife conservation (dispersal area), pastoralism, dense forest fragments
Trans Mara (2392)	980.4 ± 177.75 26.32 ± 0.67 11.72 ± 0.63	59 ± 32 (range 17–131) people 3.73%	73 cattle 17 sheep and goats 1 donkey	Highly fragmented, dense fences	Intensive small-scale agriculture, sparse forests, dense settlements, pastoralism

destroyed. 2) Tubers, including cassava (*Manihot esculenta*) and potatoes (*Solanum tuberosum*). 3) Legumes, encompassing common beans (*Phaseolus vulgaris* L.) and soya beans (*Glycine max*). 4) Fruits, comprising mangoes (*Mangifera indica*) and bananas (*Musa* spp.). 5) “Other”, representing all the other crop types plus crops not identified to species.

Livestock attacks are a major threat to the livelihoods of the Maasai pastoralists living in Narok County (Bedelian and Ogutu, 2017). To examine the preferences of wild animals, especially carnivores, we grouped livestock killed during attacks into the following four categories. 1) sheep and goats (shoats), 2) Cattle, 3) “Other”, grouping together donkeys, dogs, and poultry, and 4) “Unknown” representing livestock attack records with missing species name. As well, we tallied the number of livestock killed during attacks to quantify the losses incurred by livestock keepers during 2001–2017.

We also obtained and processed data on human (S2 Data), and livestock population (S3 Data) sizes, land use and land cover, rainfall (S4 Data) and temperature (S5 Data) to examine how they varied over time and with HWC incidents in Narok County during 2001–2017. We obtained data on human population size for each study region from the Kenya National Bureau of Statistics (KNBS). Because these data are derived from decadal national censuses, we used interpolation to estimate population size for years between successive censuses. For interpolation, we used a semi-parametric generalized linear mixed model, assuming a negative binomial error distribution and a log link function. The model allowed for a fixed intercept and year effects and random intercept and slope effects for each 5 × 5 km grid unit and a completely general (unstructured) covariance matrix parameterized in terms of variances and correlations for the random intercept and slope effects for each spatial grid unit. Further, we obtained total population estimates for cattle and shoats from the Directorate of Resource Surveys and Remote Sensing of Kenya (DRSRS) for 2000–2016. Likewise, we obtained land cover and land use data (LCLU) for 2000, 2006, 2011, 2014, and 2018 from DRSRS. We classified land use and land cover into agriculture (area under cultivation), dense, moderate and open forests, wooded and open grasslands and other, including water bodies and unclassified areas. We used the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) rainfall data for Narok Country spanning 1965–2017 (http://chg.geog.ucsb.edu/data/chirps/). We used historical rainfall and temperature data for 1965–2017 to provide a broad historical context for assessing inter-annual and seasonal variation in rainfall and temperature but used the rainfall data for 2001–2017 in the statistical analyses (S6 Data).

2.3. Statistical data analyses

We analyzed the multi-species data to establish HWC trends in Narok County during 2001–2017. The data were stratified into the four study regions for analysis. Since most of the HWC data are non-normally distributed counts, we applied mostly non-parametric statistical methods for analysis. Specifically, we used Chi-square goodness-of-fit tests to examine differences in the relative frequencies of conflicts between species and across the four study regions. We also calculated correlations between the different types of conflicts in each region to establish their spatial coherence. Since areal size can influence the absolute number of conflicts in a region, a chi-square goodness-of-fit test was used to further examine if the observed total HWC per region differed from expectation assuming a uniform distribution. We also used Spearman correlations and nonparametric linear regression analyses to quantify the strength of the association between the number of HWC conflicts and cultivated area, human population size, livestock numbers, rainfall and temperature in Narok County. Since human-wildlife conflicts are count data we also used negative binomial regression with a log link function to relate the number of conflicts to the various covariates.

Statistical analyses were done using SPSS (version 25), StataMP/15.1 (StataCorp LLC, USA) and SAS PROC GLIMMIX (SAS Institute, 2018). Maps were created using the ArcGIS® software 10.3 (Environmental Systems Research Institute, ESRI - 2014). Significance level was assessed at 0.05 unless otherwise stated.

3. Results

3.1. Frequency of human-wildlife conflicts by species

Narok County experienced substantial HWC during 2001–2017 (Table 3, Fig. 2). Overall, 13,848 conflict incidents, involving 13 wildlife species plus five species groups were reported. The elephant contributed the most to conflict incidents (46.2%) followed by nonhuman primates (11.7%). Contributions of two large herbivores, the buffalo (10.6%) and zebra (7.6%), ranked third and fourth, respectively. The giraffe (0.1%) caused the fewest conflicts. The three most common large carnivores comprising the leopard (7.3%), spotted hyena (5.8%) and the lion (3.3%) jointly contributed merely 16.4%. Overall, the number of conflicts caused by each species in Narok County differed ⟍ (χ^2_{51} = 3710.0, P = 0.001, Table 3) during 2001–2017 (H1).

3.2. The frequency of human-wildlife conflicts by outcome type and region

The distribution of conflicts differed starkly across the four regions (Table 4, Fig. 3). The elephant caused most of the conflicts in all the four regions and their contribution to the conflicts were highest in Narok North, intermediate in the Conservancy and Trans Mara and lowest in Narok South. Conflicts caused by snakes were most common in Trans Mara (Fig. 2). We expected the total number of conflicts to increase with the area of each of the four regions (H2), as it actually did (χ^2_3 = 2435.8, P <0.001). Further, we expected each outcome type of conflict to occur uniformly across the landscapes if resources are homogeneously distributed (H2) but both the relative frequency and type of conflicts varied across regions, contradicting this prediction (Table 4). Attacks on humans were the highest in the Conservancy, whereas crop raiding was more common in Narok North, Narok South and Trans Mara where crop farming is more extensive (Table 4). Livestock attacks were relatively higher than other conflict types in Trans Mara and the Conservancies, but property damage incidents were more common in Narok North (Table 4). Conflict types were not independent of each other. Thus, livestock attacks were significantly positively correlated with human attacks in the Conservancy (r_s = 0.67, P = 0.016) and crop raiding in Trans Mara (r_s = 0.62, P = 0.022). But, higher crop raiding was associated with fewer property damage incidents in Trans Mara (r_s = −0.79, P = 0.002). Overall, the relative frequency of conflicts differed significantly across conflict outcome types (χ^2_{12} = 1088.6, P = 0.001, Table 4).

3.3. Temporal patterns in HWC in Narok County

HWC incidents in Narok County varied markedly across both years (Fig. A1) and months (Fig. 3) during 2001–2017. The total annual conflicts in Narok County averaged 814.6 ± 459.1 (range 196–1848) and were the fewest in 2013 (n = 196) but the highest in 2008 (n = 1848). HWC incidents were remarkably low in 2001–2002 and 2013 but notably high in 2005–2006, 2008–2009 and 2015–2016. The troughs in HWC corresponded with high total annual rainfall whereas the peaks with severe

Table 3
Chi-squared goodness-of-fit tests of the null hypothesis that the percentage of HWC incidents attributed to each species or species group does not differ, ***n*** = total number of reported cases for each species.

No	Species	χ^2_3	***n***	***P***
1	Elephant	455.1	6401	<0.001
2	Nonhuman primates	415.9	1625	<0.001
3	Buffalo	676.5	1465	<0.001
4	Zebra	76.5	1051	<0.001
5	Leopard	794.7	1004	<0.001
6	Spotted hyena	125.0	806	<0.001
7	Lion	134.4	458	<0.001
8	Antelope	82.5	268	<0.001
9	Snake	970.4	167	<0.001
10	Other	23.3	129	<0.001
11	Wild dog	78.5	105	<0.001
12	Pigs	20.4	104	<0.001
13	Hippo	8.1	83	0.043
14	Wildebeest	35.1	73	<0.001
15	Crocodile	184.9	42	<0.001
16	Eland	4.2	40	0.242
17	Cheetah	2.1	14	0.544
18	Giraffe	43.6	13	<0.001
	Total		13848	

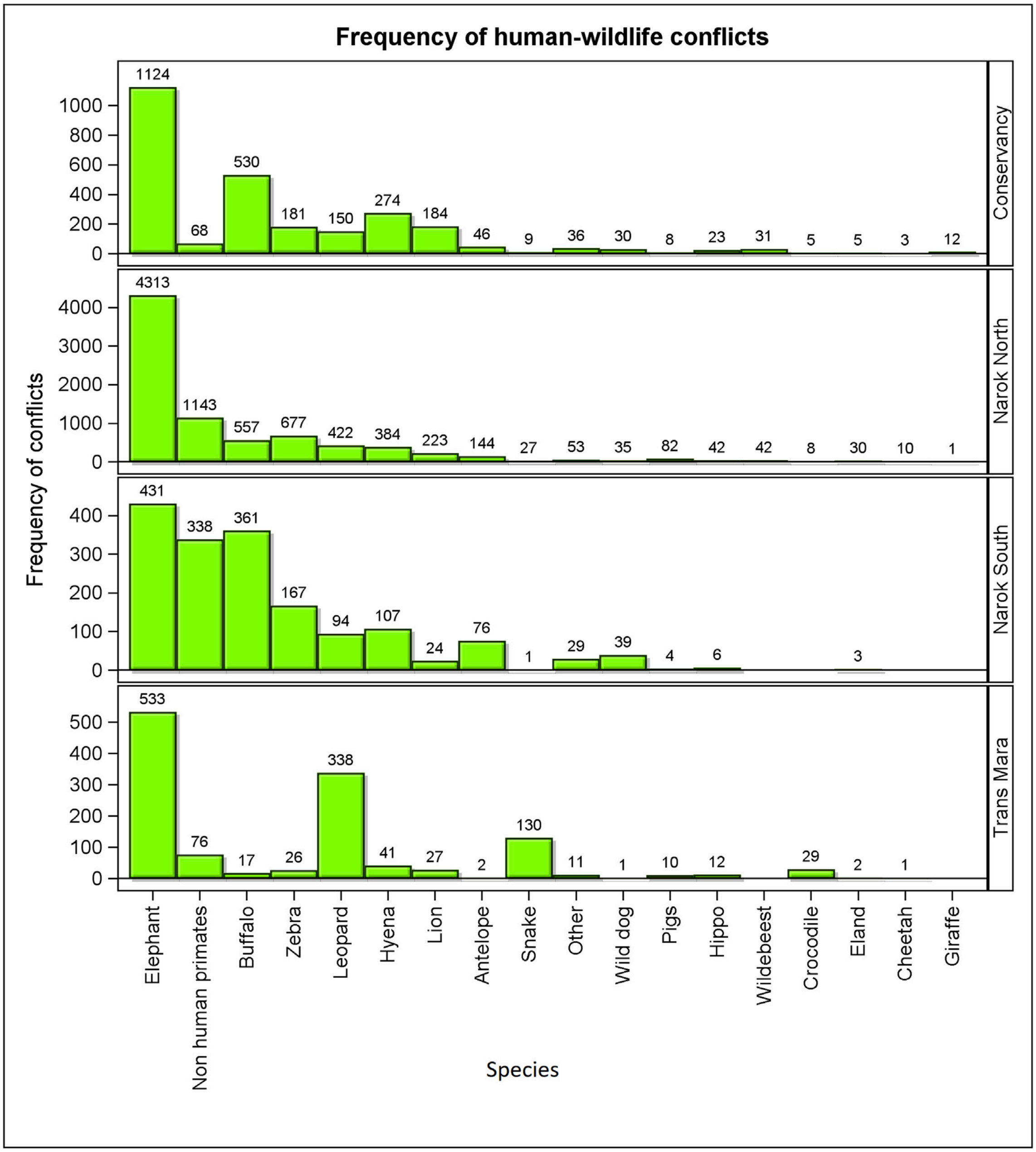

Fig. 2. Conflict frequencies for each species or species group in each of the four regions of Narok County. Data labels are the total frequencies of the HWC incidents for each species during 2001–2017.

Table 4
Chi-squared goodness-of-fit tests of the null hypothesis that the percentage contribution of each conflict type to the total conflicts does not differ across the four regions of Narok County.

Conflict type	Percentage contribution of conflict type to the regional total (100%)					Chi-square	
	Conservancy	Narok North	Narok South	Trans Mara	*n*	χ^2_4	*P*
Human attack	36.9	26.7	15.7	25.7	3774	243.2	0.001
Crop raiding	33.0	54.6	64.0	38.5	6930	581.3	0.001
Livestock attack	23.5	13.3	16.0	35.3	2438	444.6	0.001
Property damage	3.1	5.0	2.1	0.0	527	97.0	0.001
Other	3.5	0.5	2.3	0.6	179	163.8	0.001

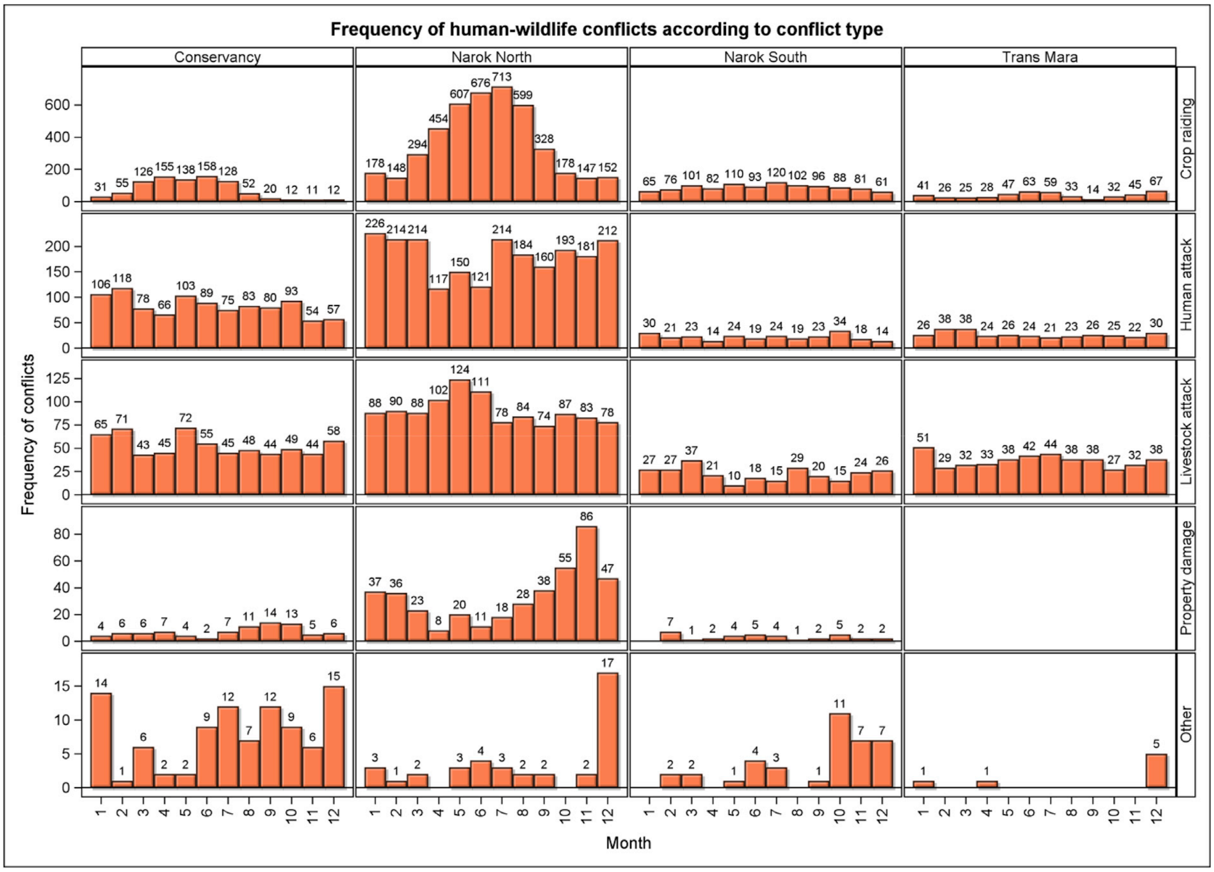

Fig. 3. Seasonal patterns in HWC for each of the four regions of Narok County during 2001–2017 (1 = January and 12 = December).

droughts in Narok County (Figs A1 and S 3). The total monthly HWC in Narok County during 2001–2017 averaged 1153.7 ± 75.14 (range 830–1583) and was the lowest in November ($n = 830$) and the highest in July ($n = 1583$) (Fig. 3). The total monthly HWC varied significantly across months ($\chi^2_{44} = 1327.4$, $P < 0.001$), demonstrating a strong influence of rainfall seasonality (H3). However, seasonality in HWC was not consistent across HWC outcome types. Notably, whereas crop raiding increased markedly from the late wet season in May to a peak in the early dry season in July, attacks on humans increased during the early wet season from December to a peak in February (Fig. 3). Thus, these results are consistent with H3 that seasonality influences occurrence and intensity of HWC.

3.4. *Wild herbivore crop type preferences during crop raiding*

Wild herbivore species differed in their preferences for crops and the most preferred crops varied across regions, reflecting seasonal and regional distinctions in the most commonly grown crops, confirming (H4.1; H4.2) respectively. More precisely, wild herbivores destroyed 55% of all crop types in Narok North, 42.9% of tubers in Trans Mara and 32.4% of vegetables in Narok South. In consequence, the percentage of crop type raided differed significantly across regions ($\chi^2_{15} = 307.7$, $P < 0.001$) (Table 5). Further, timing of peak crop raids varied with crop type, reflecting variation in the time when the different crop types are in season or are most attractive to wild herbivores. Thus, raids on cereals strikingly increased during the long rainy season in March–June, whereas raids on vegetables increased during the short-wet season in November–February (Fig. 4).

Elephants raided mostly cereals (49.6%, $n = 2677$), fruits (60.0%, $n = 21$), legumes (38.2%, $n = 82$) and vegetables (36.7%, $n = 247$). By contrast, nonhuman primates raided primarily tubers (71.4%, $n = 10$) and legumes (20.7%, $n = 44$) whereas antelopes (14.6%, $n = 31$) destroyed principally legumes. The relative frequency of damage to various crop types differed significantly across wild herbivore species ($\chi^2_{50} = 462.8$, $P < 0.001$), implying contrasting preferences as predicted by H4.3 (Table 6).

3.5. *Temporal variation in depredation incidents and large carnivore livestock species preferences*

A total of 2438 livestock attack incidents resulting in the loss of 8745 (514.4 ± 556.75) domestic animals were reported in Narok County during 2001–2017. This translates to an average loss of 450.8 ± 517.3 sheep and goats and 49.53 ± 38.40 cattle

Table 5
Chi-squared goodness-of-fit tests of the null hypothesis that the percentage contribution of each crop type to the total conflicts does not differ across the four regions of Narok County.

Crop type	Percentage contribution of crop type to crop raiding within regions (100%)				Total	Chi-square	
	Conservancy	Narok North	Narok South	Trans Mara	n	χ^2_3	*P*
Cereals	752 (83.7)	3432 (76.7)	788 (73.3)	422 (87.4)	5394	59.7	<0.001
Fruits	2 (0.2)	21 (0.5)	3 (0.3)	9 (1.9)	35	20.4	<0.001
Legumes	17 (1.9)	162 (3.6)	28 (2.6)	6 (1.2)	213	14.9	0.002
Other	53 (5.9)	480 (10.7)	38 (3.5)	30 (6.2)	601	72.1	<0.001
Tubers	0 (0.0)	8 (0.2)	0 (0.0)	6 (1.2)	14	30.0	<0.001
Vegetables	74 (8.2)	371 (8.3)	218 (20.3)	10 (2.1)	673	181.6	<0.001
Total					6930		

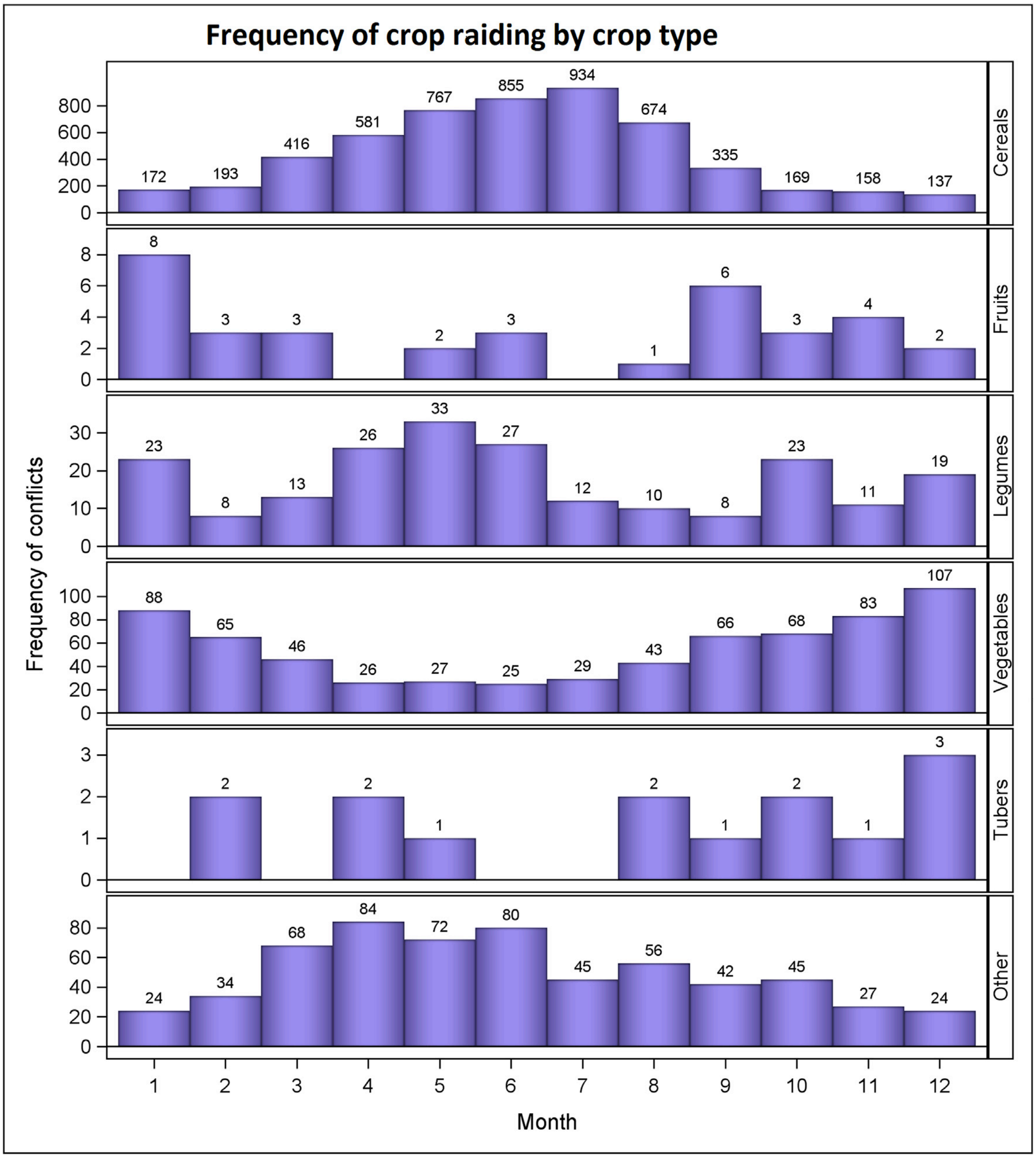

Fig. 4. Total monthly frequency of crop types destroyed during crop raiding in Narok County.

Table 6
The frequency of crop raiding by species and type of crop in Narok County during 2001–2017.

Species	Crop type												Chi-square test	
	Cereals		Fruits		Legumes		Other		Tubers		Vegetables			
	n	%	n	%	n	%	n	%	n	%	n	%	χ^2_5	P
Elephant	2677	49.6	21	60.0	82	38.5	335	55.7	4	28.6	247	36.7	65.5	<0.001
Non human primate	1033	19.2	5	14.3	44	20.7	57	9.5	10	71.4	233	34.6	158.1	<0.001
Zebra	862	16.0	1	2.9	22	10.3	93	15.5	0	0.0	46	6.8	49.9	<0.001
Buffalo	502	9.3	6	17.1	28	13.1	55	9.2	0	0.0	68	10.1	7.7	0.171
Antelope	155	2.9	0	0.0	31	14.6	24	4.0	0	0.0	55	8.2	116.5	<0.001
Pigs	74	1.4	0	0.0	0	0.0	4	0.7	0	0.0	9	1.3	5.6	0.342
Wildebeest	36	0.7	0	0.0	2	0.9	14	2.3	0	0.0	0	0.0	26.2	<0.001
Other	18	0.3	1	2.9	2	0.9	18	3.0	0	0.0	2	0.3	69.7	<0.001
Eland	28	0.5	0	0.0	2	0.9	0	0.0	0	0.0	7	1.0	7.4	0.191
Hippo	8	0.1	1	2.9	0	0.0	0	0.0	0	0.0	6	0.9	28.5	<0.001
Wild dog	1	0.0	0	0.0	0	0.0	1	0.2	0	0.0	0	0.0	4.4	0.492

per year to HWC in Narok County between 2001 and 2017. Overall, the frequency of livestock attacks differed significantly among regions (χ^2_9 = 100.2, $P < 0.001$) and was the highest for Narok North and the Conservancy (Table 7). Livestock attacks also varied significantly across months (χ^2_{33} = 87.1, $P < 0.001$, Fig. 3) and years (χ^2_{48} = 302.6, P = 0.001, Fig. 5). In particular, seasonality in livestock attacks varied regionally such that attacks peaked in the Conservancy and Narok South in the early wet season (December–March) but in Narok North in the wet season (January–June, Fig. 3). Across all regions, the total monthly livestock losses averaged 728.8 ± 152.1 (range 469–958) animals, with a peak in the early wet season (February), when the Serengeti migrants are absent from Narok, and a nadir in the late dry season (September), when most Serengeti migrants occupy Narok. The total monthly livestock losses in Narok County increased from the early (November–February) to the late (March–June) wet season, reflecting a similar underlying trend in natural prey scarcity for large carnivores in congruence with H5.2.

As expected, large carnivores predominantly killed prey species in their own body size range (H5.3) and the intensity of depredation incidents varied regionally, reflecting regional distinctions in natural prey availability, or large carnivore abundance. Thus, the small-bodied sheep and goats were killed principaly by the small-sized leopard (44.0%), spotted hyena (37.9%), wild dog (*Lycaon pictus*, 5.4%) and nonhuman primates (3.4%) and infrequently by the large-bodied lions (6.3%). But the large-bodied cattle were killed mostly by lions (63.1%) and rarely by spotted hyena (14.5%), leopard (5.7%) and wild dog (1.3%). Besides carnivores, elephants (10.8%), snakes (1.7%), and buffaloes (1.4%) also killed a few cattle. Regionally, more sheep and goats (506%, n = 3879) and cattle (48.6%, n = 409) were killed in Narok North, with lower natural prey density due to extensive crop farming and high human population density, and in the Conservancy (sheep and goats: 29.6%, n = 2270; Cattle: 36.9%, n = 311), with high large carnivore abundance in accord with H5.4.

3.6. Land use and cover influences on HWC incidents in Narok County

Narok County experienced substantial land use and cover changes between 2000 and 2014. Overall, the cultivated area increased from 2000 to 2018 in Narok North and Trans Mara but not in the Conservancy or Narok South (Fig. A2) (H6). Agricultural expansion in Narok North and Trans Mara primarily entailed conversion of wooded and open grasslands to farmlands (Fig. A2). Human-wildlife conflicts increased in the conservancy with increasing area under agriculture ($r_s = 1$, $P <$ 0.001), supporting H6. However, HWC in Narok North region decreased insignificantly ($r_s = -0.50$, P = 0.67).

3.7. Rainfall and temperature influences on HWC incidents in Narok County

We expected HWC to increase with rainfall but the total HWC, crop raiding, and attacks on humans (Fig. 6a, b, c; Table 8) but not livestock attacks (Fig. 6d; Table 8) all decreased significantly with increasing rainfall, contrary to H7. Moreover, total annual HWC were positively but insignificantly correlated with the mean annual maximum temperature ($r_s = 0.07$, P = 0.82).

Table 7
Chi-squared goodness-of-fit tests of the null hypothesis that the percentage contribution of each livestock type to the total conflicts does not differ across the four regions of Narok County.

Livestock attacked	Percentage contribution of livestock types to frequency of livestock attacks within regions (100%)				Total	Chi-square	
	Conservancy	Narok North	Narok South	Trans Mara	*n*	χ^2_3	*P*
Shoats	64.6	67.2	77.0	72.7	1673	17.7	<0.001
Cattle	31.0	18.3	18.6	20.3	537	41.2	<0.001
Other	0.5	3.9	0.4	0.9	50	32.4	<0.001
Unknown	3.9	10.6	4.1	6.1	178	33.1	<0.001

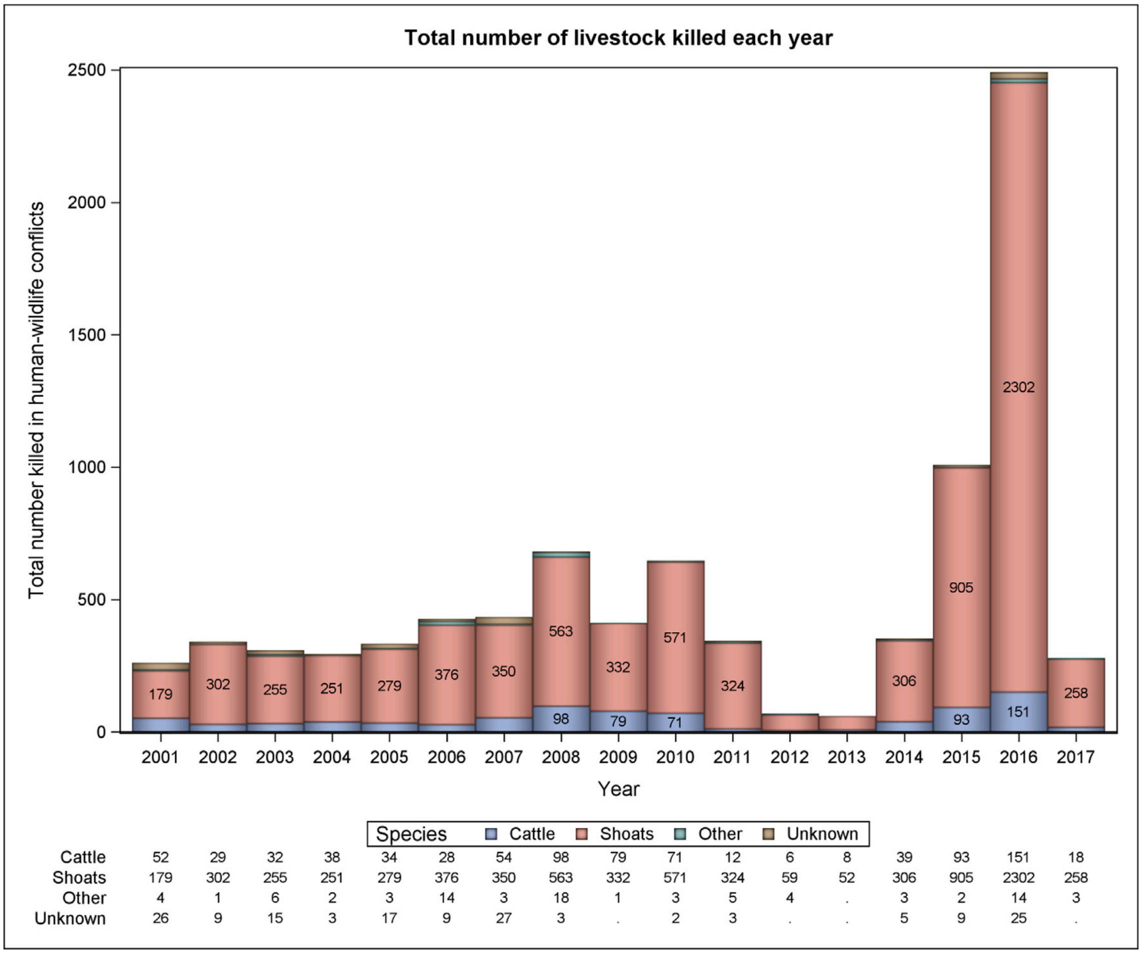

Fig. 5. Total number of livestock killed in HWC in Narok County by species during 2001–2017.

3.8. The influence of human population density on HWC incidents in Narok County

Human presence or activities disturb, displace or exclude wildlife from their feeding grounds or water points. We expected to find more HWC incidents at higher human population density as this increases the likelihood of human-wildlife encounters (H8). However, the total HWC and carnivore attacks on humans were quadratic functions of the total human population size (Fig. 6f, Table 8) and human population density (Fig. 6I; Table 8), respectively.

3.9. HWC incidents livestock density in Narok County

We also hypothesized that HWC incidents should be higher at higher livestock density due to greater competition for limiting resources (H9). However, the total HWC in Narok County increased but insignificantly with increase in the abundance of all livestock species and with the densities of cattle, sheep and goats (H5.1; Fig. 6e, g, h). Again, the total number of all livestock attacks increased with total livestock density. However, the number of cattle attacked decreased while that of shoats attacked increased with increase in the density of cattle and shoats, respectively (Fig. 6j, k, l).

4. Discussion

Human-wildlife conflicts in Narok County were attributed to multiple wildlife species at varying intensities, consistent with the prediction (H1) that HWC incidents should differ among species due to inter-specific distinctions in resource use and requirements. Six wildlife species and three species groups were jointly responsible for 95.6% of all the conflicts reported between 2001 and 2017. Of these conflicts, three large herbivores (elephant, buffalo and zebra) caused 67.3%; three large carnivores (leopard, spotted hyena and lion) caused 17.1%; nonhuman primates 12.3%; antelopes 2.0% and snakes 1.3%. As well, HWC differed regionally (H2) with Narok North reporting most of the conflicts, except for snake conflicts, which were

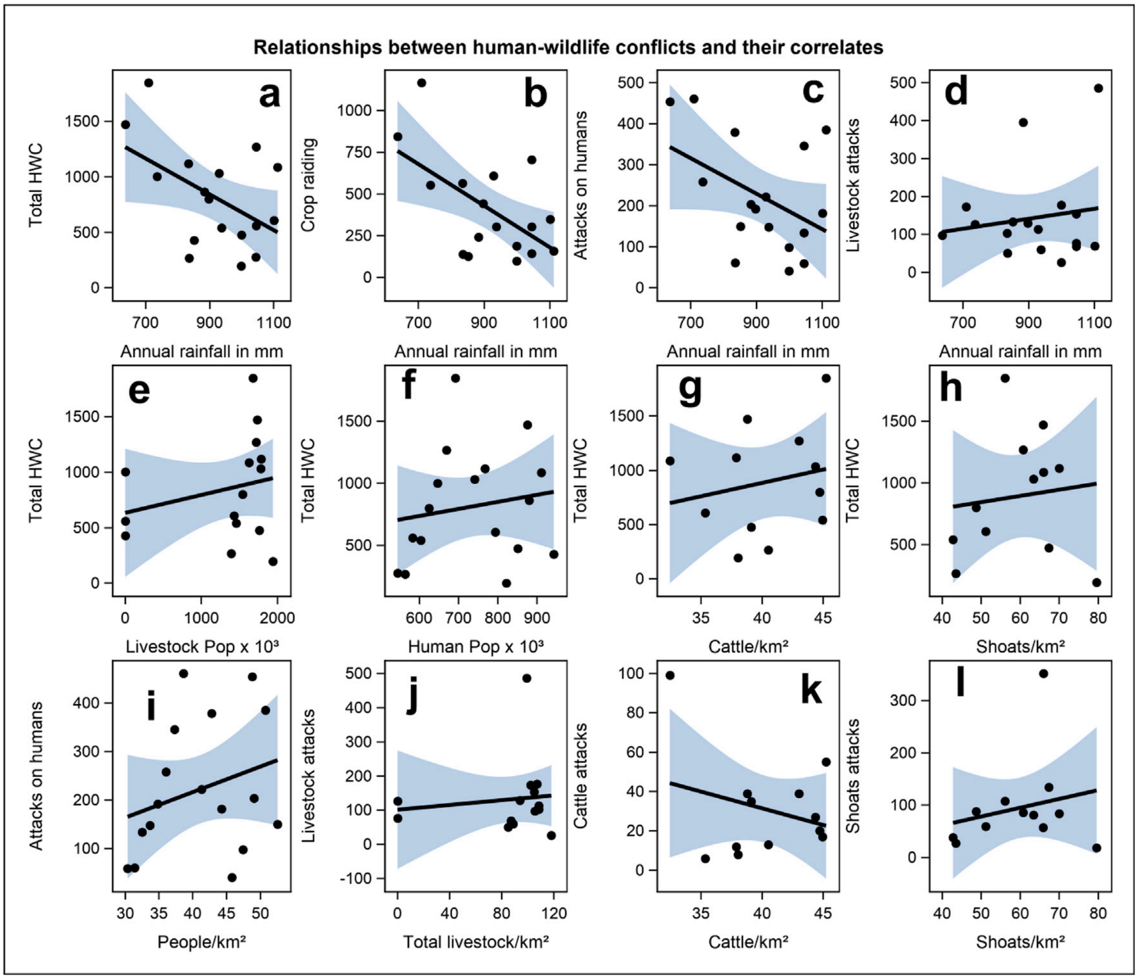

Fig. 6. Relationships between HWC and rainfall, human and livestock abundance or densities in Narok County during 2001–2017. The solid lines are the fitted linear regression lines whereas the shaded areas are the associated 95% confidence bands.

most common in Trans Mara. This implies regional heterogeneity in resource distribution (Sitati et al., 2003) and, in consequence, in conflict type and predominant conflict-causing wildlife species in Narok County. Further, the results are consistent with other studies that reported multiple HWC species (Mukeka et al., 2018a; Ravenelle and Nyhus, 2017) and that the elephant is the leading conflict causing species (Acharya et al., 2016; Gubbi, 2012). Because of their large body size, high food requirements and large home ranges, large herbivores and carnivores (Lindstedt et al., 1986; Thouless, 1996) frequently come into contact with humans when foraging. Whilst only nine species or species groups are responsible for most, other species also cause conflicts, albeit at lower frequencies. Notably, although wildebeest occur in Narok in large numbers in the dry season (July–October), they rarely caused conflicts. This is probably because of their migratory foraging style, enabling them to track spatially and temporally variable food and water resources. Other large herbivores, such as the hippo, eland and giraffe also caused few conflicts. Hippos cause conflicts when they degrade riparian vegetation for livestock (Kanga et al., 2013). Consequently, HWC mitigation measures in Narok County should take into account the multiple conflict-causing species and spatial heterogeneity in the intensity and predominant outcome of conflicts.

HWC in Narok also varied evidently seasonally and inter-annually, reflecting underlying rainfall variation as predicted by H3. The total HWC in Narok showed uni-modal seasonal distribution and increased from the late wet season in May to a peak in the early dry season in July. Crop raiding was the highest in the late wet season (May–June) to early dry season (July), when most cereal crops grown in Narok are at the maturing stages and are harvested. Due to their high nutritive quality, the crops act as caloric diets and “energy maximizers” for crop-raiding herbivores (Conover, 2001; Suba et al., 2018). Wild herbivores that feed on such nutrient-and energy-rich crops are likely to become habituated and turn into perennial raiders, returning often to the same regions every similar season using their past experience and spatial memory (Bailey et al., 1996; Howery et al., 1999; Fagan et al., 2013). This crop raiding behavior can negatively impact farmers as most crops are eaten and trampled when they are most productive, inflicting potentially immense economic losses. Because rainfall governs the amount of food

Table 8
Results of the negative binomial regression analysis relating HWC to various covariates.

Response Variable	Effect	Estimate	Standard Error	DF	t Value	Pr > |t|
Total HWC	Intercept	8.1143	0.7928	15	10.24	<0.0001
	Annual Rainfall	−0.00157	0.000853	15	−1.84	0.0857
Crop Raiding	Intercept	8.2329	0.9127	15	9.02	<0.0001
	Annual Rainfall	−0.0025	0.000983	15	−2.54	0.0226
Human attack	Intercept	6.7044	0.8819	15	7.6	<0.0001
	Annual Rainfall	−0.00145	0.000949	15	−1.53	0.148
Livestock attack	Intercept	4.1886	1.0709	15	3.91	0.0014
	Annual Rainfall	0.00084	0.001153	15	0.73	0.4779
Total HWC	Intercept	6.4615	0.3072	13	21.03	<0.0001
	Livestock population	0.000205	0.000206	13	0.99	0.3385
	Intercept	−8.4408	5.1849	14	−1.63	0.1258
	Human population size	0.04062	0.0142	14	2.86	0.0126
	Human population size^2	−0.00003	0.000009484	14	−2.8	0.0142
	Intercept	5.8204	1.5739	10	3.7	0.0041
	Cattle density	0.024	0.03877	10	0.62	0.5497
	Intercept	6.2193	1.2115	10	5.13	0.0004
	Shoats density	0.009602	0.02014	10	0.48	0.6437
Human attack	Intercept	−9.7376	5.9843	14	−1.63	0.126
	Human density	0.7125	0.2932	14	2.43	0.0291
	Human density^2	−0.00817	0.003504	14	−2.33	0.0352
Livestock attack	Intercept	4.6151	0.455	12	10.14	<0.0001
	Livestock density	0.002994	0.004862	12	0.62	0.5495
Cattle attack	Intercept	39.6351	15.9907	9	2.48	0.0351
	Cattle density	−1.8379	0.8199	9	−2.24	0.0517
	Cattle density^2	0.02303	0.01043	9	2.21	0.0546
	Intercept	2.7259	1.3754	10	1.98	0.0756
	Shoats density	0.03002	0.02282	10	1.32	0.2177

and surface water availability for savanna herbivores (Ogutu and Owen-Smith, 2005) and 2008–2009 was a severe drought year (Bartzke et al., 2018), Narok County had the highest HWC in 2008–2009, reinforcing the prediction of H3. Thus, effective and efficient HWC mitigation strategies should take seasonality into account. Furthermore animal foraging behavior is likely influenced by food resources and studies should endeavor to study whether altering its availability can be used to mitigate HWC.

Crop raiding by wild herbivores and non-human primates was seasonal (H4) and increased substantially during the late wet season as predicted by H4.1. As predicted (H4.2, H4.3, H4.4), there were also stark differences between crop types raided by the different wildlife species, such that elephant raided mostly cereals whereas nonhuman primates targeted mostly tubers probably due to their ability to use tools to dig up for food (Sugiyama et al., 1993; Van Schaik et al., 1999). Nonhuman primates including baboons have also been reported to raid root and tuber crops around the Kabale National Park in Uganda (Naughton-Treves et al., 1998). Thus, crop varieties, their vegetative morphology, and growth period all influence the conflict species (Meinecke et al., 2018). Accordingly, HWC prevention strategies should address conflicts at the crop type level, e.g., by encouraging growing of early maturing crop varieties or non-palatable crop types. The intensity of crop raiding and destruction of crops in Narok County can be attributed to land use change, especially to agriculture (H6), rainfall variation (H7) and human (H8) and livestock (H9) population expansion, that collectively reduce resource availability for humans, livestock and wildlife.

The Maasai community in Narok is changing their traditional lifestyle from semi-nomadic pastoralism to sedentary agro-pastoralism. Conversion of wildlife habitat to agriculture is being accelerated by human population growth from reproduction and immigration into Narok County. Thus, large swaths of land have been converted into large-scale farms for wheat and maize (Lamprey and Reid, 2004), the most frequently damaged crops. Small-scale horticultural farming is also expanding, stimulated by an expanding urban population. The former group ranches in Narok have been subdivided into individual holdings by a growing human population and due to the quest for individuals to invest in more enterprising agriculture and livestock rearing, thereby fragmenting, degrading and reducing wildlife habitats (Norton-Griffiths and Said, 2010; Lamprey and Reid, 2004). Land privatization and subdivision are often followed by fencing to secure grass and water for livestock from wildlife and to separate livestock and wildlife and limit the spread of zoonotic diseases, such as brucellosis (McDermott and Arimi, 2002; Enström et al., 2017). Fences not only exclude wildlife from communities (Hayward and Kerley, 2009; Evans and Adams, 2016) but also block migratory wildlife corridors (Kiringe and Okello, 2007), jeopardizing the coexistence between people and wildlife. Further, fences do not necessarily provide effective protection from nonhuman primates that are adaptable, intelligent and opportunistic and able to dig up tubers like cassava and potatoes (Conover, 2001; Woodroffe et al., 2005b; Strum, 2010). As a result, agricultural expansion driven by human population growth threatens wildlife conservation in Narok County and requires urgent remedial action, including proper land use planning and zoning.

Wildlife is getting into more frequent encounters with people, leading to more HWC especially in Narok North with more intense land use and conversion into agriculture than the other three regions (H6). Wildlife numbers are higher in the MMNR and the Conservancy Region where they are better protected (Mwiu et al., 2017) and disperse into the neighboring regions. Hence, crop raiding accentuated by range reduction is the leading HWC outcome in Narok County being a neighbor to the Conservancy Region. This strongly impacts the large-bodied mammals, such as the elephant, which require large quantities of food and water, because of increasing livestock numbers and rainfall variability in the region. The intensifying conflicts stir up negative attitudes towards, and retributive killing of, leading conflict-causing wildlife species, such as snakes and crop raiding large herbivores. This is especially pronounced among people receiving no direct benefits from wildlife such as through Conservancy land rents or wildlife tourism. Unless adequately addressed, this poses a direct and growing threat to sustainable biodiversity conservation.

The decrease in HWC at high rainfall, contrary to the prediction of H7, is probably because wildlife has largely been eliminated by high human population and settlement densities and land use developments from the high potential rainfall areas (Norton-Griffiths and Said, 2010; Norton-Griffiths et al., 2008), such as the Mau in Narok North and Trans Mara. As a result, wildlife in Narok County is becoming increasingly restricted to the lower rainfall areas, including the grasslands in the Conservancy and Narok North, where most conflicts occurred. Further, livestock numbers have increased in Narok County (Ogutu et al., 2016), heightening competition with wildlife for forage and water and the risk of crop raiding by wildlife. Regulating livestock numbers would thus be necessary to reduce competition with wildlife for the shrinking space, food and water resources.

Large carnivores killed 8097 head of livestock (H5) in Narok County over the 17- year period. Three factors appear responsible for the high livestock depredation in Narok during 2007–2017. First, the number of shoats increased by 144.4%% (H5.1, H8) whereas cattle numbers decreased by 3.2% in Narok County during 1977–2016 (Ogutu et al., 2016). Second, wildlife numbers declined markedly in Narok County between 1977 and 2016 (Ogutu et al., 2016), largely due to habitat destruction, climate change and human population expansion. Third, livestock herding in Maasai land is increasingly being undertaken by children, who cannot adequately protect livestock against large carnivores (Fratkin, 1979). The increased human attacks during livestock attacks likely occur as herders protect their livestock from predators. But the positive association of livestock attacks with crop raiding indicates increasing adoption of agro-pastoralism through small-scale subsistence cultivation close to homesteads.

Livestock depredation was strongly seasonal and dropped from June to October, when the migratory wildebeest and zebra from the Serengeti National Park occupy the MMNR, Conservancy and Narok South (Maddock, 1979; Thirgood et al., 2004; Holdo et al., 2009), vastly increasing food availability for carnivores. This releases predation pressure falling on livestock and resident wild herbivores. But livestock depredation increased in the wet season when the migrants have left Narok and migrated back to Serengeti as anticipated by H5.2. Livestock depredation also increases in the rainy season because resident ungulates disperse outside the MMNR and the conservancy to pastoral lands where most livestock are found because of shorter, nutritious and actively growing grasses maintained by heavy livestock grazing (Bhola et al., 2012; Ogutu et al., 2008). Reduced wild prey base (Karani et al., 1995) and large home ranges can lead to predators turning on to domestic livestock (Treves and Karanth, 2003). Large carnivores kill livestock when their wild prey are few and difficult to find and catch (Patterson et al., 2004) and closer to protected areas where predator densities are often high (H5.4) (Kolowski and Holekamp, 2006). Livestock depredation has also been shown to increase during the wet season in the Masai Mara region of Narok County (Kolowski and Holekamp, 2006) and in Tsavo in Kenya (Patterson et al., 2004). Elsewhere, wolf (*Canis lupus*) predation of livestock is dependent on the length of the summer grazing season in North America (Musiani et al., 2005) whereas the Indian tiger (*Panthera tigris*) kills more livestock immediately after crops are harvested near villages in India and farmers stop guarding their farms (Madhusudan, 2003). Accordingly, strategies for mitigating livestock depredation should take seasonality in depredation events into account.

Predators attacked mostly livestock species in their own body size range (H5.3). Therefore, the leopard and spotted hyena killed most of the smaller bodied shoats, whereas the lion killed most of the larger cattle. Similar size-dependent predation on livestock by large carnivores has been previously reported for the Maasai Mara (Karani et al., 1995) and the Tsavo (Patterson et al., 2004) in Kenya and Maasai steppe in Tanzania (Kissui, 2008). Livestock depredation can represent significant economic losses to livestock keepers dependent on livestock as their economic mainstay. The losses reinforce negative perceptions of carnivores by communities interacting with wildlife and fuel retaliatory killings (Kissui, 2008; Jackson and Wangchuk, 2004; Madhusudan, 2003). Although the Maasai are relatively more tolerant to wildlife (Mukeka et al., 2018a; Kolowski and Holekamp, 2006), they often kill problem carnivores that threaten their livelihood (Hazzah et al., 2009; Muriuki et al., 2017). For instance, hyena deaths caused by humans increased in Masai Mara between 1988 and 2006 (Pangle and Holekamp, 2010). The lion, leopard and the cheetah are already classified as vulnerable, while the wild dog is critically endangered (https://www.iucnredlist.org/species), hence, livestock depredation further threatens their long-term persistence in Narok and possibly elsewhere.

Finally, while attacks on humans showed no apparent seasonality, the highest number of attacks were reported in 2008 ($n = 461$) when Narok County received very low rainfall (Bartzke et al., 2018). The lack of clear seasonality thus probably indicates that attacks on humans arise from chance encounters and that people take appropriate precautions to protect themselves. The main species attacking humans were elephants (62.8%, $n = 2371$), buffaloes (20%, $n = 754$), and four carnivores (spotted hyena, leopard, lion and wild dog (7%, $n = 264$) and over 50% of these attacks occurred in Narok North and only 25% in the conservancy. Crocodile attacks were few in Narok County likely because of the scarcity of permanent water sources they inhabit. However, the notably high snake conflicts in the Trans Mara region are of concern. Similarly, increased snake conflicts have been reported for other parts of Kenya (Mukeka et al., 2018b, in review). Attacks on humans occur when people protect their property (e.g., crops from damage or livestock attacks) or during routine duties. The increasing attack on humans in Narok County can be attributed to increase in the human and livestock numbers, range contraction due to increase in land use changes and rising climatic variability and the associated increase in the likelihood of encounters with wildlife.

5. Conclusions and recommendations

1. Habitat destruction through changing land use reduces wildlife habitats and therefore ranks among the most serious threats to biodiversity loss. It adversely impacts large herbivores that forage over large areas for food and water. Preventing range contraction is thus essential for ameliorating HWC. This can be achieved by promoting profitable conservation enterprises and increasing conservation benefits to local communities. It is also essential to discourage land subdivision into smaller parcels and fencing, which obstructs wildlife movements. National and local government policies that promote land use planning and zoning can help separate human settlements, farms and livestock from wildlife.
2. Livestock attacks by carnivores is a serious threat in Narok County and the associated retaliatory killings can threaten carnivore conservation. Since most carnivore attacks occur at night (Kissui, 2008), building predator-proof holdings for livestock can help ameliorate this problem. This has proven effective in Laikipia, Masai Mara and Amboseli regions of Kenya (Manoa and Mwaura, 2016; Ogada et al., 2003). Further, providing compensation for the losses arising from the conflicts can help improve attitudes toward carnivores and enhance their survival prospects.
3. Long-term preparedness strategies should factor in the spike in HWC during droughts, which are becoming more frequent and severe in the region, including in parts of Narok County. This may include encouraging farmers to dispose of some livestock during droughts and the dry season.
4. Crop raiding can be partly addressed by growing early maturing crops to minimize habituation by crop raiding herbivores. This can also be complemented by growing crops less palatable to wildlife in some years, e.g., chilli *Capsicum* spp (Sitati and Walpole, 2006).
5. Continuing monitoring is critical to improving our understanding of the nature and dynamics in space and time of HWC as a basis for informing effective mitigation strategies. Such monitoring programs should be robust and record the precise geo-locations of the conflict incidents to enable granular analyses of HWC occurrences and tightly linking HWC events to their putative causal covariates.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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Appendix A

Table A1
The composition of the five groups of species of conflict animals used in this study

No	Species or group	Composition	†*n*
1	Non human primates	Baboons	1439
		Monkeys	186
2	Snakes	Snakes	162
		Puff adder	1
		Cobra	1
		Black mamba	1
		Python	2
3	Antelopes	Antelope	131
		Bush buck	7
		Kirk's dik-dik	2

Table A1 (*continued*)

No	Species or group	Composition	†***n***
		Grant's gazelle	44
		Impala	56
		Lesser kudu	1
		Water buck	27
4	Pigs	Warthog	37
		Wild pig	67
5	Others	Birds	12
		Cape hare	2
		Hyrax	1
		Porcupine	7
		Serval cat	1
		Unknown	106

† *n* is the number of conflicts reported between 2001 and 2017.

Table A2
List of species that were found in the datasets and mentioned or inferred in this research.

No	Common English name of species	*Scientific name of species*
1	Antelope (assorted)	*Bovidae family*
2	Baboons	*Papio* spp.
3	Birds	Class: Aves
4	Bohor reedbuck	*Redunca redunca*
5	Buffalo	*Syncerus caffer*
6	Bush buck	*Tragelaphus scriptus*
7	Cheetah	*Acinonyx jubatus*
8	Common duiker	*Sylvicapra grimmia*
9	Crocodile	*Crocodylus niloticus*
10	Eland	*Taurotragus oryx*
11	Elephant	*Loxodanta africana*
12	Giraffe	*Giraffa camelopardalis*
13	Grant's gazelle	Gazella *granti*
14	Hippopotamus	*Hippopotamus amphibius*
15	Impala	*Aepyceros melampus*
16	Kirk's dik-dik	*Rhynchotragus kirkii*
17	Leopard	*Panthera pardus*
18	Lesser kudu	*Tragelaphus imberbis*
19	Lion	*Panthera leo*
20	Monkeys	*Cercopithecus* spp.
21	Nonhuman primates	*Family cercopithecidae*
22	Oribi	*Ourebia ourebia*
23	Porcupine	*Apis mellifera scutellata*
24	Puff adder	*Bitis arietans*
25	Python	*Python sebae*
26	Serval cat	*Leptailurus serval*
27	Snake	*Serpentes suborder*
28	Spotted hyena	*Crocuta*
29	Thomson's gazelle	*Gazella thomsonii*
30	Topi	*Damaliscus korrigum*
31	Warthog	*Phacochoerus africanus*
32	Waterbuck	*Kobus ellipsiprymnus*
33	Wild dog	*Lycaon pictus*
34	Wild pig	*Sus scrofa*
35	Wildebeest	*Connochaetes taurinus*
36	Zebra	*Equus quagga*

Every effort has been made to identify each species. Where it was not possible, we used the lowest taxon group possible.

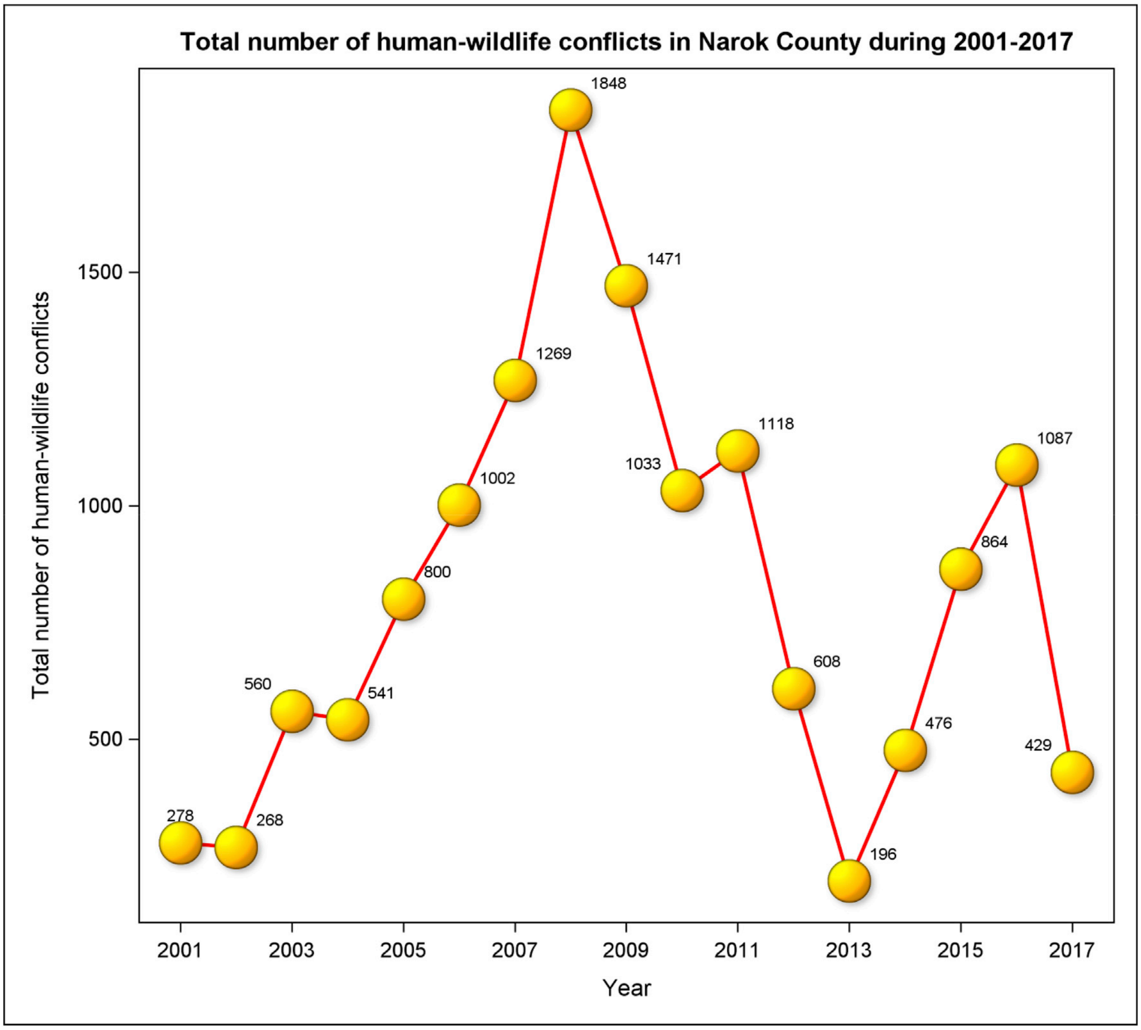

Fig. A1. Temporal variation in human-wildlife conflicts in Narok County during 2001–2017.

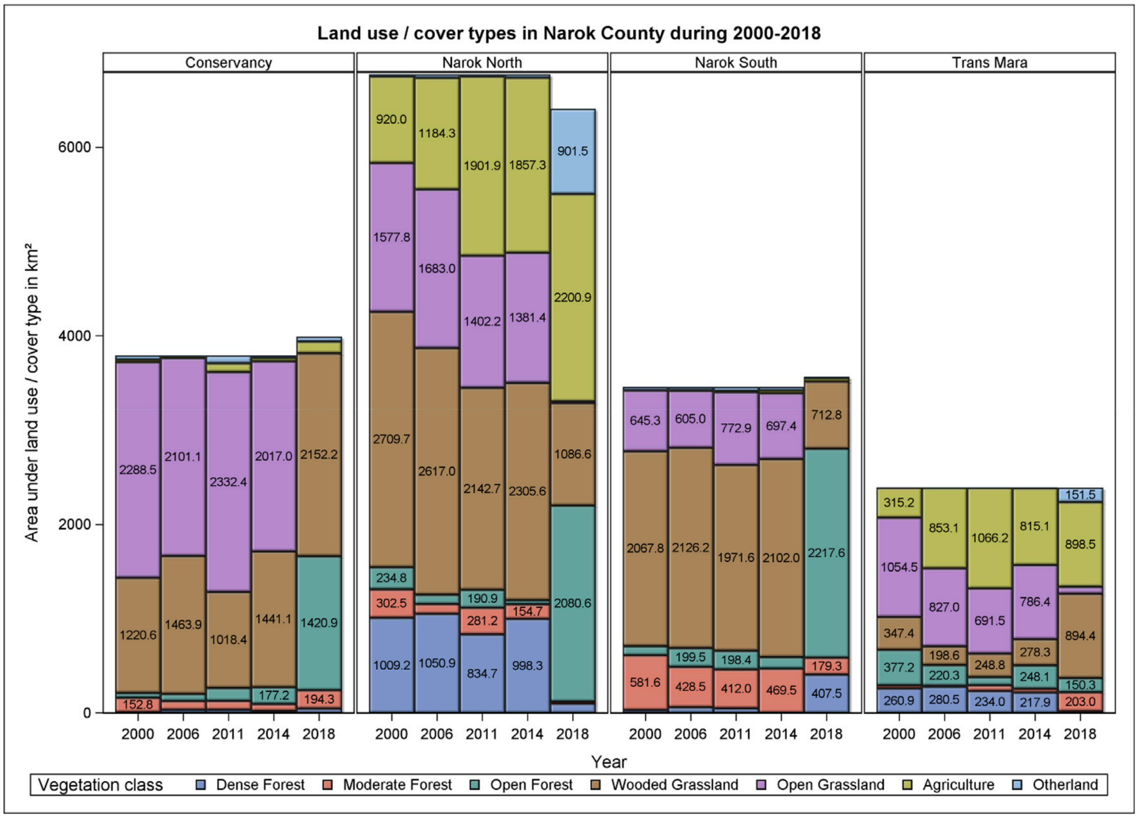

Fig. A2. Land use transformation in Narok County.

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00620.

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