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Joseph Mbyati Mukeka

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Thesis for the Degree of
Philosophiae Doctor
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PREFACE

This work is the product of collaboration with, assistance of, and dedication by many people. First, I would like to extend my sincere gratitude to my three supervisors led by Professor Eivin Røskaft, Dr. Joseph O. Ogutu, and Dr. Erustus Kanga. The conception of this work occurred when I was attending the first AfricanBioServices Consortium Meeting in Mugumu - Tanzania, where I was representing the Kenya Wildlife Service (KWS). I recall being asked to come up with a brief concept of something interesting that I could achieve within a record three years of the project's time lines. Thus, my supervisors from then on, guided me in developing a research proposal that eventually saw me admitted to NTNU courtesy of Prof Eivin Røskaft. Special thanks to Joseph Ogutu for his patience and careful guidance through the manuscript development as well as the very great artistic figures he helped develop. Thanks to Erustus Kanga for introducing me to the AfricanBioServices project without which I would not be here writing this now.

This study was made possible by the AfricanBioServices Project which received funding from the European Union's Horizon 2020 research and innovation programme under Grant Agreement No. 641918. JOO was additionally supported by a grant from the German Research Foundation (DFG, Grant No. OG 83/1-1). I would like also to thank my employer, the Kenya Wildlife Service (KWS) for granting me study leave so I could pursue my dreams. Further, I would like to thank KWS for giving me the permission to access and use the long term data upon which this research is based. I hope that the findings of the research reported here will be useful in guiding conservation of biodiversity, the national mandate of KWS.

I would like to extend my sincere gratitude to the many KWS researchers based in Tsavo and Maasai Mara Research Centers for their assistance in collecting, cleaning and verifying the many years' of data that have been used in this research. To the wardens also in both regions, it was enlightening and informative interacting and sharing ideas with you on the subject of human-wildlife conflicts in your zones of administration. At the KWS headquarters, I was able to work with the Community wing of KWS and specifically Mr. Moses Maloba who assisted with cleaning the data and helped me understand some of the important issues involved in compensation to victims of human-wildlife conflicts. My gratitude goes to all my colleagues at KWS, who supported me in various ways during my studies.

Thanks also to those in the NTNU community who made my life here livelier, e.g., through the impromptu dinners at Prof Eivin Røskaft's house, the lunch bites and sometimes the sugarless coffee that would wake my nerves. It was wonderful being part of such a great institution and wonderful people!

My being away in Trondheim separated me from my family, to whom I would like to extend my deepest gratitude for their understanding, support, and enduring my prolonged absence. To my wife Mwende, our three lovely sons, Mutinda, Mumo and Mukeka aka Toto Junior, who always wondered why I could not come to see him every weekend! - **THIS IS DEDICATED TO YOU**.

Joseph Mbyati Mukeka

Trondheim

June - 2019

CONTENTS

SUMMARY

Human-wildlife conflict (HWC) is a common phenomenon around the world and occurs when resource use by humans overlaps with that of wildlife resulting in competition. The major factor exacerbating this situation is human population growth whose secondary effects cascade to land use change, habitat fragmentation, increased livestock numbers, settlements and anthropogenic climate change. Africa, and in particular Kenya, is faced with rapid population growth and highly variable climatic conditions such as extreme floods and prolonged droughts. Furthermore, Kenya lies in the tropics, is blessed with a wide taxonomic array of wildlife found in terrestrial (forest and savanna), fresh water and marine ecosystems. Thus, HWC is common in Kenya because of the high wildlife population and diversity and because most wildlife are found in communal lands outside protected areas (PA). Wildlife also wander beyond the unfenced protected areas and often come in contact with people, resulting in conflicts. The major conflict types in Kenya are crop raiding, attacks on humans (causing death or injury), livestock depredation, and property damage. Because most Kenyans depend on agriculture and livestock raising, HWC affects the lives and livelihoods of the most vulnerable in the society, the many rural communities. HWC negatively impacts the livelihoods of these people and therefore people often retaliate by killing the offending wildlife using poison, spears and arrows, or building fences to keep wildlife away. Thus, HWC threatens biodiversity conservation and may lead to local extinction of some species.

In Kenya, two regions contain most of the wildlife, namely the Mara Region in Narok County which hosts the famous Maasai Mara National Reserve (MMNR) and the Greater Tsavo Ecosystem (GTE) spanning seven Counties, i.e., Taita Taveta, Kajiado, Makueni, Kitui, Tana River, Kilifi, and Kwale. The GTE comprises of Tsavo National Parks (East and West), Chyulu National Park, South Kitui National Reserve, and the adjoining wildlife conservation ranches in Taita Taveta, Galana, Kulalu and wildlife dispersal areas to the north and west of the Tsavo National Parks. The two regions are inhabited by people who have adopted different lifestyles to earn their livelihoods. The Mara region is settled predominantly by the pastoral Maasai community and the GTE is occupied mostly by different communities who practice agriculture. The common fauna in both the Mara and Tsavo consist of the African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer)*, hippopotamus (*Hippopotamus amphibius)*, giraffe

(*Giraffa camelopardalis*), Burchell's zebra *(Equus quagga),* Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*), and the critically endangered black rhino *(Diceros bicornis)*. However, wildebeest (*Connochaetes taurinus*), Burchell's zebra and Thomson's gazelle (*Gazella thomsonii*) are found in far larger numbers in the Mara region than in the Tsavo. Large carnivores, such as the lion (*Panthera leo),* leopard (*Panthera pardus),* and spotted hyena (*Crocuta crocuta)* are also found in large numbers as are nonhuman primates, including baboons and monkeys, in the two regions. Given the similarity in species composition, but major differences in land use types between these two regions, we analyzed whether there were differences in the relative frequencies of HWC over the course of the 15 years spanning from 2001 to 2016 based on data collected by the Kenya Wildlife Service (KWS). The elephant was the leading species causing crop damage, followed by nonhuman primates and buffalo. The lion and spotted hyena were the leading causes of livestock depredation. Interestingly, fewer people felt threatened by wildlife in the Mara than in the Tsavo region, likely because of the historical co-existence and tolerance of wildlife by the Maasai community.

These findings are interesting, general and yielded insights into regional HWC differences. We next focused on each region and conducted in-depth analyses for each to provide a more detailed understanding of HWC occurrence. We first focused on the Greater Tsavo Ecosystem (GTE), the single largest contiguous protected area in Kenya. For the Greater Tsavo Ecosystem we analyzed spatial, seasonal and inter-annual variation in human-wildlife conflicts, conflict species and management responses to the conflicts during 1995 - 2017. We correlated HWC with human populations and modeled seasonal and annual variation in HWC. The elephant and nonhuman primates caused most crop raiding conflicts, but distinct spatial differences were apparent such that the Taveta region was an elephant conflict hotspot while snake conflicts were the highest in Mutomo. Moreover, elephant conflicts were positively and linearly related with human, elephant and livestock densities.

For the Mara region, we analyzed HWC and their correlates for the period 2001 - 2017. In particular, we related HWC with human population density, rainfall, maximum temperature, land conversion to agriculture, seasons, total number of livestock killed, crop preferences by herbivores, and regional differences in HWC. Three carnivores caused most livestock depredation with the lion killing most of the cattle whereas the leopard and spotted hyena killed the smaller sheep and goats. The elephant was the leading crop raiding species and preferentially fed on maize and wheat while the nonhuman primates were responsible for most tuber crop destruction.

HWC leads to loss of human life and causes injuries to humans, jeopardizing harmonious co-existence and thus threatening biodiversity conservation. One method of ameliorating these conflicts is compensation for losses by national governments. We therefore analyzed compensation payments by the government of Kenya between 2007 and 2016. Snakes were the leading cause of human deaths and injuries in dry regions of Kenya. As well, HWC increased with increase in the percentage area under protection in each county. HWC also varied with population demography such that more males than females and more adults than children suffered from HWC incidents.

Hence, HWC portray regional and spatial distinctions that should also be reflected in the level of resource allocated for preventing or mitigating HWC. Seasonality in HWC can be addressed by adopting crops that mature at different times and are less palatable where the risk of crop raiding is high. High livestock depredation can be minimized through better husbandry practices. People living with wildlife also need to benefit more from conservation. Finally, the national compensation scheme for HWC losses requires adequate funding to cater for the increasing HWC cases.

LIST OF PAPERS

The PhD thesis comprises the following four papers:

1. Mukeka, J., Ogutu, J.O., Kanga, E., & Røskaft, E. (2018). Characteristics of Human-Wildlife Conflicts in Kenya: Examples of Tsavo and Maasai Mara Regions. *Environment and Natural Resources Research, 8*(3), 148.

2. Mukeka, J., Ogutu, J.O., Kanga, E., & Røskaft, E. (2018). Spatial and temporal dynamics of human-wildlife conflicts in the Greater Tsavo Ecosystem, Kenya. (Provisionally accepted)

3. Mukeka, J., Ogutu, J.O., Kanga, E., & Røskaft, E. (2019). Human-Wildlife Conflicts and their correlates in Narok County, Kenya. (Accepted April 2019: *Global Ecology and Conservation*)

4. Mukeka, J., Ogutu, J.O., Kanga, E., & Røskaft, E. (2019). Trends in compensation for human-wildlife conflict losses in Kenya. (Accepted March 2019: *International Journal of Biodiversity and Conservation)*

INTRODUCTION

Human-wildlife conflicts (HWC) are negative interactions between humans and wildlife (Messmer, 2009) and threaten conservation of biodiversity worldwide. HWC conflicts occur in many countries, including in the US (Conover, 2001; Messmer, 2009), European countries (Røskaft, Händel, Bjerke, & Kaltenborn, 2007), India (Gubbi, 2012; Karanth, Gupta, & Vanamamalai, 2018), China (Li, Buzzard, Chen, & Jiang, 2013), Israal (Nemtzov, 2003), and Africa (Hemson, Maclennan, Mills, Johnson, & Macdonald, 2009; Holdo, Fryxell, Sinclair, Dobson, & Holt, 2011; Mukeka, Ogutu, Kanga, & Røskaft, 2018; Patterson, Kasiki, Selempo, & Kays, 2004). HWC have been attributed to many factors, including exponential human population growth, land use change and the associated degradation, fragmentation and loss, climatic change, livestock and wildlife population increase (Distefano, 2005; Thirgood, Woodroffe, & Rabinowitz, 2005). These factors reduce food, water and other resources that wildlife require for survival and reproduction. As a result, wildlife are forced to move over longer distances in search of essential resources, increasing the frequency of encounters with humans. Furthermore, over 65% of wildlife in Kenya is found outside protected areas (PA) (Western, Russell, & Cuthill, 2009) and those found in PA often wander beyond the protected area boundaries since most parks and reserves are not fenced. The four main conflict types are attacks on humans, livestock depredation, crop raiding and property destruction (Conover, 2001; Messmer, 2000). Attacks on humans can result in different outcomes ranging from death, injury, and general insecurity. Livestock depredation refers to attacks on domesticated animals such as cattle, donkeys, sheep, goats, and poultry. Crop raiding leads to destruction of farmed crops for human consumption, while property damage encompasses damage to such things as fences, water pipes and houses (Distefano, 2005; Messmer, 2009).

Human-wildlife conflicts are more frequent in developing countries in Africa and Asia, with high human population growth rates and where the majority of the people still rely on land-based economic activities, such as agriculture and livestock herding (Distefano, 2005). For example, Kenya's human population size has grown 6-fold from 8 million people in 1962 to 49 million currently and is expected to reach 80 million by 2050 (http://www.worldbank.org/).

Widening climatic variability and change in Kenya are associated with recurrent severe droughts, flush floods and reduced resources for humans and wildlife alike. In consequence, the more drought resistant livestock species, especially sheep and goats, camels and donkeys, have increased in the Kenyan rangelands but the less drought resistant cattle have concurrently declined (Ogutu et al., 2016).

Wildlife based tourism contributes about 10% to Kenya's Gross Domestic Product (GoK, 2010) besides providing important business and employment opportunities. Therefore, by threatening biodiversity conservation, HWC can negatively impact Kenya's economic growth prospects. The outcome of HWC in Kenya ranges from crop raiding by large herbivores like the African elephant (*Loxodonta africana)* (Evans & Adams, 2016; Graham, Notter, Adams, Lee, & Ochieng, 2010), livestock depredation by carnivores such as the lion (*Panthera leo),* leopard (*Panthera pardus),* and spotted hyena (*Crocuta crocuta)* (Kolowski & Holekamp, 2006; Patterson et al., 2004)*,* and attacks on humans by poisonous snakes, leading to human deaths and injuries (Mukeka et al., 2018). Therefore, conflicts threaten lives and livelihoods of people, especially of the rural communities that heavily depend on farming and livestock rearing (Smith & Kasiki, 2000). Where these conflicts occur but no adequate mitigation measures are instituted, people resort to retaliatory wildlife killings. For instance, lions and spotted hyenas are persecuted for killing Maasai livestock (Goldman, de Pinho, & Perry, 2013; Périquet, Fritz, & Revilla, 2015), while the elephant is killed because of crop raiding (Okello, Njumbi, Kiringe, & Isiiche, 2014). These animals are critical to biodiversity conservation and wildlife-based tourism. Consequently, HWC not only threatens the very economic fabric of Kenya, but also species of conservation importance.

Since factors that intensify HWC vary over time and given that long term data are difficult to obtain and thus are rare, studies of HWC using long-term data can yield potentially valuable insights. This study thus analyzes HWC in Kenya using long-term monitoring data collected by the Kenya Wildlife Service (KWS).

AIM

The over-archiving aim of this thesis is to broaden our understanding of long-term human-wildlife conflicts in two important conservation regions of Kenya, the Mara and Tsavo regions.

Further, it evaluates the monetary costs of HWC by analyzing trends in compensation payments to victims of HWC by the government of Kenya.

The specific objectives of the thesis are as follows:

1. Analyze reported incidents of human-wildlife conflicts in the Tsavo and Mara regions, identify and characterize the conflicts caused by wildlife species and the variation across seasons, years and between the two study regions, 2001 - 2016 (Paper I).
2. Analyze spatial, seasonal and inter-annual variation in human-wildlife conflicts, conflict - species and management responses to the conflicts in the Greater Tsavo Ecosystem (GTE) during 1995 - 2017. We also test predictions of four hypotheses (Paper II).
3. Seek answers to the questions: (1) What are the long-term temporal trends in HWC for each of the 18 common wildlife species in each of the four regions of Narok County? (2) What are the crop type preferences of the conflict herbivore species based on the type of crops they damage? (3) How many people are killed or injured and how many individuals of the different livestock species are killed by particular large carnivore species and when? (4) 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? (Paper III).
4. Search for answers to the questions. 1) What is the inter-annual and seasonal pattern of HWC compensation claims? 2) What are the common human-wildlife conflict causing species, the types and number of conflicts they cause? 3) How are wildlife attacks on humans spread across the two key demographic attributes of gender and age? 4) How are HWC incidents distributed across Kenya's administrative Counties? 5) How do HWC vary with the proportion of a county that is protected, human population density, rainfall, maximum temperature, and predominant type of agro-climatic zone in each county? 6) What is the monetary cost of HWC compensation payments per wildlife species, conflict type and county and how efficient was the Kenya National Compensation Scheme (KNCS) during 2007 - 2016? 7) How does the amount of money paid for compensation claims compare with tourism revenue earnings by the Kenyan state during 2007 - 2016? (Paper IV).

METHODS

STUDY AREA

The first three papers cover two of the most important wildlife concentration and conservation regions in Kenya. These include the Mara region (in Narok County) that encompasses the world famous Maasai Mara National Reserve (MMNR) and the Greater Tsavo Ecosystem (GTE), containing the largest contiguous protected area (23,000 km^2) and the largest elephant population 13,000 (Ngene et al., 2017) in Kenya. The fourth paper covers the whole of Kenya. A brief description of each of these study areas is provided below.

KENYA

General Description

Kenya borders Somalia, Ethiopia, Sudan, Uganda, Tanzania, and the Indian Ocean in East Africa (Figure 1). It straddles the equator and lies between longitudes 33°50'E - 41°58'E and latitudes 5°2'N - 4°45'S and has a total area of 582,646 km^2. Kenya's human population has grown exponentially from about 8 million people in 1962 to about 49 million people in 2017 (https://data.worldbank.org/) distributed across 47 administrative Counties. Altitude ranges between 0 and 5199 m, the highest peak of Mount Kenya. Rainfall in Kenya is mostly bimodal with short rains occurring during November - December and the long rains during March-May (Ogutu, Piepho, Dublin, Bhola, & Reid, 2008). Kenya is divided into seven agro-climatic zones (I to VII), four (IV to VII) of which are hot, dry and receive little and often unreliable rains. The latter four zones have very limited agricultural potential, cover the largest percentage of Kenya and are often referred to as rangelands. The rangelands are inhabited by pastoral communities and harbour a wide variety of wildlife species that are adapted to the harsh climatic conditions (Pratt & Gwynne, 1977). Kenya has 63 protected areas, including 23 terrestrial national parks, 26 terrestrial national reserves, four marine national parks, six marine national reserves and four national sanctuaries that account for about 8% of Kenya’s total land surface area (Kanga, Ogutu, Piepho, & Olff, 2013). Most protected areas are not fenced and therefore wildlife move freely to human-dominated landscapes bringing them into frequent interaction with people and their livestock.

Figure 1: A map of Kenya showing the 47 administrative County boundaries, protected areas (PA), and the two (Narok and Tsavo) study regions. Notice the KWS stations in areas where there are no PAs.

THE MARA REGION (OR NAROK COUNTY)

Location and Climate

The Mara region (referring to the entire 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. Southern Narok is the northern-most section of the Greater Mara-Serengeti Ecosystem (GMSE) (Figure 1).

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 geographic 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 (Norton-Griffiths, Herlocker, & Pennycuick, 1975; Ogutu & Dublin, 2004, Mukhopadhyay, Ogutu, Bartzke, Dublin, & Piepho, 2018 - in press). As well, temperatures range from a low of 13 °C to a high of 28 °C. 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.

Biodiversity

A rich diversity and abundance of large mammalian herbivores are found within the MMNR, wildlife conservancies and community areas in Narok County (Broten & Said, 1995; Ottichilo, De Leeuw, Skidmore, Prins, & Said, 2000). Maasai Mara National Reserve (MMNR), famous for its rich biodiversity, including the great wildebeest (*Connochaetes taurinus*) and Burchell's zebra (*Equus quagga*) migration from the Serengeti in Tanzania to Maasai Mara in Narok County in Kenya (Maddock, 1979; Thirgood et al., 2004; Ogutu, Piepho, Dublin, Bhola, & Reid, 2008; Holdo et al., 2011). The common resident large herbivores include the African elephant, the Maasai giraffe (*Giraffa cameleopardalis*), the Cape buffalo (*Syncerus caffe*r) and hippopotamus (*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 (*Panthera pardus*) and cheetah (*Acinonyx jubatus*) constitute the common large carnivores in Narok.

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 (Figure 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).

THE GREATER TSAVO ECOSYSTEM (GTE)

Location and Climate

The study region lies between Longitudes 37° 7' E - 39° 59' E and latitudes 0° 58' S - 4° 22' S in south-eastern Kenya. It comprises four functional protected areas, Tsavo East (TENP) - 11,747 km^2 and Tsavo West (TWNP) - 9,065 km^2, Chyulu National Park - 736 km^2, and South Kitui National Reserve (SKNR) - 1,133 km^2, situated to the north of TENP. This region has the largest contiguous protected area in Kenya covering some 22,681 km^2 (Figure 1). The PA and its surrounding six regions, covering a total area of about 66,300 km^2 is the Greater Tsavo Ecosystem (GTE). Rainfall (200-700 mm/year) is bimodal and erratic, with the short rains falling in November - December and the long rains between March and May (Van Wijngaarden 1985). Rainfall increases with altitude in the ecosystem and averages about 1185 mm at the highest altitude of about 1,810 m in Chyulu Hills (Pócs and Luke 2007).

Biodiversity

The common large herbivores found in the Greater Tsavo Ecosystem include the African elephant, buffalo, hippo and critically endangered black rhinoceros whereas large carnivores include the lion and leopard (Van Wijngaarden 1985). Indeed, the fauna in Tsavo is largely similar to that found in Mara, the only difference being the population differences for some species, e.g., wildebeest that are more abundant in the Mara. Moreover, the Tsavo region harbors the largest elephant population in Kenya, numbering about 13,000 individuals (Ngene et al. 2017).

The vegetation is dominated by several tree species, including *Commiphora* spp and *Acacia* spp, forming three broad types of communities; namely 1) *Commiphora-Lannea*, 2) *Commiphora-Acacia* and 3) *Acacia-Schoenefelda* (van Wijngaarden 1985). Elephants and anthropogenic influences, e.g., human-caused fires, vegetation destruction through charcoal burning and harvesting trees for building materials, fuel wood and fences play key roles in modifying these broad types (Van Wijngaarden 1985). As a result, grasslands and wooded bushlands are also found in the ecosystem. The Chyulu Hills have open glades with pockets of montane and mist forests (Pócs and Luke 2007). Further details on the fauna, flora, climate, soils and other characteristics of the ecosystem can be found in van Wijngaarden (1985).

HUMAN-WILDLIFE CONFLICT DATA ACQUISITION AND PRE-PROCESSING

Kenya Wildlife Service (KWS) was established in 1989 by the government of Kenya to perform the following functions: 1) formulate policies on conservation, management and utilization of wildlife, 2) manage all protected areas (PA) (parks and reserves), and 3) provide information on establishment of more PAs (http://www.kenyalaw.org/). KWS has established an elaborate radio network that connects all field stations in Kenya to regional level headquarters (Figure 1) and with the command and control center at the KWS' national headquarters in Nairobi. Using this network KWS gathers detailed data on threats to wildlife such as human-wildlife conflicts and poaching. These data are often captured in daily occurrence books and sometimes input into databases. We used the HWC data for the Narok County and the Greater Tsavo Ecosystem for the period 1995 to 2017. As well, we used the KWS national compensation data covering the period 2007 - 2016. The information collected on HWC incidents include the date (day, month and year) and type of incident (crop raiding, attack on humans resulting in either death or injury, livestock depredation, and property damage) and the common name of the species causing the conflict. If a compensation claim is filed, then the details collected include the amount paid, gender and age of victim, etc. More details on the data collected can be found in the individual papers.

We performed quality control checks on the data before the statistical analyses, including cross-checking the digital records against the hand/written records in the occurrence books. We further verified the datasets with the help of the researchers in each region, the person in charge of the databases and by visiting the KWS stations. Finally, we processed the datasets to extract relevant information for the analyses.

In addition to the HWC datasets, we obtained data on the following variables:

- Kenya's human population census data for the study regions (1962, 1979, 1989, 1999, 2009) from the Kenya National Bureau of Statistics (KNBS)
- Livestock numbers (sheep, goats, donkeys and cattle for 1977 - 2016) from the Directorate of Resource Surveys and Remote Sensing (DRSRS) of Kenya.
- Rainfall data from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) rainfall data for Narok Country 1965 – 2017 (http://chg.geog.ucsb.edu/data/chirps/).
- Temperature data from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) rainfall data for Narok Country 1965 – 2017 (http://chg.geog.ucsb.edu/data/chirps/).

Likewise, to the HWC data, these data also required processing prior to the analyses. For instance, human censuses are normally conducted decadally and therefore we used interpolation to estimate values for years between censuses and extrapolation to estimate population size for the period from 2010 to 2017.

SUMMARY OF RESULTS

PAPER I

Characteristics of Human-Wildlife Conflicts in Kenya: Examples of Tsavo and Maasai Mara Regions

The study revealed that both the type and severity of conflicts varied among species such that the African elephant was the leading conflict species in both the Tsavo (64.3%) and Mara (47.0%) ecosystems. The other notorious conflict causing animals, in decreasing order, were nonhuman primates (Tsavo 11.4%; Mara 11.8%), African buffalo (Tsavo 5.5%, Mara 11.3%), lion (Tsavo 3.6%; Mara 3.3%) and spotted hyena (Tsavo 2.4%; Mara 5.8). Of the four major conflict types, crop raiding was the most common conflict, followed by human and livestock attacks and property damage. The severity of conflicts also varied markedly seasonally and inter-annually. Crop raiding peaked in May-July, during and toward the end of the wet season when crops are maturing. Attacks on humans and livestock increased more than other conflict types in both Tsavo and Mara. Relatively fewer people in Mara than in Tsavo felt threatened by wildlife, suggesting that the Maasai people are more tolerant of wildlife.

PAPER II

Spatial and temporal dynamics of human-wildlife conflicts in the Greater Tsavo Ecosystem, Kenya.

Analyses of data collected over 23-years (1995 - 2017) revealed that five wildlife species contributed most to HWC incidents including the elephant (61.6%), nonhuman primates (11.5%), buffalo (6.2%), lion (4.2%) and hippo (3.8%). HWC incidents showed spatial distinctions across the six regions, such that Taveta (43.3%) was the leading human-elephant conflict (HEC) hotspot and Mutomo was the epicenter of non-human primate, snake and python conflicts. Taveta, Rombo and Mutomo were leading in livestock attacks by large carnivores particularly the lion, spotted hyena and leopard. HWC showed marked inter-annual and seasonal variation related to similar variations in the availability, quality and distribution of food and water governed by rainfall fluctuations. HEC were positively and linearly related with human, elephant and livestock population densities. The Kenya Wildlife Service (KWS) responded to

HWC reports and the rate of these responses peaked in 2017 when KWS staff attended to over 90% of the reported conflicts.

PAPER III

Human-Wildlife Conflicts and their correlates in Narok County, Kenya.

We analyzed how HWC varied across multiple wildlife species, seasons, years, and regions to quantify their extent, causes and consequences 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%), attack 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%) and spotted hyena (37.9%) killed most sheep and goats whereas the lion (63.1%) and spotted hyenas (14.5%) killed most cattle. 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.

PAPER IV

Trends in compensation for human-wildlife conflict losses in Kenya

We analyzed inter-specific, spatial, inter-annual and seasonal variation in human-wildlife conflicts, conflict outcome and the associated monetary costs of compensation in Kenya during 2007 - 2016. A total of 18,794 compensation claims were filed with the Kenya National Compensation Scheme (KNCS) during 2007 - 2016. Snakes made the greatest contribution to the total cases (44.8%), human fatalities (43.1%) and human injuries (76.9%). The elephant was the second leading conflict causing species (22.3%) and was responsible for 18.8% of human deaths and over 75% of crop and property damage. The spotted hyena, leopard and lion, caused 85% of livestock predation cases. Most human fatalities occurred in the arid Tana River and Wajir counties, whereas most human injuries occurred in Kitui and Wajir counties. Crop damage was the highest in counties with high agricultural potential (Meru and Taita Taveta) but livestock predation was the highest in counties with large protected areas (Samburu and Taita Taveta). Human fatality and injury were higher among males than females and adults than children. Over the 10-year period, the Kenya government spent about 3 billion Kenya shillings on compensation of about 30% of all filed claims.

DISCUSSION

HUMAN-WILDLIFE CONFLICT CAUSING SPECIES AND TYPES OF CONFLICTS

Human-wildlife conflicts in Kenya are caused by a wide array of wildlife species in varying intensities. Further, our study identified four major conflict types including crop raiding, livestock depredations, attacks on humans and less common property damage, all of which were caused by different or the same species. Among the herbivores, the elephant is the species most frequently responsible for raiding crops such as wheat and maize in the Narok region. Other herbivores including the buffalo, zebra and hippo caused considerable crop raiding incidents. Nonhuman primates raided tuber crops like cassava (*Manihot esculenta*) and potatoes (*Solanum tuberosum*). Increased herbivore conflicts in Kenya can be attributed to a number of factors: 1) Increased human population growth that has fragmented wildlife habitat (Lamprey & Reid, 2004; Okello et al., 2014). 2) Increased herbivore population, specifically the elephant population in the Greater Tsavo Ecosystem (Ngene et al., 2017). 3) Living in proximity to protected areas (Hill, 1997; Karanth et al., 2018; Sarker & Røskaft, 2014). 4) Widening climatic variability leading to less but more variable rainfall and hence reduced food and water availability for herbivores (Ogutu et al., 2008, 2016). Their large body size, high food requirements, and large ranging home sizes (Lindstedt, Miller, & Buskirk, 1986; Thouless, 1996) often force large herbivores to raid planted crops to fulfill their dietary requirements. Multiple species cause human-wildlife conflicts (Ravenelle & Nyhus, 2017). Specifically, the elephant is a leading cause of crop damage elsewhere as well, including the Laikipia region of Kenya (Evans &

Adams, 2016; Graham et al., 2010) and in India (Acharya, Paudel, Neupane, & Köhl, 2016; Gubbi, 2012).

Large carnivores including the lion, leopard and spotted hyena contributed over 80% of livestock depredation in Kenya. Other carnivores involved in livestock depredation, albeit in fewer incidents, were the wild dog and cheetah. Likewise to crop raiding, livestock depredation conflicts can be attributed to a few key factors: 1) increased livestock numbers (easy to catch prey) by pastoralists and consequent decrease in prey density (Ogutu et al., 2016; Patterson et al., 2004), and 2) poor livestock herding practices that render livestock vulnerable to carnivore attacks, e.g., poor enclosures and child herding that offer less protection against predators (Fratkin, 1979; Kissui, 2008). The study also showed that carnivores attacked livestock preferentially based on body size such that lions mostly attacked cattle while spotted hyena and leopard attacked most sheep and goats. Other studies have also found that size dependent attacks are prevalent in livestock depredation, e.g., in the Mara (Karani, Dublin, & Koehler, 1995; Kolowski & Holekamp, 2006) and Tsavo (Patterson et al., 2004), both in Kenya and in the Maasai steppe in northern Tanzania (Kissui, 2008).

Attacks on humans that resulted in deaths and injuries were mostly caused, in decreasing order, by snakes, elephant, and buffalo. Further, attacks on humans were skewed in favor of females than males and children than adults. Thus, gender can influence attitude (Kellert & Berry, 1987) and is a useful predictor of human attacks. Also, a large proportion of snake related attacks occurred in the most arid Counties of Kitui, Wajir, and Marsabit. These Counties are inhabited predominantly by pastoral communities except Kitui County. Human vulnerability to snake attacks in these regions is exacerbated by under-development that forces people to live in poorly built houses, general lack of medical facilities and high cost of antivenoms (Chippaux, 2011; Chippaux, Massougbodji, Diouf, Baldé, & Boyer, 2015). Snakes cause about 7,000 human deaths and 10,000 permanent disabilities annually on continental Africa (Chippaux, 2011). In India, about 49,000 people succumb to snake bites annually (Mohapatra et al., 2011).

Consequently, HWC certainly affect people's lives and livelihoods especially in developing countries where the majority live in the rural areas (Smith & Kasiki, 2000). These losses increase intolerance to wildlife by the affected communities and aggravate retaliatory killings (Hazzah, Borgerhoff Mulder, & Frank, 2009; Muriuki, Ipara, & Kiringe, 2017; Pangle & Holekamp, 2010). Thus, HWC threaten biodiversity and conservation efforts. If left uncontrolled, HWC can lead to reduced wildlife populations and accelerate local extinctions especially of the critically endangered species, such as the wild dog.

TEMPORAL AND SPATIAL OCCURRENCE OF HUMAN-WILDLIFE CONFLICTS

HWC occurrences varied in both time and space reflecting corresponding variation in rainfall. Thus, crop raiding was more frequent in Meru, Taita Taveta and Mt Kenya counties with high agricultural potential. In contrast, attacks on humans and livestock depredation were high in Kitui, Wajir, Marsabit and Laikipia counties that are of low agricultural potential. At regional levels, there were higher crop raids in the Taveta region in the GTE and Narok North in Narok County. Further, crop raiding incidents also showed monthly and inter-annual variation governed by rainfall variation. For instance, crop raiding peaked in the GTE and Narok County during 2008 - 2009 characterized by a severe drought (Bartzke et al., 2018; Ogutu et al., 2014). This is because rainfall controls the quantity and quality of food and water available for herbivores in savannas (Boutton, Tieszen, & Imbamba, 1988; Deshmukh, 1984). Further, crop raiding incidents increase nationally and regionally toward the end of the wet season when crops are mature and are being harvested. Crops are more nutritive than most wild forage and often result in habituation, making animals perennial crop raiders (Bailey et al., 1996; Howery, Bailey, & Laca, 1999). Farmers who lose their crops to wildlife during this stage are likely to suffer immense economic losses and will often be non-receptive to conservation. HWC mitigation measures can focus on reducing conflicts by providing water when droughts occur, e.g., through construction of widely spaced water dams and adoption of early maturing crops to respond to animal behavior.

COMPENSATION FOR HUMAN WILDLIFE CONFLICT LOSSES IN KENYA

The current wildlife legislation in Kenya, The Wildlife Conservation and Management Act 2013 (Act 2013) is robust and allows for compensation to be made for multiple wildlife species and different conflict outcomes. During the three years (2014 - 2016) Act 2013 was in operation, a total of about Kenya shillings (KES) 2.7 billion was paid out as compensation. However, during

2007 - 2013 when the repealed Wildlife (Conservation and Management) Act, Chapter 376 (Cap 376) was in force about KES 300 million was paid out in the comparatively longer seven-year period. However, only 35% of the cases filed for compensation were approved by the Kenya National Compensation Scheme (KNCS) during this period. In Nepal, a country with almost similar economic condition to Kenya, 31% of HWC were compensated for in one year (Karanth, Gopalaswamy, Prasad, & Dasgupta, 2013). However, in Kenya, half of the total compensation payments (about KES 3 billion) was spent on snake related incidents underlying the seriousness of this problem given that no crop damage or livestock depredation claims were paid. Nevertheless, Kenya fell below the budget requirement for compensating all human-wildlife conflict related losses. Elsewhere, the US the government spent $60 million in 2001 (Treves, Wallace, Naughton-Treves, & Morales, 2006), which is far less than the estimated annual losses of $2 billion (Messmer, 2000) incurred by American farmers due to HWC losses.

Compensation for HWC losses is essential to foster positive community attitudes toward wildlife conservation. In Kenya, wildlife based tourism is an important source of revenue, accounting for about 10% of the Gross Domestic Product (GDP) (GoK, 2010; Kibara, Odhiambo, & Njuguna, 2012). If HWC losses are not compensated as required by law, then this can negatively impact conservation efforts by aggravating retributive killing of conflict causing wildlife. Thus, the Kenya government should seriously consider increasing funds for compensating deserving human-wildlife conflict cases and expanding the range of conflict types that can be compensated as stipulated in Act 2013.

CONCLUSION AND RECOMMENDATIONS

Human-wildlife conflicts in Kenya and specifically the two most important wildlife regions, Maasai Mara and Greater Tsavo Ecosystems are caused by multiple wildlife species. The large herbivores led by the African elephant cause considerable crop damage together with non-human primates. Further, livestock depredation is largely caused by three carnivores, the lion, leopard and spotted hyena. Most human attacks that result in deaths or injuries are caused by a wide array of poisonous snakes. Conflicts also vary spatially because resources are heterogeneously distributed, closely mirroring rainfall distribution. Hence, crop raiding incidents occurred in areas of high agriculture potential whereas livestock depredation was higher in low potential agricultural zones. Further, seasonality plays a key role in influencing the frequency and intensity of HWC such that livestock attacks peaked during wet seasons when wild prey are in peak body condition, more dispersed and difficult to catch, while crop raiding peaked toward the end of the wet season when crops attain maturity. For this reason, HWC can result in immense economic losses affecting people's lives and livelihoods. Consequently, the government of Kenya spends considerable amounts of money on compensating HWC caused losses.

We suggest the following recommendations to address HWC and to enhance conservation of biodiversity in Kenya and possibly elsewhere:

1. Human population growth in Kenya is threatening biodiversity conservation. Education improves preference for smaller families (Lutz, Cuaresma, & Sanderson, 2008). Therefore, Kenya should target educating its general population especially the girls to help reduce human population growth and thus prevent the related negative impacts on biodiversity conservation. Exponential human population growth is responsible for habitat destruction through changes in land use, e.g., to agriculture that reduces wildlife habitat.

2. Scarcity of water in savannas caused by erratic rainfall due to climatic variation can be countered by providing water for wildlife in protected areas. This will reduce impacts of seasonality such that wildlife do not move outside parks and reserves in search of water at least for the large water deficient regions like the Tsavo region. Hence, long term planning should factor in spikes in HWC during droughts. This can be achieved through increased seasonal river and earth dams as well as encouraging farmers to dispose excess livestock during these periods of scarce resources. However, it is crucial to spatially plan and carefully manage artificial water sources to avoid habitat degradation around the areas as has happened elsewhere.

3. The central government of Kenya and devolved county governments need to review national and county policies on land use and spatial planning. These policies should integrate creation and protection of conservation corridors, wildlife dispersal areas and other critical habitats. Preventing habitat fragmentation and maintaining connectivity

ensures continuing migration of wildlife and therefore sustains genetic diversity. Existing policies should be effectively implemented to reduce HWC and enhance conservation.

4. Sustainable conservation in communal areas where most wildlife in Kenya are found is contingent upon economic benefits accruing to local communities from conservation. Hence, conservation needs to be developed to compete with other land use options such as agriculture and livestock keeping. The perception that conservation primarily helps enrich few local elites should be addressed specifically because it is the poor rural households that bear the brunt of most human-wildlife conflicts.

5. Compensation for losses caused by human-wildlife conflicts is a strategy the government of Kenya practices as a means of mitigation. However, the scheme is grossly underfunded. Processing compensation claims is also too slow and cumbersome. Increased funding will ensure that more victims are compensated to improve attitudes toward peaceful co-existence with potentially dangerous wildlife.

6. HWC monitoring databases should be enhanced to capture more useful details such as by specifying why an animal was killed during conflicts, e.g., as part of problem animal control, retaliatory killing by local communities, or to make a political statement and for attack on humans e.g. under what situations the attacks occurred to help guide the development of targeted response strategies. Further, the databases should provide a breakdown of the nature and timeliness of responses undertaken by wildlife managers in response to complaints about human-wildlife conflicts.

7. Continuing monitoring is critical to improving our understating 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 incidences to enable granular analyses of HWC occurrences and tightly linking HWC events to their putative causal covariates. KWS should thus, invest more on modern equipment, strengthen regional HWC databases by procuring more computers and Geographic Position System (GPS) receivers.

PROSPECTS FOR FUTURE RESEARCH

I. Snake related attacks on humans that result in the loss of many lives and injuries should be further investigated. Specifically, research should focus on what renders people vulnerable to snake attacks and what can actually be done to reduce such attacks.

II. It is important to investigate whether monetary compensation scheme for losses due to human-wildlife conflicts has any positive consequences toward conservation. This is likely to yield important information on the performance of this scheme which can lead to improved administration.

III. Examining livestock depredation by large carnivores relative to availability of wildlife biomass would be interesting. This can lead to a better understanding of why and when carnivores are killing more livestock.

IV. Future research should also aim to understand HWC at a higher spatial resolution, e.g., by getting the exact geo-location of the conflict incidents and including more information on the circumstances during the occurrence of conflict.

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Characteristics of Human-Wildlife Conflicts in Kenya: Examples of Tsavo and Maasai Mara Regions

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Abstract

Human-wildlife conflict (HWC) is a widespread and persistent challenge to conservation. However, relatively few studies have thus far examined long-term monitoring data to quantify how the type, and severity of HWC varies across species, seasons, years and ecosystems. Here, we examine human-wildlife conflicts in Tsavo and Maasai Mara, two premier wildlife conservation areas in Kenya. Using Kenya Wildlife Service (KWS) data (2001-2016), we show that both the type and severity of conflicts vary among species such that the African elephant (*Loxodonta africana*), is the leading conflict species in both the Tsavo (64.3%, n= 30664) and Mara (47.0%, n=12487) ecosystems. The next four most notorious conflict animals, in decreasing order, are nonhuman primates (Tsavo 11.4%, n=3502; Mara 11.8%, n=1473), African buffalo (*Syncerus caffer,* Tsavo 5.5%, n=1676; Mara 11.3%, n=1410), lion (*Panthera leo,*Tsavo 3.6%, n=1107; Mara 3.3%, n=416) and spotted hyena (*Crocuta crocuta,* Tsavo 2.4%, n=744; Mara 5.8%, n=729). We group the observed conflict incidences (n= 43,151) into four major conflict types, including crop raiding, the most common conflict type, followed by human and livestock attacks and property damage. The severity of conflicts also varies markedly seasonally and inter-annually. Crop raiding peaks in May-July, during and at the end of the wet season when crops are maturing but is lowest in November during the late dry season and beginning of the early rains. Attacks on humans and livestock increased more than other conflict types in both Tsavo (from 2001) and Mara (from 2013). Relatively fewer people in Mara (7.2%, n=901) than in Tsavo (38.2%, n = 11714) felt threatened by wildlife, suggesting that the Maasai people are more tolerant of wildlife. Minimizing HWC is tightly linked to successfully resolving the broader conservation challenges, including enhancing ecosystem connectivity, community engagement and conservation benefits to communities.

Keywords: Human-wildlife conflicts; crop raiding; human and livestock attacks; African elephant; Tsavo and Mara ecosystems

1. Introduction

Wildlife often interacts with humans in different ways, however, when such interactions adversely affect or are perceived to affect the lives and livelihoods of people, then conflicts occur (Woodroffe, Thirgood, & Rabinowitz, 2005). These negative interactions result in human-wildlife conflicts (HWC), the most common of which include: crop raiding, livestock depredation, and attacks on humans (Thouless, 1994; Woodroffe et al., 2005). Conflicts are caused by different wildlife species and occur at different intensities in different countries or parts of the same country. The African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants are key conflict animals and are involved in crop raiding and attacks on humans in these two continents (Gadd, 2005; Sitati, Walpole, Smith, & Leader-Williams, 2003; Sarker & Røskaft, 2014). Carnivores such as lions *(Panthera leo*), tigers (*Panthera tigris*), brown bears (*Ursus arctos*) and wolves (*Canis lupus*) often attack, and injure or kill people and livestock in many countries (Kolowski & Holekamp, 2006, Woodroffe et al., 2005; Patterson, Kasiki, Selempo, & Kays, 2004; Löe & Røskaft, 2004).

The main factors driving human-wildlife conflicts include human population increase, changing land use, habitat loss, degradation and fragmentation, high livestock population density, low abundance and restricted distribution of wild prey, high wildlife population density, and climatic factors. Further, stochastic events such as fires and increasing interest in ecotourism and access to nature reserves also contribute to increased HWC (Distefano, 2005). These factors contribute to human-wildlife conflicts differentially in different regions of the world. For instance, in Kenya, human-elephant conflicts (HEC) are attributed to increasing human population and changes in land use (Hoare, 1999; Thouless, 1994), that has increased the interphase between people and wildlife. Human-dominated areas are more likely to be settled by people who practice agriculture, a major pull factor for elephants as a source of alternative succulent and nutritious forage (Røskaft et al., 2014).

1.1 Human-Wildlife Conflicts in Kenya

Kenya, like many other countries, is experiencing fast human population growth and the associated demand for more space for agriculture, human settlements, and other developments. Human population increase is accompanied with progressive habitat fragmentation and demand for space as people seek alternative livelihoods. Nevertheless, tourism is an important foreign exchange earner in Kenya (Kenya Government, 2005) and is based mainly on wildlife watching. As a result, wildlife conservation is given a high priority by the Kenyan Government. The Kenya Wildlife Service (KWS), created in 1989, has the aim of overseeing wildlife conservation in all protected and non-protected areas in Kenya, including wildlife parks, reserves, sanctuaries, and community conservancies.

Wildlife in Kenya faces many threats including poaching, habitat loss, competition for water and food with livestock and human-wildlife conflicts (HWC). KWS has been collecting data on HWC since the early 1990s for some of the areas under its jurisdiction, such as the Tsavo and Maasai Mara (Mara) regions. These two regions support most of the wildlife in Kenya (as described in details below), including the largest terrestrial mammal in the world (Ogutu et al., 2016), the African elephant, as well as some of the largest felid species, such as the lion (*Panthera leo*) and leopard (*Panthera pardus*).

Here, we use HWC monitoring data collected by KWS during 2001-2016 for both Tsavo and Mara to analyze variation in human-wildlife conflicts across species, seasons, years and regions. Specifically, we examine and compare HWC patterns for 19 wildlife species in these two important transboundary conservation ecosystems in Kenya. Our analysis differs from previous studies in these regions that have mostly concentrated on single species (e.g., Smith & Kasiki, 2000; Sitati et al., 2003; Kaelo, 2007, Kanga et al., 2012; Mijele et al., 2013) by seeking to understand HWC patterns over the two regions during 2001-2016. HWC analyses involving multiple species monitored over long time frames are scarce because of the dearth of reliable long-term monitoring data. Kanga et al., (2012) used 12 years' (1997-2008) data from KWS to study hippopotamus *(Hippopotamus amphibius)* conflicts in Kenya and found a peak in June-August during crop harvest. Patterson et al., *(*2004) used data for four years to study livestock depredation in Tsavo and found that lions and spotted hyenas (*Crocuta crocuta*) killed most cattle, while cheetah (*Acinonyx jubatus*) killed only sheep and goats. In the Mara, over 50% of livestock attacks during one year of study were attributed to the spotted hyena (Kolowski & Holekamp, 2006). Sitati et al., (2003) examined human-elephant conflicts (HEC) in the Mara and noted that crop raiding by elephants could be predicted from the area of cultivated land. Habitat fragmentation due to cultivation and increasing human settlements have also been identified as major drivers of HECs in the Maasai Mara Wildlife Conservancies (Kaelo, 2007; Røskaft et al., 2014). Besides, these studies are based on a single region or ecosystem, and none of them have attempted to understand the patterns of HWC between two important wildlife areas in Kenya. In this study, we examined interspecific and temporal variation in HWC in the two premier conservation regions of Kenya.

Our main objective was to analyze reported incidences of human-wildlife conflicts in the Tsavo and Mara regions, identify and characterize the conflicts caused by wildlife species and the variation across seasons, years and between the two study regions. We test the following six hypotheses:

H1: Human-elephant conflicts are more likely to occur where there are high elephant densities, close to protected areas and in areas with high human population densities. Furthermore, there is likely to be more HEC in landscapes in which agriculture is the dominant land use than in landscapes where traditional pastoralism is the predominant land use. Because of the high elephant population and the fact that the major land use outside the Tsavo National Parks is agriculture, we therefore, expect relatively more conflicts with elephants in Tsavo than in Mara. Human-elephant conflicts can be expected to be more intense in landscapes whenever these land uses are practiced.

H2: Elephant is the leading animal species in terms of crop raiding, as well as attacks on humans. Among the other large herbivores, we expect buffalo (*Syncerus caffer*) and hippopotamus to have frequent conflicts with humans, because they occur in relatively large numbers in the Tsavo and Mara regions and have been shown to frequently cause conflicts with humans (Woodroffe et al., 2005); Dunham, Ghiurghi, Cumbi, & Urbano, 2010; Kanga et al., 2012).

H3: Among large carnivores, we hypothesize that lions will have the highest levels of reported cases of attacks on both humans and livestock. Other large carnivores such as spotted hyenas and leopards will also occasionally have conflicts with humans while cheetah and African wild dogs (*Lyacaon pictus*) only rarely attack humans or their livestock.

H4: We also postulate that many nonhuman primates will be involved in conflicts related to crop raiding. Baboons (*Papio spp*) and vervet monkeys (*Cercopithecus spp.*) are adapted to living at the edges of protected areas and raid farms when wild fruits are scarce.

H5: We expect more HWC to occur during the dry than the wet season when food and water are plenty. During the dry season, surface drinking water sources are fewer and wildlife move and congregate around a few permanent water sources outside of protected areas where people and their livestock are found.

H6: We expect to find fewer people in the Mara feeling threatened than in the Tsavo during HWC encounters. This is because the Mara is predominantly inhabited by the Maasai people who have a long history of co-existence with, and tolerance of, wildlife because of their traditional nomadic and pastoral lifestyles (Guggisberg, 1975; Okello, 2005; Conroy, 2013). Further, we expect to find more human fatalities during conflicts involving attacks on humans, particularly by mega-herbivores and the big cats.

2. Study area

2.1 Tsavo Region

The Tsavo ecosystem covers a total area of about 66,500 km^2 and lies between longitudes 37°7'E - 39°59'E and latitudes 0°58'S - 4°22'S to the south of Kenya. Rainfall is bimodal but erratic, with the short rains occurring in November - December and the long rains in March- May (Van Wijngaarden, 1985). Two major rivers, the Galana and the Tsavo, pass through this extensive area. It harbors the highest number of elephants (about 13000, Ngene et al., 2017) in a contiguous land mass in Kenya. The Tsavo Ecosystem consists of two of the largest National Parks (Tsavo East: 11,747 km^2 and Tsavo West: 9065 km^2) in Kenya plus Chyullu National Park (736 km^2), an important water catchment. South Kitui National Reserve (1133 km^2) is situated to the north of Tsavo East NP. The Taita Ranches, sandwiched between Tsavo West and East National Parks, is an important wildlife dispersal area and is home to the Taita people. The Taita Hills found here are densely populated owing to high rainfall and intensive agriculture (Van Wijngaarden, 1985; Figure 1). The regions adjacent to the protected areas serve as important seasonal wildlife dispersal areas.

The fauna in Tsavo consist of large herbivores, including the African elephant, African buffalo, hippopotamus, giraffe (*Giraffa camelopardalis*), Burchell's zebra *(Equus quagga*), eland (*Taurotragus oryx)*, waterbuck (*Kobus ellipsiprymnus*), Coke's hartebeest *(Alcelaphus buselaphus cokii),* Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), lesser kudu (*Tragelaphus imberbis*), gerenuk (*Litocranius walleri),* warthog (*Phacochoerus africanus*), fringe-eared oryx (*Oryx gazella callotis)* and black rhino *(Diceros bicornis)*. A wide array of large carnivores are found in the region, including the lion, cheetah, leopard, spotted hyena and the African wild dog. The population numbers of these species are monitored by KWS through tri-annual aerial surveys (once every three years) and annual ground animal censuses. For instance, between 2014 and 2017, elephant abundance increased by 4.9% while about 8600 buffaloes were counted in 2017 (Ngene et al., 2017). Long-term monitoring of elephants in the Tsavo region indicates continuous elephant population growth from 9447 (1999) through 9284 (2002), 11742 (2005), 11733 (2008), 12573 (2011), 11217 (2014) to 12866 (2017) individuals (Ngene *et al.,* 2017). The major land use types include agriculture, which is both practiced in small- and large-scale farms that rely on either rainfall or irrigation. Closely related to this is livestock keeping either in small or large-scale farms, wildlife conservation in ranches adjacent to the two Tsavos, intensive infrastructure development, and settlements in towns such as Voi (Ngene *et al.,* 2017). The human population has also been increasing at a similar rate as the rest of Kenya in the areas around Tsavo, especially in the Taita Taveta County (1999, n = 469,244; 2009, n = 720,352) (https://www.knbs.or.ke). In 1999, about 2.7 million people lived in and adjacent to the Tsavo region (https://www.knbs.or.ke). This population increased to about 4.5 million people in 2009 (https://www.knbs.or.ke), translating to a population growth rate of about 4.0% per annum.

2.2 Maasai Mara region

The Mara region (18,500 km^2) is found within Narok County between longitudes 34°34'E - 36°26'E and latitudes 0°24'S - 2°6'S to the southwestern part of Kenya, bordering Tanzania. The famous Maasai Mara National Reserve (MMNR) (1510 km^2) to the south-west of Narok County adjoins the Serengeti National Park (SNP) in

Tanzania to form the Greater Mara-Serengeti Ecosystem (GMSE). The Mara River, which originates from the Mau Forest ranges slithers through Narok County and the MMNR into SNP. Like the Tsavo Ecosystem, the Mara also harbours a large migratory population of wildlife. In earlier years, wildlife in the MMNR used to roam over the entire extent of Narok County up to the Mau ranges. However, recently this has changed drastically as the communal ranches that made this possible have been subdivided into individual holdings and fenced, cultivated or settled (Lamprey & Reid, 2004) thereby greatly impeding animal movements within the Narok county. We use the term Mara here to refer to the area covered by the MMNR and extending outwards to cover the entire Narok County (Figure 1).

The fauna of the Mara is similar to that of the Tsavo except for wildebeest (*Connochaetes taurinus*), Burchell's zebra and Thomson's gazelle (*Gazella thomsonii*) are found in very large numbers compared to Tsavo. Like for Tsavo, KWS continuously monitors wildlife in the Mara and, based on the latest census in 2017, elephants numbered 2493 and buffaloes 9466. These figures exclude about 450 km^2 overlapping area traditionally counted in the Tanzanian side but not covered in the 2017 survey. The Mara region has experienced a variable (due to cross-border movements) although increasing elephant population since 1999 (1577 individuals) to 2493 individuals in 2017, and these numbers have always been above 1500 except for a low of 820 elephants in 2003 and a high of 3051 elephants in 2010 (KWS, Unpublished data). Pastoralism is the predominant form of land use in the Mara and sheep, goats and cattle are the most commonly herded species. In 2017, KWS estimated 350,000 shoats (sheep and goats) and 800,000 cattle (Mwiu et al., 2017, unpublished report). Human immigration into this area has led to the conversion of large areas into large-scale wheat and maize farms. Wildlife conservancies are found adjacent to the MMNR, while to the northern part of the County (Mau), forest conservation is a major form of land use. Human population size in Narok County was about 470,000 in 1999 and increased to about 720,000 in 2009 (https://www.knbs.or.ke). This translates to an average human population growth rate of about 3.5% per annum and, therefore, Narok will likely have an estimated human population size of about 1,000,000 by 2019.

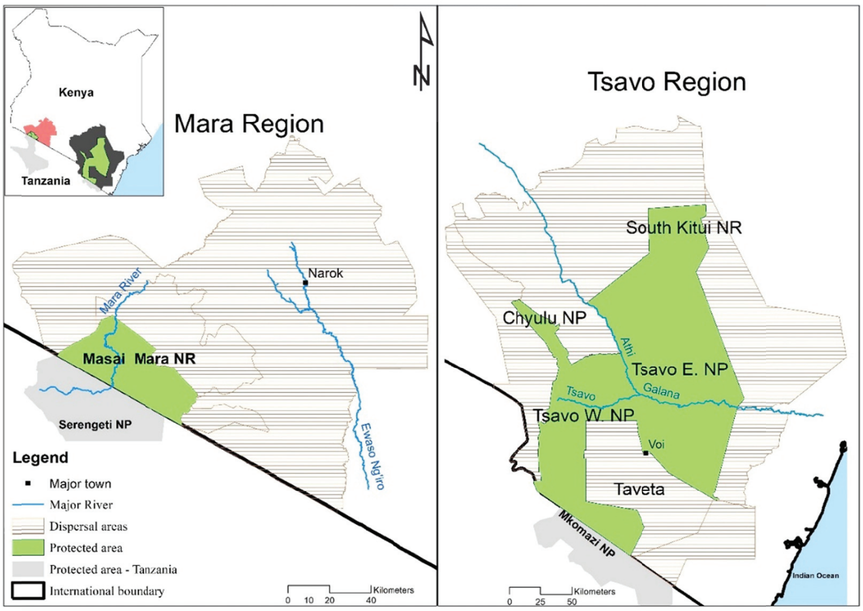

Figure 1. Map showing the Mara and Tsavo study regions in Kenya (top left corner) with surrounding dispersal areas (shaded) where human-wildlife interactions are reported. Notice the location of Taveta in the Tsavo region sandwiched between the two sections of the protected area

3. Methods

3.1 Human-Wildlife Conflict Database

KWS established an elaborate radio network covering the whole of Kenya and its headquarters in Langata, Nairobi. Every event or incident observed by KWS field personnel, or reported to KWS by communities, conservation Non-Governmental Organizations (NGOs) and governmental agencies are relayed as radio messages through the network. As a result, KWS has been able to record numerous HWC incidences since 1990. These datasets assist KWS to appropriately respond to reports concerning HWC and act as evidence for compensation claims relating to HWC fatalities and injuries. The HWC variables reported and recorded include the date (day, month and year) of occurrence; conflict types (human death, i.e., at least one person is killed during the animal attack; human injury, i.e., at least one person is physically injured during the animal attack; human threat, i.e., at least one person felt threatened by the encounter, however, no person was injured or killed). Other variables included obstruction (wildlife obstructing school going children, vehicles, or herders); crop damage (wildlife invade farms and damage crops), and property damage (water pipes, grain stores or other property damage); livestock killed or injured; species involved (i.e., species responsible for the conflict). Mostly, one species is involved in the conflict, however, at times multiple species are involved, and sometimes the conflict species is not identified.

Based on these variables, we identified four main human-wildlife conflict types; 1) attack on humans, 2) livestock attack, 3) crop raiding and 4) property damage. Attacks on humans refer to those conflicts where a wild animal is involved in an encounter with humans, and the incident is captured in the database as human death, human injury, a threat to humans, or obstruction to school-going children or general public insecurity. Livestock attacks include incidences where livestock are killed or injured and are captured in the database as livestock depredation. Crop raiding refers to incidents where crops are either destroyed or eaten by wildlife when farms are invaded or raided. Property damage denotes incidents including damage to property such as water pipes, grain stores, and houses. The last form of conflicts is referred to as "others" and includes any other reported human-wildlife incident involving one or more than one wildlife species and incidents such as automobile accidents involving wildlife.

In some cases, we pooled together several species commonly involved in conflicts in one group. Thus, the term antelope is used to group together Kirk's dik-dik *(Madoqua kirkii,* n = 4), common duikers (*Sylvicapra grimmia,* n = 1), hartebeest (*Alcelaphus buselaphus,* n = 1), impala (n = 77) bushbuck (n = 21), lesser kudu (n = 2), reedbuck *(Redunca fulvorufula,* n = 3), Thomson's gazelle (n = 10), Grant's gazelle (Gazella *granti,* n = 39), wildebeest (n = 95) or when term "antelope" was used as an umbrella conflict "species" (n = 135) in the data. Small carnivores such as the serval cat (*Leptailurus serval*, n = 17), caracal (*Caracal caracal*, n = 4), jackal (*Canis Spp.*, n = 4), mongoose (family *herpestidae,* n = 7), honey badger (*mellivora capensis*, n=19) and civets (family *Viverridae*, n =1) are also pooled into one group. Furthermore, primates mean baboons *(Papio spp.*, n = 4328) and monkeys *(Cercopithecus spp.*, n = 647) (all nonhuman primates), while bush pigs (*Potamochoerus larvatus*, n = 50), warthogs (*Phacochoerus africanus*, n = 52) and wild pigs (*Sus scrofa*, n = 74) are grouped as pigs. The last species type, “others” pools together records for which no species was indicated (n = 152), plus conflict incidents involving birds (eagles, vultures (accipitrids) and guinea fowls (numidids), n = 30), bees (*Apis mellifera scutellata,* n = 4), porcupine (*Hystrix cristata,* n = 9), squirrel (sciurids*,* n = 3), scorpions (bothrirurids, n = 1), as well as mixed conflict instances (several species, n = 16) and vehicles (n = 7). Thus, the final list comprised 19 wildlife species and one group labeled "others" (Table 1).

We also added another variable to the database called conflict outcome to denote the severity of conflicts involving humans based on a scale of 0 to 3; 0 = nothing happened to humans, 1 = humans felt threatened, 2 = humans were injured, and 3 = humans were killed. We examine whether the conflicts resulted in any one of these four outcomes.

We use the term livestock to refer to all types of domesticated animals such as cattle, sheep, goats, donkeys, camels, dogs and poultry. Livestock attacks are grouped into three outcome categories, 0 = nothing happened to livestock, 1 = livestock were injured, and 2 = livestock were killed.

We associate each conflict with the month in which it occurred to enable seasonal analysis. It is important to note that, although the total area of the Tsavo region is comparatively larger than that of the Mara, we compare relative frequencies of conflict cases which are independent of area and not the absolute human conflict numbers between the two regions.

Statistical analyses were done using SPSS, version 24.0 (IBM Corp. Release 2016. NY, USA). Since our data were count data, we used descriptive statistics as well as cross tabulations to compare relative frequencies between the two conservation regions. Most statistical tests were non-parametric Chi-square goodness of fit tests while few were cumulative frequency bar charts. Statistical significance is assessed at alpha = 0.05.

4. Results

4.1 The Relative Contribution of Species to Conflict by Region

A total of 45,151 cases of human-wildlife conflicts were reported between 2001 and 2016 for Tsavo and Mara combined. Tsavo had a total of 30,664 conflict cases compared to 12,487 cases for the Mara. This translates to an average of 1,900 human-wildlife conflict incidences per year for the Tsavo and 780 incidents for the Mara.

Most of the reported cases of conflict involved the African elephant for both the Tsavo (64.3%) and Mara (47.0%). However, the percentage of conflict incidences involving elephants was significantly higher for Tsavo than the Mara (Table 1, P = 0.001). Primates were the second most common cause of conflicts and their relative contributions to the total conflict incidents in Tsavo (11.4%), and Mara (11.8%) did not differ between the two regions (Table 1). Buffalo was the third most frequent conflict animal in both regions but was almost twice as likely to cause conflicts in the Mara (11.3%) as in Tsavo (5.5%, Table 1). The hippopotamus (2.6%) and zebra (2.5%) were the seventh and eighth most common causes of conflicts, respectively. However, while hippo conflict incidences were more common in Tsavo than in the Mara, the converse was the case for zebra (Table 1).

Among the carnivore species, lions had the highest but non-significant number of reported cases (3.5%) followed by the spotted hyena (3.4%) and the leopard (2.8%, Table 1). The cheetah and the wild dog ranked 16th and scored low overall (0.3%) and together with small carnivores (0.1%) made negligible contributions to the conflict incidences (Table 1). Carnivores made a minor contribution to the conflicts relative to the large herbivores. Conflicts involving reptiles were due to pythons as well as unidentified snakes and ranked ninth (1.6%) and tenth (1.5%), respectively. Moreover, the crocodile often considered likely to cause conflicts, was ranked behind snakes at the 13th position (0.5%; Table 1). However, the relative frequencies for all these animals differed significantly between the two regions (Table 1).

The antelopes (0.9%) had somewhat many reported cases in Mara (2.50%). Waterbuck (0.10%, n = 64) and giraffe (0.10%, n = 26) were only very rarely reported as conflict species (Table 1). The "others" group was also an insignificant source of conflicts and was ranked 13th (0.5%, n = 222; Table 1). Overall, our results indicate significant differences between the two regions (χ^2 = 5451.2, df = 19, P < 0.001).

Table 1. The common English and scientific names of the human-wildlife conflicts species, ordered by the number of cases of conflicts involving each species in Tsavo and Mara, and chi-squared goodness of fit tests for the null hypothesis that the percentage contribution of each species to the total conflicts differs between the two regions (n = number of reported cases, % is n expressed as a percentage of the total number of cases for the region)

No	Common English name of species	*Scientific name of species*	Tsavo		Mara		Pearson Chi-square test		
			n	%	*n*	%	X^2	df	P < 0.05
1	Elephant	*Loxodonta africana*	19719	64.3	5875	47.0	1094.8	1	0.001
2	Primates	Cercopithecidae family	3502	11.4	1473	11.8	1.2	1	0.267
3	Buffalo	*Syncerus caffer*	1676	5.5	1410	11.3	453.6	1	0.001
4	Lion	*Panthera leo*	1107	3.6	416	3.3	2.0	1	0.155
5	Spotted hyena	*Crocuta crocuta*	744	2.4	729	5.8	313.3	1	0.001
6	Leopard	*Panthera pardus*	526	1.7	698	5.6	483.3	1	0.001
7	Hippopotamus	*Hippopotamus amphibius*	1032	4.4	71	0.6	278.7	1	0.001
8	Zebra	*Equus quagga*	64	0.2	1013	8.1	2277.9	1	0.001
9	Python	*Python sebae*	695	2.3	0	0.0	287.6	1	0.001
10	Snake	*Serpentes suborder*	596	1.9	70	0.6	111.7	1	0.001
11	Antelope (assorted)	Bovidae family	73	0.2	315	2.5	519.8	1	0.001
12	Eland	*Taurotragus oryx*	275	0.9	37	0.3	44.6	1	0.001
13	Others*[1]		100	0.3	122	1.0	73.5	1	0.001
13	Crocodile*[1]	*Crocodylus niloticus*	199	0.6	14	0.1	52.1	1	0.001
15	Pigs (assorted)*[3]	Suidae family	86	0.3	90	0.7	42.4	1	0.001
16	Cheetah*[2]	*Acinonyx jubatus*	130	0.4	13	0.1	27.5	1	0.001
16	Wild dog*[2]	*Lycaon pictus*	35	0.1	104	0.8	142.8	1	0.001
18	Waterbuck*[3]	*Kobus ellipsiprymnus*	38	0.1	26	0.2	4.3	1	0.039
18	Small carnivores*[3]	*[4]	52	0.2	0	0.0	21.2	1	0.001
18	Giraffe*[3]	*Giraffa camelopardalis*	15	0.0	11	0.1	2.3	1	0.133
	Total		30664	100	12487	100	5451.2	19	0.001

*[1-3] These species had an equal overall frequency contribution to HWCs (0.5%, 0.3%, and 0.1%) respectively.

*[4] Families - Viverridae, Canidae, Herpestidae, Felidae, and Mustelidae

4.2 Frequency of Conflict Types by Species Between Tsavo and Mara

The elephant emerged as the leading conflict animal in three out of the five conflict types, namely attacks on humans (Tsavo = 74.6%, Mara = 64.8%), crop raiding (Tsavo = 65.8%, Mara = 47.3%) and property damage (Tsavo = 90.5%, Mara = 89.4%), with Tsavo reporting a relatively higher number of cases. However, the leading species causing livestock attacks was the lion (Tsavo = 31.8%, Mara = 16.7%) and the spotted hyena (Tsavo = 23.2%, Mara = 35%). The contributions of primates to crop raiding incidences were similar for the Tsavo (20.8%) and Mara (19.8%). There were higher attacks on humans incidents ascribed to buffalo in the Mara (20.9%) than in the Tsavo (8.0%). The spotted hyena (Mara = 35%, Tsavo = 23.2%) and leopard (Mara = 30.3%, Tsavo = 14.9%) accounted for higher livestock attacks in the Mara than Tsavo. Pythons attacked humans (4.8%) and livestock (1.4%) only in Tsavo. Snake bite incidences were relatively higher for Tsavo (4.3%, n = 578) than Mara (1.6%, n = 62) (Table 2).

Table 2. Conflict types by species

The contribution of each of the 10 leading conflict species to the most prevalent conflict types in both Tsavo and Mara. The Chi-squared goodness of tests for the null hypothesis that each species makes a uniform contribution to all the conflict types in each region

			Attacks on humans		**Crop raiding**		**Livestock attack**		**Property damage**		**Other**		**Pearson Chi-square test**		
	NO	Species	n	%	n	%	n	%	n	%	n	%	X^2	df	P <0.05
Tsavo	1	Elephant	10093	74.6	9094	65.8	84	3.1	446	90.5	2	2.9	5391.8	4	0.001
	2	Primate	182	1.3	2869	20.8	410	14.9	20	4.1	21	30.9	2634.4	4	0.001
	3	Buffalo	1083	8.0	565	4.1	13	0.5	5	1.0	10	14.7	382.3	4	0.001
	4	Lion	219	1.6	9	0.1	876	31.8	1	0.2	2	2.9	6971.6	4	0.001
	5	Hyena	97	0.7	7	0.1	637	23.2	1	0.2	2	2.9	5499.9	4	0.001
	6	Leopard	110	0.8	5	0.0	410	14.9	1	0.2	0	0.0	3142.5	4	0.001
	7	Hippo	262	1.9	751	5.4	6	0.2	5	1.0	8	11.8	373.8	4	0.001
	8	Zebra	10	0.1	48	0.3	0	0.0	2	0.4	4	5.9	136.3	4	0.001
	9	Python	654	4.8	2	0.0	38	1.4	1	0.2	0	0.0	739.6	4	0.001
	10	Snake	578	4.3	3	0.0	15	0.5	0	0.0	0	0.0	691.9	4	0.001
Mara	1	Elephant	2193	64.8	3051	47.3	90	4.6	463	89.4	78	47.6	2227.8	4	0.001
	2	Primate	59	1.7	1279	19.8	112	5.7	16	3.1	7	4.3	844.4	4	0.001
	3	Buffalo	708	20.9	650	10.1	14	0.7	12	2.3	26	15.9	588.6	4	0.001
	4	Lion	78	2.3	1	0.0	329	16.7	0	0.0	8	4.9	1345.5	4	0.001
	5	Hyena	37	1.1	0	0.0	688	35.0	3	0.6	1	0.6	3608.9	4	0.001
	6	Leopard	98	2.9	3	0.0	597	30.3	0	0.0	0	0.0	2746.2	4	0.001
	7	Hippo	58	1.7	9	0.1	0	0.0	3	0.6	1	0.6	110.9	4	0.001
	8	Zebra	5	0.1	998	15.5	0	0.0	7	1.4	3	1.8	969.6	4	0.001
	9	Python*											-		-
	10	Snake	62	1.8	0	0.0	6	0.3	0	0.0	2	1.2	141.2	4	0.001

*Python conflict incidents were not reported in the Mara region.

4.3 Frequency of Conflict Types in Tsavo and Mara

Crop raiding was the leading type of conflict in both the Mara (51.7%, n = 6455) and Tsavo (45.1%, n = 13820) and accounted for 47% of all the reported cases in both regions. The number of attacks on humans were higher for Tsavo (44.1%, n = 13532) than the Mara (27.1%, n = 3382) and accounted for 39.2% of all the conflict cases for both regions combined. Livestock attack was the third most common conflict type (10.9%), but was relatively higher for the Mara (15.8%, n = 1968) than the Tsavo (9.0%, n = 2751). Other conflict types were far fewer even though property damage accounted for 2.3% of the cases in both regions (Table 3). The overall relative frequency differed significantly between the two regions for all the conflict types ($P < 0.001$, Table 3) when the two regions are combined.

Table 3. The contributions of the different conflict types in Tsavo and Mara for the period 2001-2016 and the chi-squared tests of independence for the null hypothesis that each conflict type makes a similar contribution to the total in both regions

Conflict type	Tsavo		Mara		Pearson Chi-Square test		
	n	%	n	%	X^2	df	P<0.05
Crop raiding	13820	45.1	6455	51.7	156.3	1	0.001
Attack on humans	13532	44.1	3382	27.1	1081.8	1	0.001
Livestock attack	2751	9.0	1968	15.8	419.9	1	0.001
Property damage	493	1.6	518	4.1	250.3	1	0.001
Other	68	0.2	164	1.3	197.7	1	0.001
Total	30664	100.0	12487	100.0	1555.7	4	0.001

4.4 Seasonal Variation in the Frequency of the Common Conflict Types

The most frequent type of conflict was crop raiding and peaked in May-July when the frequencies were pooled across both regions (Figure 2). However, when considered for each region separately, crop raiding was more pronounced in March-September in Mara and January-February and May-July in Tsavo than in the rest of the year (Fig. 3). Attacks on humans were the next most frequent conflict type after crop raiding followed by livestock attacks, property damage, and others, in decreasing order. These human-wildlife conflict types were not only relatively rare but also displayed no evident seasonality in both regions (Figs 2 and 3).

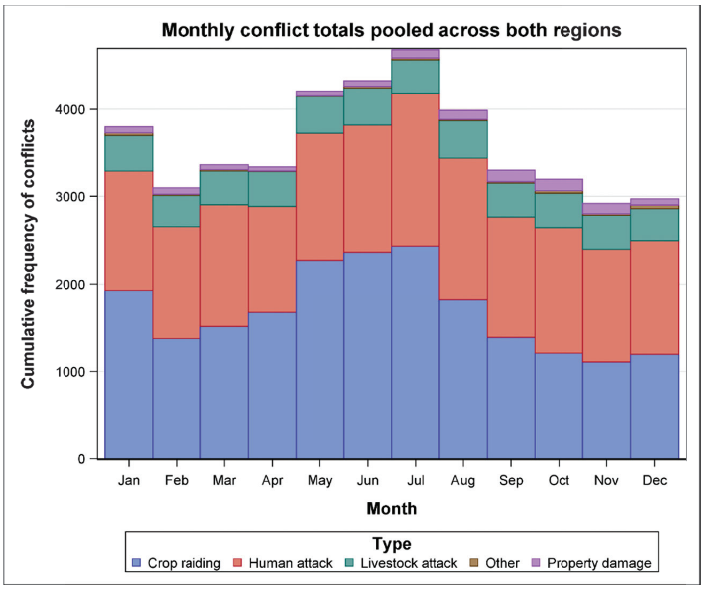

Figure 2. The distribution of the cumulative frequency of the common conflict types across months. The frequency of each conflict type has been pooled over the Tsavo and Mara regions

Crop raiding incidences in the Mara increased from March to a unimodal peak in July and then declined thereafter (Figure 3). Unlike for the Mara, Tsavo experienced a bimodal peak in crop raiding with a secondary peak in January-February and a primary peak in May-Jul (Figure 3).

4.5 Inter-Annual Variation in the Frequency of the Common Conflict Types

There were evident temporal trends in the major conflict types, but the trends differed between the two regions. In Tsavo, crop raiding was the most common conflict type during 2001-2007 but dropped precipitously to a low in 2010 before increasing steadily again during 2011-2016. However, the frequency of crop raiding in 2016 was still lower than the levels attained in 2001-2007. In sharp contrast to crop raiding, attacks on humans increased strikingly from 2001 to 2016 and surpassed crop raiding as the most common conflict type during 2009-2016 (Figure 4). Though relatively less frequent, livestock attacks also increased from 2001 to 2016, similarly to crop raiding (Figure 4). In the Mara, crop raiding and attacks on humans increased markedly from 2001 to peak in 2008-2009 and declined steadily thereafter. However, livestock attacks remained relatively stable during 2001-2013 and began increasing in 2014 (Figure 4). Conflicts related to property damage showed no apparent temporal pattern in both regions (Figure 4).

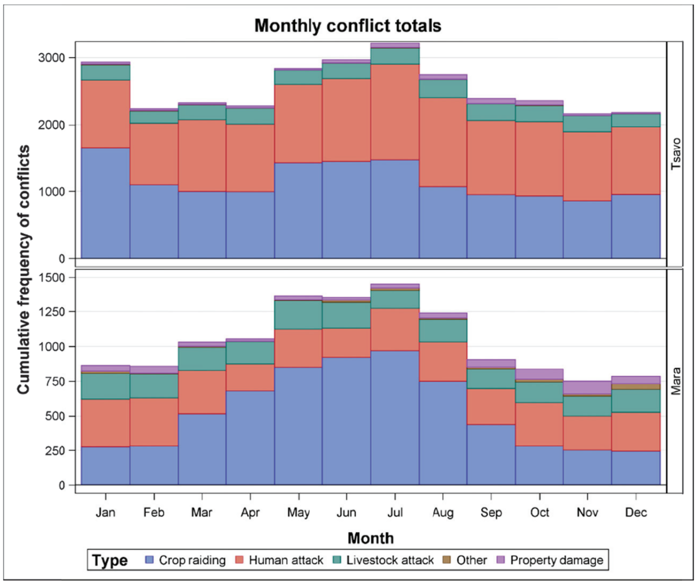

Figure 3. The distribution of the cumulative frequency of conflict types across months in Tsavo (top) and Maasai Mara (bottom) regions

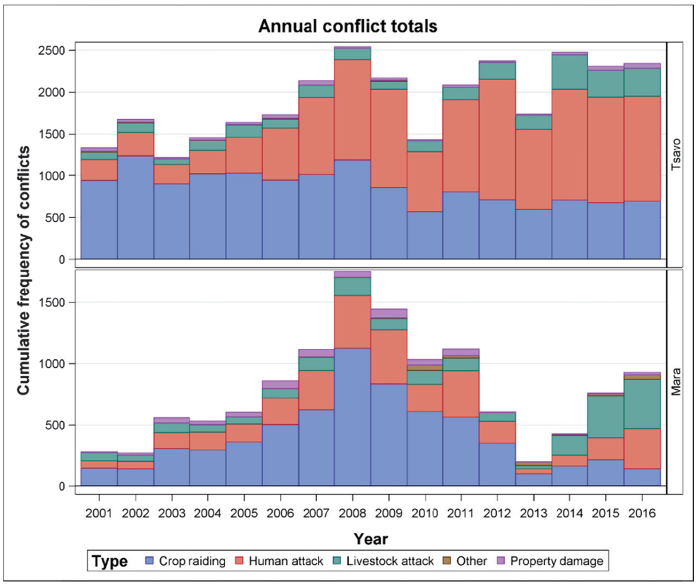

Figure 4. The inter-annual variation in the cumulative frequency of the common conflict types for the Tsavo (top) and Mara (bottom) regions

4.6 Conflict Type Outcome Differences between Tsavo and Mara

Here, we examine the outcomes of conflicts involving human and livestock attacks. Humans either felt threatened, were injured or killed during many conflict incidents in both the study regions (Table 4).Twice as many people were killed in Tsavo (0.9%, n = 278) as in the Mara (1.0%, n = 126) during 2001-2016 though the difference was not statistically significant (P = 0.316). In contrast, more conflict incidents reported for the Mara (89%, n = 11113) than for Tsavo (56%, n=17174) did not involve human injury, death or threats to people (Table 4).

Table 4. Outcomes of conflicts involving humans in the Tsavo and Mara regions

Conflict outcome	Tsavo		Mara		Pearson Chi-square test		
	n	%	n	%	n	df	P<0.05
Nothing happened to humans	17174	56.0	11113	89.0	4276.7	1	0.001
Humans felt threatened	11714	38.2	901	7.2	4118.1	1	0.001
Humans were injured	1498	4.9	347	2.8	96.2	1	0.001
Humans were killed	278	0.9	126	1.0	1.0	1	0.316
Total	**30664**	**100**	**12487**	**100**	**4480.4**	**3**	**0.001**

4.7 Human Wildlife Conflict Outcomes in Tsavo and Mara

Conflicts involving attacks on humans resulted in the highest cases of humans getting killed (2.4%, n = 398), human injuries (10.7%), and humans feeling threatened (74.6%). Tsavo had relatively higher frequency of incidents in which humans either felt threatened (86.6%, n = 11712; 26.6%, n = 901) or were injured (10.8%, n = 1466; 10.2%, n = 344) but fewer incidents involving human fatalities (2.0%, n = 272; 3.7%, n = 126) than the Mara.

During conflicts involving livestock attacks, very few cases also resulted in humans being either killed or injured. Tsavo had more cases of human injuries (0.9%, n = 25) during livestock attacks than the Mara (0.1%, n = 2). The Mara reported no cases of humans being killed during livestock attacks between 2001 and 2016 as opposed to Tsavo (0.2%, n = 5).

Though they were the most frequently recorded conflict types, conflicts involving crop or property damage were rarely associated with human injuries. Thus, for the Tsavo region, crop damage (0.0%, n = 6) was hardly associated with human injuries (See Table S5 in the appendix)

4.8 Livestock Attack Conflict Outcomes

Livestock attacks resulted in livestock either being killed (59.3% of the cases) or not (35.2%). In addition, a small proportion of livestock attacks (5.5%) resulted in livestock being injured (Table 6). Livestock was also either injured (0.1%) or killed (3.4%) during conflicts classified as property damage. Some attacks on humans (0.3%) and crop raiding (0.1%) incidents also resulted in livestock being killed.

Livestock attacks resulted in relatively more incidents of livestock being killed in Tsavo (81.3%, n = 2237) than the Mara (28.5%, n = 561), while Mara (13.1%, n = 257) had relatively higher incidences of livestock injuries than Tsavo (0.1%, n = 4). Tsavo region also had livestock killed during property (6.9%, n = 34) and human (0.4%, n = 50) attacks, while similar outcomes were relatively rare for the Mara (Table S6 in the supplementary materials).

5. Discussion

5.1 Prevalence of Human Elephant Conflicts in Tsavo and Mara Regions

The results reveal that the African elephant is the leading wildlife conflict species in both Tsavo and Mara regions, but there are higher relative conflict incidences for the Tsavo than for the Mara. This supports hypotheses **H1** and **H2**. In H1, we hypothesized that human elephant conflicts (HEC) are more likely to occur where elephant density is high, close to protected areas and where human population density is high. According to the KWS' aerial survey of 2017, there are 12866 elephants in the Tsavo region and the southern part of the Tsavo East National Park has 7.01 elephants/km^2, Taveta has 1.86 elephants/km^2, and Tsavo West National Park has 2.99 elephants/km^2 (Ngene et al., 2017). However, in Mara, a KWS' aerial survey of 2017 found a total of 2493 elephants with a density ranging from 1.73 elephants/km^2 in the protected area to 0.01 elephants/km^2 in the adjacent dispersal area (Mwiu et al., 2017, unpublished report). The Tsavo region is surrounded to the southern, south western and northern sides by the Taita and Kamba communities who practice agriculture in small farms adjacent to the protected areas. Further, the Kasigau corridor (important for wildlife) joins Tsavo East and Tsavo West NP through Taita area (Wildlife Works, 2013). This makes them more vulnerable to HEC conflicts due to the increasing elephant and human populations. This is unlike in the Mara where the indigenous Maasai people predominantly practice pastoralism, which is more compatible with wildlife conservation (Conroy, 2013, Okello, 2005). The trend of increasing HEC observed in the Mara region is due to the gradual sedentarization of these once nomadic pastoralists and the increasing conversion of land to large-scale wheat farming and human settlements. Nomadic pastoralism in Kenya is decreasing principally due to the scarcity of land and water (Okello, 2005) and is giving way to agro-pastoralism as a form of livelihoods for the Maasai. The elephant is the largest living terrestrial mammal and requires large amounts of food and water per day, and hence have large home ranges to obtain these resources. These movements lead to frequent conflicts between elephants and humans. This supports H2 which predicts that elephants should lead in crop raiding and attacking humans. Further, buffalo accounted for 7.2% and the hippopotamus for 2.6% of the reported cases of conflict. Buffalo was second to elephants in terms of attacks on humans, while hippopotamus was linked to crop raiding as earlier reported by Kanga et al. (2013). Indeed, based on these results, the elephant may be labeled as the 'most notorious' conflict species in Kenya, accounting for 80% of all conflict types and being the leading conflict species in four out of five conflict types. Persistent human-elephant conflicts pose great challenges to conservation managers as a form of land use, and the Kenyan state will likely have to shoulder greater compensation burdens for human fatalities in future. Land use entails a tradeoff between what local communities perceive to be more lucrative, which is often agriculture (Okello, 2005), and this threatens wildlife conservation by reducing conservation space.

5.2 Occurrence and Differences in Human Carnivore Conflicts for Tsavo and Mara

Overall, our results indicate that the lion is the leading cause of large carnivore-related conflicts. A closer examination of conflict types revealed differences between the Tsavo and the Mara regions. In the Mara, livestock attack conflicts were most likely to be caused by the spotted hyena, the leopard, and the lion. These results are consistent with those of Kolowski and Holekamp (2006) who also found livestock attacks in the Mara to be caused mainly by the spotted hyena (53%), the leopard (32%) and the lion (15%). In the Tsavo region, by contrast, livestock attacks were most often caused by the lion, the spotted hyena, and the leopard. However, the lion accounted for more incidences of attacks on humans in both the Tsavo and Mara, followed by the leopard and the hyena. This accords with **H3** which predicts that lions should have the highest reported cases of attacks on both humans and livestock while other large carnivores, such as spotted hyenas and leopards (Tweheyo et al., 2012) should less frequently cause conflict with humans. Carnivores are known to kill livestock (Patterson et al., 2004) as they experience reduced range and where their wild prey base has been reduced, and other forms of land use are being practiced. There were relatively more incidences of livestock attacks by the spotted hyena and leopard in the Mara than the Tsavo. The Mara is experiencing drastic land use changes and population increase (from births and immigration) which jeopardize the harmony that once existed between traditional pastoralism and wildlife (Lamprey & Reid, 2004; Kolowski & Holekamp, 2006; Schuette et al., 2013) resulting in increased HWC. It is likely that conflict incidences associated with the spotted hyena and leopard in the Mara involve primarily sheep and goats that are kept in large numbers, as they are more tolerant to droughts and can be kept in smaller land parcels than cattle. The once pastoral Maasai community has changed progressively to agro-pastoralism, thus fragmenting wildlife habitats (Okello, 2005; Conroy, 2013). Sheep and goat numbers increased in Narok County during 1977-2016 (Ogutu et al., 2016). However, this regional difference can also be attributed to differences in carnivore densities and husbandry practices (Kolowski & Holekamp, 2006). There were rare but noteworthy wild dog conflict incidences reported for the Mara, which abuts the Serengeti National Park in Tanzania. Lyamuya et al., (2014) and Holmern et al., (2007) have recently reported livestock predation by wild dogs in Serengeti, Tanzania. It is likely that these conflicts will persist in the future in both regions. Increased livestock depredation is likely to lead to decreased tolerance of carnivores (Kolowski & Holekamp, 2006) by local communities and therefore compromise their conservation.

5.3 Occurrence of other HWC Including Primates, Pythons, and Snakes in Tsavo and Mara

Our results also indicate that primates are a major cause of HWC in Kenya, second only to the elephant. Primates were mainly responsible for crop raiding and livestock attacks but rarely attacked humans. This supports hypothesis **H4** predicting frequent conflicts related to crop raiding by baboons and monkeys. Like other wildlife, the primates, too, are faced with shrinking habitats and are often forced to co-exist with humans. This often results in baboons and monkeys becoming 'primate pests' due to their role in crop raiding (Strum, 2010; Hill, 1997) and being negatively perceived by local communities and thus becoming of conservation concern (Dickman, 2012). Python and snakes made greater contributions to HWC occurrences in Tsavo than in the Mara. This makes python and snake bites an important conflict type for humans. In Uganda, pythons have been reported as responsible for livestock attacks (Tweheyo et al., 2012). In Kenya, the Wildlife Conservation and Management Act 2013 recognizes that snakes can often lead to fatal or serious human injuries and therefore provides that victims be compensated, unlike the previous Act of 1989, which lacked this provision.

Other wildlife species also played key roles in the HWC conflicts in the two regions. However, giraffe caused the least number of conflicts and was ranked the last species in order of relative frequencies of conflict incidences. This shows that all other wildlife species, such as giraffe, though they only rarely come into conflicts with humans can cause conflicts. For instance, the crocodile often considered a very dangerous animal and feared by many people, accounted for few of the conflict incidences in Tsavo (0.6%, n = 199) and Mara (0.1%, n = 14). The few cases of crocodile conflicts in these two regions do not necessarily reflect the national threat posed to humans and livestock by crocodiles and may reflect the fact that crocodiles inhabit sections of large rivers within protected areas with low human and livestock populations. Small carnivores also had few reported incidences, although most of their conflicts, e.g., targeting poultry, may often go unreported.

5.4 Seasonality and Inter-Annual Variation in Human-Wildlife Conflicts

Severe droughts can lead to serious water and food shortages for wildlife and therefore increase competition for resources between humans and livestock (Kanga et al. 2013). Crop raiding, the most frequent type of conflict peaked in May - July for the two regions. May is the time of year when most crops reach maturity while June and July are the typical harvesting times for most crops grown in these regions. This implies succulent and nutritious food that is attractive to wild herbivores is abundant during these three months. This is consistent with **H5** that seasonality is an important predictor of HWC and that there are fewer HWC during the wet than the dry season (Tweheyo et al., 2012) when food and water resources are scarce. Patterson et al., (2004) found that there was a higher incidence of lion depredation on livestock in Tsavo in the wet season. The extended continuous period for incidences of crop raiding in Mara (March-September) compared to Tsavo (January-February and May-July) reflect the fact that the two regions receive rains at different times but may also indicate other underlying factors not considered in this study. For instance, the Tsavo region receives bimodal rainfall with very distinctive short and long dry seasons (Van Wijngaarden, 1985). All these periods correspond to harvesting times for most crops (e.g., wheat and maize). Other conflict types were not seasonal, likely reflecting their nature and causes, e.g., attacks on humans can occur during any time of the year irrespective of season.

Human disturbance of wildlife habitats (Lamprey & Reid, 2004; Ogutu et al., 2014) increase HWC but its effects differ from one region to another. The temporal trends in conflict incidences show that incidences of attacks on humans have been increasing in the Tsavo regions since 2001 and surpassed crop raiding, which was at its lowest in 2010. Livestock attacks in the Mara, by contrast, have been increasing since 2013. We suggest that more attacks on humans are occurring in Tsavo due to increasing human and wildlife populations in the protected and adjacent areas while increasing livestock numbers (Ogutu et al. 2011; 2016) in the Mara are responsible for increasing livestock attacks there. Furthermore, KWS has stepped up a fencing programme around the Tsavo protected areas hence keeping crop raiding elephants away from farms, but this fails to prevent the smaller-bodied carnivores from moving out.

5.5 Conflict Type Outcomes for Tsavo and Mara

Conflicts involving attacks on humans resulted in many incidences of people feeling threatened, injured or killed. Occasionally, people are injured or killed during livestock attacks and property damage as they try to protect their livestock from depredation or property from being damaged. In Tsavo (38.2%), more people reported feeling threatened than in the Mara (7.2%). That relatively fewer people felt threatened by wildlife in the Mara reflects the historically relatively more harmonious co-existence of the Maasai community with wildlife (**H6**). This is unlike in the Tsavo where the people living in the dispersal areas are agriculturists and are more likely to report any wildlife they encounter to the government. The Maasai people are known to tolerate wildlife unless their livestock or lives are in danger and it is not rare to find cattle grazing together with wildlife (Conroy, 2013).

We also examined the outcomes of conflicts involving livestock based on three outcome categories (nothing happened to livestock, livestock were injured or killed) for the five conflict types. The most frequent incidents of livestock being killed occurred during livestock attacks. That livestock was rarely killed or injured during other conflict types, such as property damage, shows that human-wildlife conflicts can occur in multiple dimensions. Relatively more livestock attack incidences in Tsavo (81.3%) resulted in livestock being killed than in the Mara (28.5%). This could be because the Maasai have morans (warriors) who aggressively protect their livestock from predators when attacked (Lyamuya et al., 2016). This underlies the problem of depredation of livestock in Tsavo and Mara regions.

6. Conclusions and Recommendations for Wildlife Conservation and Management

Human-wildlife conflicts differ starkly in their types and frequencies between the Mara and Tsavo regions of Kenya. However, crop raiding is the most common type of HWC in both regions. Although the wildlife species involved in HWC also differ between the two regions, the elephant is the leading HWC species regardless of region. Non-human primates are the second most important group of wildlife species causing HWC in both regions. Elephant and primates are also the two leading groups of crop raiding wildlife species, not only in the two study regions but also elsewhere in Kenya (Strum, 1994, Graham, Notter, Adams, Lee, & Ochieng, 2010, Conroy, 2013). Thus, a recent trend of decreasing crop raiding and increasing attacks on humans in Tsavo implicates either shifting land use or effective HEC mitigation measures. For example, KWS has recently intensified fencing efforts around Tsavo PAs to limit elephant movements (Wambua et al., Unpub Report).

Rainfall seasonality is a key driver of HWC in both the Mara and Tsavo regions. However, climate change, by reducing or making rainfall more erratic, can amplify the effect of rainfall seasonality on HWC. A marked change in rainfall seasonality can heighten HWC by aggravating competition for food and water between livestock, wildlife, and people (Reed, 2012). Unsurprisingly, crop raiding conflicts peak immediately after the wet season, when food and water become limiting.

Thus, the following alternatives for addressing human-wildlife conflicts in Kenya are envisioned:

1) HWC mitigation measures should aim to reduce the influence of rainfall seasonality on wildlife and local communities through the provision of water (to homesteads and wildlife) and other interventions that minimize resource competition. Effective strategies and methods are needed to counteract the harmful impacts of HWC on wildlife and human communities. Ideally, such methods should take account of distinctions in HWC incidence types and frequencies across regions, seasons, predominant land use types and wildlife species. Methods developed thus far to combat crop raiding by elephants and other large herbivores in Kenya include erecting fences, barriers (vegetative, moats and ditches, stone walls), and active management (scaring, translocations, problem animal control (PAC)). In contrast, approaches used for primates mostly involve active management, such as translocation, guarding farms and PAC. For carnivores, the most widely used methods in Kenya are predator-proof livestock holdings (Hill, 1997, Omondi, Bitok, & Kagiri, 2004). The strategy adopted in particular localities vary depending on the type of HWC and the target wildlife species. However, HWC mitigation strategies are not always effective. For example, translocating a problem animal can work well in some situations, but can amount to transferring the problem in others (Dickman, 2010, Massei, Quy, Gurney, & Cowan, 2010,White & Ward, 2011). Technology is being increasingly used to aid HWC prevention and mitigation measures. For example, HWC prevention is being enhanced by geo-fencing in both study regions and elsewhere in Kenya by fitting elephants and lions with GPS-enabled collars to allow timely responses to problem animals. This is already producing useful data for understanding species movements in space and time, enabling timely responses to HWC incidences.

2) Fencing is one of the widely used interventions to contain HWC. Even so, the effects of fences are contested in conservation circles (Packer et al., 2013, Woodroffe, Hedges, & Durant, 2014). Fences (electric or non-electric) need to be built and maintained (both expensive) along PA boundaries to prevent large herbivores from raiding farms, as predator-proof livestock enclosures, and to protect agricultural farms and schools. However, fences are not an effective solution to HWC for all species and are often ineffective for primates, birds, burrowing animals and other species. The future of wildlife conservation in the two study areas, as in most others, will thus most strongly depend upon the good will and support of the local communities. These can be enhanced by conservation education targeting communities living adjacent to PAs or within human-dominated pastoral systems (Gadd, 2005, Gambay, 2014, Mmassy & Røskaft, 2014).

3) A growing threat to biodiversity conservation that is increasing HWC is spiraling human population density. If well- educated people prefer smaller households and care more for the environment (Lutz, Cuaresma, & Sanderson, 2008), then investing in better education may help to reduce human population and hence HWC. Better conservation benefits to communities and more equitable benefit sharing schemes can encourage positive community attitudes toward and support for wildlife conservation (Kala & Maikhuri, 2011). As tourism is a leading foreign exchange earner for Kenya escalating HWC poses serious challenges not only to wildlife conservation but also to national development. Economic benefits to local communities from ecotourism enterprises in the two study regions, and the rest of Kenya, have encouraged communities to set community-based wildlife conservancies that have greatly expanded the space available for wildlife conservation in recent years. This has also reduced HWC by reducing contacts between people,

livestock and wildlife as landowners voluntarily vacate their land parcels for wildlife conservancies in return for land rents and resettle elsewhere (Bedelian & Ogutu 2017; Ogutu et al. 2017).

4) The prevention and mitigation of HWC in Kenya and hence the success of conservation is complicated by the interplay of several other factors, including land use change, privatization of land ownership, land subdivision and declining traditional pastoralism, which was more compatible with wildlife conservation (Lamprey & Reid, 2004). The Kenyan state needs to seriously consider reviewing the national policy on land use and spatial planning, and giving greater priority to protecting wildlife habitats, including dispersal and migratory corridors to reduce HWC and promote wildlife conservation. This will reduce habitat fragmentation and maintain habitat connectivity for migratory and wide-ranging wildlife species. Close monitoring and effective law enforcement are needed to ensure that the intended goals are achieved.

5) Combating HWC places a huge burden on wildlife managers, conservationists, and communities and requires substantial human and financial resources. The Kenyan state and the international community would do well to work together to address this growing challenge as well as establishing a functional mechanism for funding compensation schemes for HWC-related losses. A similar approach is also needed in the provision of anti-venom drugs for snake bites, which are common in the Tsavo region. This will encourage and improve local communities' good will and support for conservation.

6) Because the Tsavo and Mara are cross-border ecosystems shared by Kenya and Tanzania, HWC prevention and mitigation strategies should ideally involve transboundary collaboration between the two states. HWC represents a serious and mounting challenge to contemporary conservation. Securing the future of wildlife and their ecosystems in the context of the expanding human population, changing land use developments, climate change and other factors calls for enhancing investments in conservation to improve HWC prevention and mitigation strategies.

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Appendixes

Table S5. The contributions of the common conflict types to outcomes involving threats to humans, human injuries or fatalities in the Tsavo and Mara regions

Conflict type		Attacks on humans		Crop raiding		Livestock attack		Property damage		Other		Pearson Chi-square test		
Conflict outcome		n	%	n	%	n	%	n	%	n	%	X^2	df	p
Tsavo	Nothing happened to humans	82	0.6	13814	100.0	2719	98.8	491	99.6	68	100.0	30172.4	4	0.001
	Humans felt threatened	11712	86.6	0	0.0	2	0.1	0	0.0	0	0.0	23983.1	4	0.001
	Humans were injured	1466	10.8	6	0.0	25	0.9	1	0.2	0	0.0	1848.1	4	0.001
	Humans were killed	272	2.0	0	0.0	5	0.2	1	0.2	0	0.0	329.3	4	0.001
Mara	Nothing happened to humans	2011	59.5	6455	100.0	1966	99.9	517	99.8	164	100.0	4131.6	4	0.001
	Humans felt threatened	901	26.6	0	0.0	0	0.0	0	0.0	0	0.0	2614.3	4	0.001
	Humans were injured	344	10.2	0	0.0	2	0.1	1	0.2	0	0.0	938.4	4	0.001
	Humans were killed	126	3.7	0	0.0	0	0.0	0	0.0	0	0.0	342.7	4	0.001
Tsavo and Mara	**Nothing happened to humans**	**2093**	**12.4**	**20269**	**100.0**	**4685**	**99.3**	**1008**	**99.7**	**232**	**100.0**	**34839.8**	**4**	**0.001**
	Humans felt threatened	**12613**	**74.6**	**0**	**0.0**	**2**	**0.0**	**0**	**0.0**	**0**	**0.0**	**27638.0**	**4**	**0.001**
	Humans were injured	**1810**	**10.7**	**6**	**0.0**	**27**	**0.6**	**2**	**0.2**	**0**	**0.0**	**2808.9**	**4**	**0.001**
	Humans were killed	**398**	**2.4**	**0**	**0.0**	**5**	**0.1**	**1**	**0.1**	**0**	**0.0**	**602.6**	**4**	**0.001**

Table S6. Outcomes of conflicts involving livestock in the Tsavo and Mara regions (separately and pooled) and the contributions of the common conflict types to the outcomes

		Conflict type										Pearson Chi-square test		
		Attack on humans		Crop raiding		Livestock attack		Property damage		Other				
		n	%	n	%	n	%	n	%	n	%	X2	df	p
Tsavo	Nothing happened to livestock	13482	99.6	13796	99.8	510	18.5	459	93.1	68	100.0	23300.3	4	0.001
	Livestock were injured	0	0.0	5	0.0	4	0.1	0	0.0	0	0.0	17.0	4	0.002
	Livestock were killed	50	0.4	19	0.1	2237	81.3	34	6.9	0	0.0	23309.4	4	0.001
Mara	Nothing happened to livestock	3373	99.7	6453	100.0	1150	58.4	517	99.8	164	100.0	4590.7	4	0.001
	Livestock were injured	1	0.0	1	0.0	257	13.1	1	0.2	0	0.0	1380.7	4	0.001
	Livestock were killed	8	0.2	1	0.0	561	28.5	0	0.0	0	0.0	3074.1	4	0.001
Mara and Tsavo	**Nothing happened to livestock**	**16855**	**99.7**	**20249**	**99.9**	**1660**	**35.2**	**976**	**96.5**	**232**	**100.0**	**25646.0**	**4**	**0.001**
	Livestock were injured	**1**	**0.0**	**6**	**0.0**	**261**	**5.5**	**1**	**0.1**	**0**	**0.0**	**2059.9**	**4**	**0.001**
	Livestock were killed	**58**	**0.3**	**20**	**0.1**	**2798**	**59.3**	**34**	**3.4**	**0**	**0.0**	**23280.7**	**4**	**0.001**

Table S7. Seasonal variation in each conflict types for the Tsavo and Mara regions

			Month												Pearson Chi-Square test		
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	X^2	df	P<0.05
Tsavo	Attack on humans	n	1010	929	1080	1018	1180	1246	1437	1336	1117	1119	1041	1019			
		%	7.5	6.9	8.0	7.5	8.7	9.2	10.6	9.9	8.3	8.3	7.7	7.5	195.8	11	0.001
	Crop raiding	n	1657	1095	996	992	1422	1442	1466	1067	948	928	856	951			
		%	12.0	7.9	7.2	7.2	10.3	10.4	10.6	7.7	6.9	6.7	6.2	6.9	350.6	11	0.001
	Livestock attack	n	225	182	221	239	214	229	242	272	249	242	242	194			
		%	8.2	6.6	8.0	8.7	7.8	8.3	8.8	9.9	9.1	8.8	8.8	7.1	62.8	11	0.001
	Property damage	n	32	26	26	29	20	46	66	67	76	63	26	16			
		%	6.5	5.3	5.3	5.9	4.1	9.3	13.4	13.6	15.4	12.8	5.3	3.2	110.6	11	0.001
	Other	n	12	9	7	4	2	5	6	5	3	8	2	5			
		%	17.6	13.2	10.3	5.9	2.9	7.4	8.8	7.4	4.4	11.8	2.9	7.4	16.6	11	0.096
Mara	Attack on human	n	348	352	311	192	273	209	304	282	258	318	250	284			
		%	10.3	10.4	9.2	5.7	8.1	6.2	9.0	8.3	7.6	9.4	7.4	8.4	474.5	11	0.001
	Crop raiding	n	274	279	517	682	850	921	969	750	440	279	246	243			
		%	4.2	4.3	**8.0**	**10.6**	**13.2**	**14.3**	**15.0**	**11.6**	**6.8**	4.3	3.8	3.8	1070.9	11	0.001
	Livestock attack	n	184	173	165	161	206	186	135	162	140	148	143	163			
		%	9.4	8.8	8.4	8.2	10.5	9.5	6.9	8.2	7.1	7.5	7.3	8.3	113.9	11	0.001
	Property damage	n	40	49	30	17	28	18	28	36	54	72	92	54			
		%	7.7	9.5	5.8	3.3	5.4	3.5	5.4	6.9	10.4	13.9	17.8	10.4	281.2	11	0.001
	Other	n	17	4	8	2	4	16	17	9	13	20	15	39			
		%	10.4	2.4	4.9	1.2	2.4	9.8	10.4	5.5	7.9	12.2	9.1	23.8	126.3	11	0.001

Paper II

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Spatial and temporal dynamics of human-wildlife conflicts in the Greater Tsavo Ecosystem, Kenya.

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Abstract

Biodiversity conservation in developing countries, including in Africa, is faced with many and mounting challenges, especially human-wildlife conflicts (HWC). We analyze patterns in HWC data consisting of multiple wildlife species. These data were collected over 23-years (1995 - 2017) from six regions constituting the Greater Tsavo Ecosystem (GTE), containing the largest protected area in Kenya. Overall, five wildlife species that contributed most to HWC incidents were the elephant (*Loxodonta africana*, 61.6%), nonhuman primates (11.5%), buffalo (*Syncerus caffer,* 6.2%), lion (*Panthera leo,* 4.2%) and hippo (*Hippopotamus amphibius*, 3.8%). HWC incidents showed spatial distinctions across the six regions, such that Taveta (43.3%, n = 10,427) was the leading human-elephant conflict (HEC) hotspot and Mutomo was the epicenter of primate, snake and python conflicts. Taveta, Rombo and Mutomo were leading in livestock attacks by large carnivores particularly the lion, spotted hyena *(Crocuta crocuta)* and leopard (*Panthera pardus)*. HWC showed marked inter-annual and seasonal variation during 1995 - 2017 related to similar variations in the availability, quality and distribution of food and water governed by rainfall fluctuations. HEC was positively and linearly related with human, elephant and livestock population densities. The Kenya Wildlife Service (KWS) responded to HWC reports and the rate of these responses peaked in 2017 when KWS attended to over 90% of the reported conflicts. HWC cases in Tsavo were not only substantial but increased strikingly over time. Hence, sustainable biodiversity conservation in human-dominated landscapes is contingent upon communities deriving meaningful benefits from wildlife conservation. Far-sighted measures and different conservation approaches are required to mitigate HWC in communal areas neighboring protected areas.

Keywords: Biodiversity, conservation, land use change, climate change, human population growth

Introduction

Human-wildlife conflicts (HWC) pose major challenges to biodiversity conservation in many ecosystems worldwide and particularly in Africa with diverse species of wildlife which compete directly with humans for land, forage and water. The conflicts contribute to biodiversity loss and adversely affect ecosystem services upon which the economies of over 80% of less-industrialized nations depend (Mooney et al. 1997, Solomon 2007). Further, biodiversity loss is often irreversible (Reed 2012), and therefore it is crucial to forestall such losses. HWC occur when resources are limited, leading to competition and conflicts between humans and wildlife (Graham et al. 2005). Increasing human population pressures and climate change in Africa thus pose serious conservation challenges as rising demand for resources exacerbates degradation and fragmentation of wildlife ecosystems. Climate change, in particular reduced rainfall and rising temperatures, aggravate food and water scarcity for wildlife. Notably, temperatures are increasing faster in Africa than the global average (Collier et al. 2008). This has significant implications for the frequency and intensity of HWC. Furthermore, bush meat harvesting can severely impact on ungulate off take and therefore change population dynamics (Rentsch and Packer, 2015, Allendorf and Hard 2009) leading to increased livestock depredation.

The Tsavo Ecosystem located in south eastern Kenya is the largest contiguous protected area system in Kenya. Even so, wildlife wander regularly outside this protected area in search of food and water (Okello 2005). Once outside the protected area, wildlife cause conflicts with humans through livestock depredation, crop damage, property damage, human deaths, injuries, threats, and general insecurity (Thirgood et al. 2005). Communities experiencing these conflicts tend to develop negative attitudes toward wildlife because they derive no benefits from the various programmes of wildlife utilization thus making wildlife a liability to their livelihood and therefore resort to persecuting wildlife through retaliatory killings to protect their lives or sources of livelihoods (Smith and Kasiki 2000, Packer et al. 2005, Røskaft et al. 2007, Hemson et al. 2009). Human-wildlife conflicts in the Tsavo are not new but date back to the late 20th Century when the Kenya-Uganda railway was being built. Tsavo became famous then for the 'Tsavo man eaters'; lions that hunted and killed many railway workers during this period (Kerbis Peterhans and Gnoske 2001).

Here, we analyze HWC for 20 wildlife species around the Tsavo Protected Area (PA). Our analysis expands upon and extends to multiple species, previous analyses in this region that have concentrated on single species or taxons, such as, the African elephant (*Loxodonta africana*, Smith and Kasiki 2000), lion (*Panthera leo),* cheetah (*Acinonyx jubatus*) or leopard (*Panthera pardus*) (Patterson et al. 2004). Such single species or single taxon studies are limiting in the sense that they often ignore the contribution of other species to HWC. HWC studies involving multiple species are very rare and have hardly been undertaken in Kenya (but see Okello 2005, Omondi 1994). Yet, only HWC studies involving multiple species are able to capture the full range of conflicts and their consequences. Such studies can therefore inform accurate resource allocation by managers, such as the amount and type of manpower to deploy, and the development of suitable methods for HWC control. Moreover, our study differs from the earlier ones by analyzing temporal and spatial dynamics of HWC and the associated conflict species for 23 years from 1995 to 2017. To do this, we use data on HWC collected by the Kenya Wildlife Service (KWS) at the Tsavo Research Center (TRC) from 1995 to 2017 and on wildlife mortality due to HWC collected by the KWS Security Division from 1995 to 2016. Such long-term HWC data sets provide a rare opportunity to unravel temporal patterns in and responses to HWC (Smith and Kasiki 2000).

Our main objective was to analyze spatial, seasonal, and inter-annual variation in human-wildlife conflicts, conflict species and management responses to the conflicts in the Greater Tsavo Ecosystem during 1995 - 2017. We also sought to identify and quantify common human-wildlife conflict types, outcomes and hotspots. We use HWC data collected daily for 23 years on all conflict-causing species in the Greater Tsavo Ecosystem to evaluate predictions of hypotheses relating to our initial expectations about conflict types, their frequencies and consequences.

H1: Human-elephant conflicts (HEC), including human attacks, should occur more frequently in areas with high elephant and human population densities and close to protected areas. H1.1: We therefore expect the Taveta region to experience higher HEC than all the other five regions comprising the Greater Tsavo Ecosystem because this region has a high human population density and is sandwiched between the two largest national parks (Tsavo East and West) in Kenya. H1.2: We expect, furthermore, to find more human-wildlife conflicts caused by crop raiding in the densely populated Taveta, Kibwezi and Rombo regions bordering the protected areas than in any of the other three regions in Tsavo. H1.3: HEC often results in elephant mortalities through government control and community retaliatory killing; as a result, increasing human-elephant conflicts over time should lead to more elephant deaths.

H2: Besides elephant and buffalo (*Syncerus caffe*r), we expect the leading HWC-causing species in the Greater Tsavo Ecosystem to also include large carnivores, specifically the lion, leopard and spotted hyena (*Crocuta crocuta)*, which cause livestock depredation. Other notable HWC-causing species should include crop raiding primates, snakes and pythons (*Python sebae)* that attack humans and the hippopotamus (*Hippopotamus amphibius*).

H3: We expect to find significant seasonal differences in HWC because some large herbivores (such as elephant and buffalo) require high amounts of food and water both of which vary seasonally. We therefore expect HWC to peak in the dry season months when water and food availability are most limiting in savannas.

H4: We expect to find an increasing trend in responses to HWC incidents over time. Such responses are important for sustaining community support for wildlife conservation on communal lands outside protected areas.

Methods

Study area

Our study region lies between latitudes 0° 58' S - 4° 22' S and longitudes 37° 7' E - 39° 59' E in south-eastern Kenya. It comprised four functional protected areas, Tsavo East (TENP) - 11,747 km^2 and Tsavo West (TWNP) - 9,065 km^2, Chyulu National Park - 736 km^2, and South Kitui National Reserve (SKNR) - 1,133 km^2, situated to the north of TENP. This region has the largest contiguous protected area in Kenya covering some 22,681 km^2 (Fig. I). We refer to the PA and its surrounding six regions, covering a total area of about 66,300 km^2 as the Greater Tsavo Ecosystem (GTE). This ecosystem is the focus of our study. Rainfall (200 -7 00 mm/year) is bimodal and erratic, with the short rains falling in November and December and the long rains between March and May (Van Wijngaarden 1985). Rainfall increases with altitude in the ecosystem and averages about 1,185 millimeters at the highest altitude of about 1,810 meters in Chyulu Hills (Pócs and Luke 2007).

The common large herbivores found in the Greater Tsavo Ecosystem include the African elephant, buffalo, hippo and the critically endangered black rhinoceros (*Diceros bicornis*) (Emslie. R. 2012), whereas large carnivores include the lion and leopard (Mukeka et al. 2018). The region harbors the largest elephant population in Kenya, numbering about 13,000 individuals (Ngene et al. 2017).

The vegetation is dominated by two tree communities, including *Commiphora* spp and *Acacia* spp, forming three broad types of communities; namely 1) *Commiphora-Lannea*, 2) *Commiphora-Acacia* and 3) *Acacia-Schoenefelda* (van Wijngaarden 1985). Elephants and anthropogenic influences, such as human-caused fires, vegetation destruction through charcoal burning and harvesting trees for building materials, fuelwood and fences play key roles in modifying these broad types (Van Wijngaarden 1985). As a result, grasslands and wooded bushlands are also found in the ecosystem. The Chyulu Hills have open glades with pockets of montane and mist forests (Pócs and Luke 2007). Further details on the fauna, flora, climate, soils and other characteristics of the ecosystem can be found in van Wijngaarden (1985).

Based on how KWS administers responses to HWC-related incidents, we subdivided the GTE into the following six regions. The Taveta region, encompassing Taita Ranches sandwiched between the Tsavo East and West national parks, is home to the Taita people and is an important wildlife dispersal area. The Taita Hills found in Taveta have high human density owing to high local rainfall (Van Wijngaarden 1985). Bachuma is a wildlife dispersal area and corridor that connects Tsavo East and the Shimba Hills National Reserve (NP) near the Indian Ocean coast.

The Galana Ranch forming the eastern part of the study region is used for extensive cattle ranching as well as a wildlife dispersal area. The Mutomo region is located to the north of Tsavo East, while the Kibwezi region is found to the east of Chyulu NP running northward along the Mombasa-Nairobi road, with Athi River as its boundary with Mutomo. Kibwezi and Mutomo regions both lie within Makueni and Kitui Counties, respectively. To the west of Chyulu NP and Tsavo West NP and extending southward up to Oloitokitok Town along the Tanzania-Kenya border is the Rombo region. The six regions adjoining the protected areas serve as important wildlife dispersal areas and are often centers of many HWC (Table 1, Figure 1).

Land use varies significantly across the six regions. Within the Taveta region, wildlife conservation and cattle ranching in 28 ranches are the prime land uses. These ranches are owned by local communities (n = 9 ranches), Kenya government (n = 8) and private entities (n = 11) (Taita Taveta County Government, 2012, unpublished report). Further, small-scale agriculture, sisal plantations and mining are also practiced whereas intensive infrastructure development and settlements are found in towns, such as Voi (Ngene et al. 2017, Table 1).

Bachuma is located in Kwale County. The most common land uses here include small-scale agriculture, settlements, mining and quarrying as most of the region is very arid and held under trust land. Trust land in Kenya is land held by the state on behalf of the communities inhabiting a region (Thompson, Serneels, Kaelo, and Trench 2009). Galana includes Kulalu Ranch in Kilifi and Tana River Counties, and is used predominantly for wildlife conservation and commercial livestock farming. However, recently there have been efforts by the Kenya Government to convert part of Galana into an irrigated farmland, incompatible with wildlife conservation (Ombaka 2014). In Rombo, intensive agriculture, both rain fed as well as irrigated, horticulture and wildlife conservation (in Kuku ranch) are practiced. The local Maasai community practice primarily livestock rearing in this region (Okello 2005). Agriculture is practiced more intensely in Kibwezi than Mutomo, which is drier than the former. As well, the local Kamba community inhabiting both Makueni and Mutomo regions keep fewer livestock than their Maasai counterparts in the Rombo region (Figure 1, Table 1).

Human population has been growing steadily in all the six regions. Data from the Kenya National Bureau of Statistics (KNBS), show that humans living in all six regions combined numbered 1,316,898 in 1989 and 1,825,299 in 2009. KNBS also projected the expected total human population size in the six regions by 2017 at about 2.1 million (KNBS 2017, Table 1, Figure A.1 associated files).

Table 1:

Summary descriptions of the six study regions constituting the Greater Tsavo Ecosystem

Region	**Area (km^2)**	**% average annual human population growth rate (1989-2017)**	**Habitat characteristics**	**Predominant land use**
Bachuma	2,900	2.97	Highly degraded in some parts	Wildlife conservation, settlements
Taveta	5,900	2.94	Partly intact in ranches, borehole water. Highly fragmented by settlements	Wildlife conservation, forests, livestock, small-scale agriculture, sisal plantations
Rombo	5,000	2.94	Fragmented on the southern part.	Agriculture (horticulture), wildlife conservation, pastoralism

Region	Area (km^2)	% average annual human population growth rate (1989-2017)	Habitat characteristics	Predominant land use
Kibwezi	7,000	1.66	Highly fragmented	Small-scale agriculture, forests, settlements
Mutomo	11,600	1.11	Fragmented	Small-scale agriculture, forests, settlements
Galana	11,200	2.97	Least disturbed	Livestock ranching, wildlife conservation

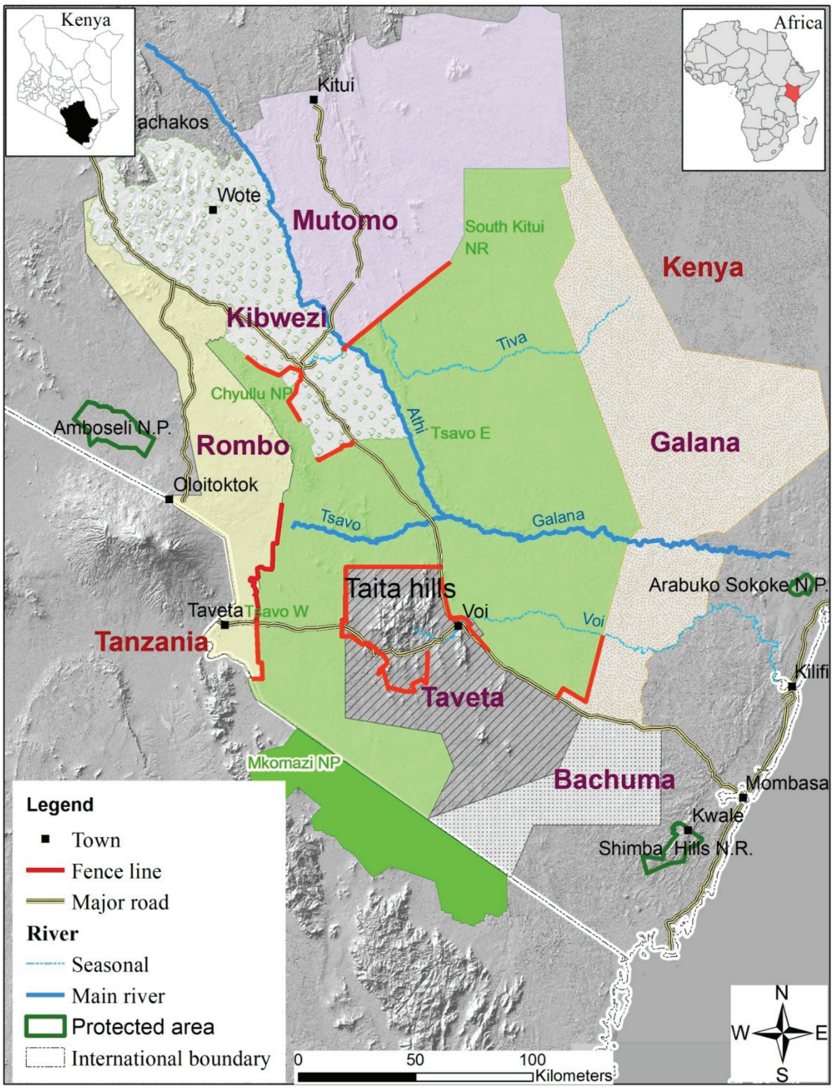

Figure 1: Map showing the PA and the six adjoining regions that jointly make up the GTE. Notice the fences put up to reduce HWC around the Tsavo PA. Taita Hills lies to the west of Voi Town.

The Greater Tsavo Ecosystem is connected to Mkomazi NP in Tanzania. Although a protected area, Mkomazi NP located in Tanzania, is omitted from our study because we did not have HWC data for it. We also obtained rainfall data from the Tsavo Research Center to represent the temporal trend in rainfall for the Tsavo region and relate it to the HWC trend for the region. Rainfall decreased steadily in the Greater Tsavo Ecosystem and hence the availability of food and water for wild herbivores (Figure A.2, associated files).

Human-wildlife conflict data preparation

KWS has partitioned Kenya into eight conservation regions for effective wildlife management and administration and to enable fast responses to wildlife-related issues (Kanga et al. 2012). The Tsavo Conservation Area (TCA) is one of these regions. We obtained HWC data from the Tsavo Research Center for the period 1995 - 2017. Data entered in daily occurrence books at stations within TCA, such as Mutomo, Kamboyo and Bura are collected periodically for compilation and archiving. The information collected on HWC include the date of incidents, wildlife species involved, conflict types (crop damage, human death, injury or threat, livestock killed or injured). A comprehensive list of the variables collected on HWC incidents can be found in Mukeka et al. 2018. Four main human-wildlife conflict types are identified: (1) attack on humans, (2) livestock attack, (3) crop raiding, (4) property damage, and (5) 'other' less common types involving multiple species (Mukeka et al. 2018). We also include a variable indicating how KWS responded to reported HWC incidents based on records in the occurrence books. These records indicate whether KWS attended to or did not attend to HWC incidents, or if the status of the response to the HWC incident was not specified. KWS attended to reported HWC cases by visiting conflict sites to scare away conflict animal(s), assess property or crop damage, or rescue communities in distress. KWS did not attend to all HWC reports due to logistical constraints or other reasons. Finally, some HWC reports did not specify whether KWS took action or not. A total of 14 species of conflict animals, five groups each comprising two or more species and a sixth 'other' group were identified (Mukeka et al. 2018). Further details are found in associated files (Table A.1 & A. 2)

The consequence of HWC sometimes leads to killing of the wildlife species involved either by KWS, or the affected communities. KWS occasionally kills animals that threaten people or their livelihoods through its problem animal control (PAC) program. Communities can also kill animals that threaten people or damage property through retaliatory killings (Achaet al. 2018). We also obtained data from KWS on all HWC- related elephant fatalities for the period 1995 - 2016 for the Tsavo region.

Using human population growth rates obtained from KNBS, we interpolated the number of people between 1995 and 2009 and extrapolated up to 2017 because human censuses are carried out once every 10 years in Kenya. We used the human population data to examine the effect of HEC incidents on elephant mortality in the Greater Tsavo Ecosystem. We further computed the total length (in kilometers) of the boundary each region shares with the PA to examine the effect of proximity to the PA on HWC. Finally, we stratified the data into the six regions (Bachuma, Taveta, Rombo, Kibwezi, Mutomo and Galana) constituting the Greater Tsavo Ecosystem based on the locations of conflict occurrence (Figure 1). We used these regions to examine spatial variation in HWC incidents in the GTE.

Statistical data analyses

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 across the six study regions. We used Kruskal Wallis H tests and multiple pairwise comparisons with a Bonferroni adjustment for multiplicity to examine regional and temporal differences in mean HWC across years. We also used simple bivariate correlations (Spearman's rank) and linear regression to quantify the strength of the relationship between the shared length of the boundary between the PA and the six regions, number of elephant conflicts and human population size and elephant population size, and between HWC-induced elephant mortalities, livestock numbers and the number of elephant conflicts. Since areal size can influence the number of conflicts in a region, a chi-square goodness-of-fit test was used to further examine if the observed distribution of the total HWC across regions differed from expectation assuming a distribution proportional to the area of each region. We conducted the analysis of temporal variation in the total monthly conflicts across all the six regions in the Greater Tsavo Ecosystem using the Unobserved Components Model (UCM), a special case of the Gaussian state space model. The UCM model decomposes the conflict series into a level (a time-varying level), two cyclical components, a seasonal component of length = 12 months, and an irregular component (or unexplained error). We fit this model with the diffuse Kalman filtering and smoothing algorithm (De Jong 1991, Selukar 2011).

We conducted statistical analyses using SPSS (version 24), StataMP/15.1 (StataCorp LLC, USA), R Studio (Version 1.0.153 – © 2009-2017 RStudio, Inc), and the GLIMMIX and UCM procedures of SAS (SAS Institute 2018). We created maps using ArcGIS® software

(Environmental Systems Research Institute, ESRI). We assessed significance level at alpha equal to 0.05, unless otherwise stated.

Results

Spatial variation in human-wildlife conflicts in the Greater Tsavo Ecosystem

Frequency of HWC occurrence in Tsavo region.

HWC incidents varied substantially across the six regions. Overall, 39,022 HWC incidents were recorded for all six regions adjoining the PA from 1995 to 2017 (Table 2). The total HWC incidents for each region over 1995 - 2017 averaged 6,503.7 ± 5,568.1. The lowest average of the regional total HWC incidents was 411 in Galana region whereas the highest was 14,240 in Taveta region. Wildlife species contributed to conflicts at varying intensities. African elephants were implicated in the highest number of conflict incidents overall and in five of the six regions (Figure 2). Primates were the second most likely group of species to cause conflicts but the vast majority of these (90%) occurred in Rombo (Figure 2). Large herbivores other than elephant were involved in far fewer and more localized conflicts. Thus, the buffalo and hippo contributed the highest HWC in Rombo whereas zebra and giraffe did so in Taveta (Figure 2). Large carnivores caused considerably fewer conflicts than the large herbivores and most of those conflicts were in Taveta. The overall contribution of large carnivore species to HWC, in decreasing order, were lion, leopard and hyena. The lion was the leading conflict carnivore species in Taveta followed by Galana whereas the spotted hyena and leopard were the most common conflict carnivores in Mutomo (Figure 2 and Fig A.3 associated files). Pythons and snakes were the fourth most notorious causes of conflicts after large carnivores albeit in smaller proportion, but important because of injury and death to humans. The majority of python and snake conflicts occurred in Mutomo, whereas one third occurred in Taveta. The giraffe was the least conflict-causing species attacking one human every two years and very few crop raiding incidents. Nine of the 14 common species accounted for 95.3% of all the conflict incidents in the Greater Tsavo Ecosystem. A detailed breakdown of the conflicts by species and region is provided in Table A.3 in the associated files. Overall, differences in the relative frequencies of conflicts across the six regions were statistically significant (Table 2, Figure 2). Similarly, the relative contribution to the overall HWC cases of the 20 species differed among the six regions.

Table 2:

Chi-squared goodness-of-fit test of the null hypothesis that the percentage HWC incidents attributed to each species or species group does not differ across the six regions. n = total number of reported cases for each species, df = 5 for all the tests.

No	**Species**	χ^2	n	**P-value**
1	Elephant	5850.1	24032	<0.001
2	Primates	3853.0	4480	<0.001
3	Buffalo	145.4	2432	<0.001
4	Lion	489.7	1645	<0.001
5	Hippo	2102.8	1497	<0.001
6	Hyena	573.5	925	<0.001
7	Snake	3546.6	789	<0.001
8	Python	4321.9	709	<0.001
9	Leopard	280.5	672	<0.001
10	Eland	286.7	363	<0.001
11	Waterbuck	432.7	322	<0.001

No	Species	χ^2	n	P-value
12	Crocodile	373.7	319	<0.001
13	Cheetah	71.6	167	<0.001
14	Antelope	62.1	155	<0.001
15	Pigs	92.6	153	<0.001
16	Others	67.7	124	<0.001
17	Zebra	27.3	122	<0.001
18	Small carnivores	38.4	55	<0.001
19	Wild dog	25.8	39	<0.001
20	Giraffe	23.9	22	<0.001

All the P-values are statistically significant at P<0.01

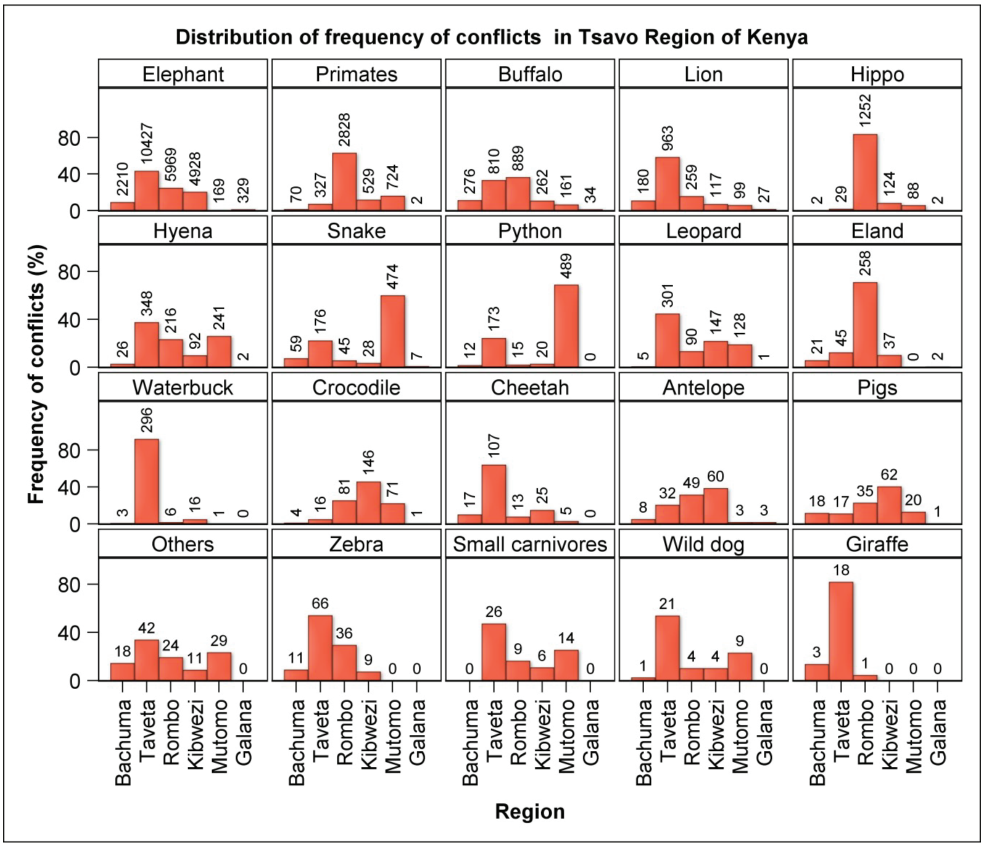

Figure 2: Percentage conflict frequencies for each species or species group in each of the six study regions. Data labels are the total frequencies of the HWC incidents for each species during 1995-2017.

Quantifying differences in HWC across the six study regions during 1995 - 2017.

We expected HWC to vary spatially in correspondence with spatial variation in the level of critical resources, such as water and food that are rarely homogeneously distributed across landscapes. As expected, there was a highly significant overall difference in HWC incidents among the six regions ($\chi^2_5 = 88.590$, $P < 0.001$; Table 3). The highest number of conflict incidents were found in Taveta (n = 14,240) and Rombo (n = 12,079; Figure A.4 associated files). We also expected spatial differences in HWC incidents to increase with the length of the boundary shared between a region and the PA through its impact on the number and frequency of HWC incidents in the region. Although, this relationship was positive it was very weak (r^2 = 0.15, $F_{1,5}$ = 0.72, P = 0.445). Remarkably, the Taveta region shared over 70% of its boundary with the protected areas.

Furthermore, the number of HWC incidents differed significantly (χ^2_5 = 43,055, P < 0.001) across the six regions. As a result, the relative frequency of occurrence of conflicts in the Greater Tsavo Ecosystem did not simply reflect the size of a region. Thus, larger regions like Galana and Mutomo experienced far fewer conflict incidents than smaller regions such as Taveta and Rombo (Table 3). Thus HWC in the GTE are caused by other underlying factors besides expansiveness of the region.

Table 3:
Multiple pairwise comparisons of the relative frequency of HWC incidents among the six study regions adjoining the Tsavo PA.

Pair of regions compared	**Observed**	**Expected**	**Kruskall-Wallis H**	**aP-value**
Bachuma-Taveta	2944|14240	2609 |5301	5.18	0.001*
Bachuma-Rombo	2944|12079	2609 |4457	4.43	0.001*
Bachuma-Kibwezi	2944|6623	2609 |6227	2.45	0.22

Pair of regions compared	Observed	Expected	Kruskall-Wallis H	aP-value
Bachuma-Mutomo	2944|2725	2609 |10405	.26	1.00
Bachuma-Galana	2944|411	2609 |10019	2.76	0.09
Taveta-Rombo	14240|12079	5301|4457	0.76	1.00
Taveta-Kibwezi	14240|6623	5301|6227	2.73	0.09
Taveta-Mutomo	14240|2725	5301|10405	5.44	0.001*
Taveta-Galana	14240|411	5301|10019	7.69	0.001*
Rombo-Kibwezi	12079|6623	4457|6227	1.98	0.71
Rombo-Mutomo	12079|2725	4457|10405	4.68	0.001*
Rombo-Galana	12079|411	4457|10019	6.97	0.001*
Kibwezi-Mutomo	6623|2725	6227|10405	2.70	0.10
Kibwezi-Galana	6623|411	6227|10019	5.09	0.001*
Mutomo-Galana	2725|411	10405|10019	2.51	0.18

[a]P- values have been adjusted for multiple tests. *Indicates statistically significant differences in relative frequencies of HWC between pairs of regions. A vertical bar (|) is used to separate observed and expected values for the pair of regions being compared.

HWC frequency distribution by conflict types and region.

There were four common conflict types and their relative frequencies varied markedly across regions. Crop raiding (47.2%) was the most frequent conflict type followed by attacks on humans (41.3%), livestock attacks (9.5%), property damage (1.7%) and others (0.4%) (Table 4, Figure 3). Crop raiding was 1.6, 2.4, 7.3, 11.6 and 44.4 times more likely to occur in Rombo than in Taveta, Kibwezi, Bachuma, Mutomo or Galana, respectively. The distribution of the frequency of attacks on humans across regions followed the same pattern as crop raiding except that attacks on humans were most prevalent in Taveta. Livestock attacks were predominantly concentrated in Taveta and Rombo. Incidents involving property damage were extremely rare in Mutomo and Galana compared to the other four regions (Table 4, Figure 3). Similar results were obtained after weighing the total number of conflicts per region with the area of the region. Overall, Chi-square goodness-of-fit tests indicated significant differences in the relative frequencies of conflict types across the six regions (χ^2_5 = 3,829.1 P = 0.001).

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 six regions around the Greater Tsavo Ecosystem, df = 5 for all the chi-square tests.

Conflict type	**Percentage contribution of conflict type to the regional total (100%)**							**Chi-square**	
	Bachuma	Taveta	Rombo	Kibwezi	Mutomo	Galana	n	χ^2_5	P-value
Crop raiding	37.2	35.9	65.8	51.0	25.1	43.6	18404	3094.0	<0.001
Human attack	49.5	50.0	26.5	41.5	51.2	45.5	16106	1726.1	<0.001
Livestock attack	7.5	11.3	6.8	6.2	22.6	6.8	3707	801.1	<0.001
Property damage	5.4	2.4	0.6	1.1	0.2	3.6	668	432.2	<0.001
Other	0.4	0.4	0.3	0.2	0.9	0.5%	137	30.9	<0.001

All the P-values are statistically significant at P<0.01.

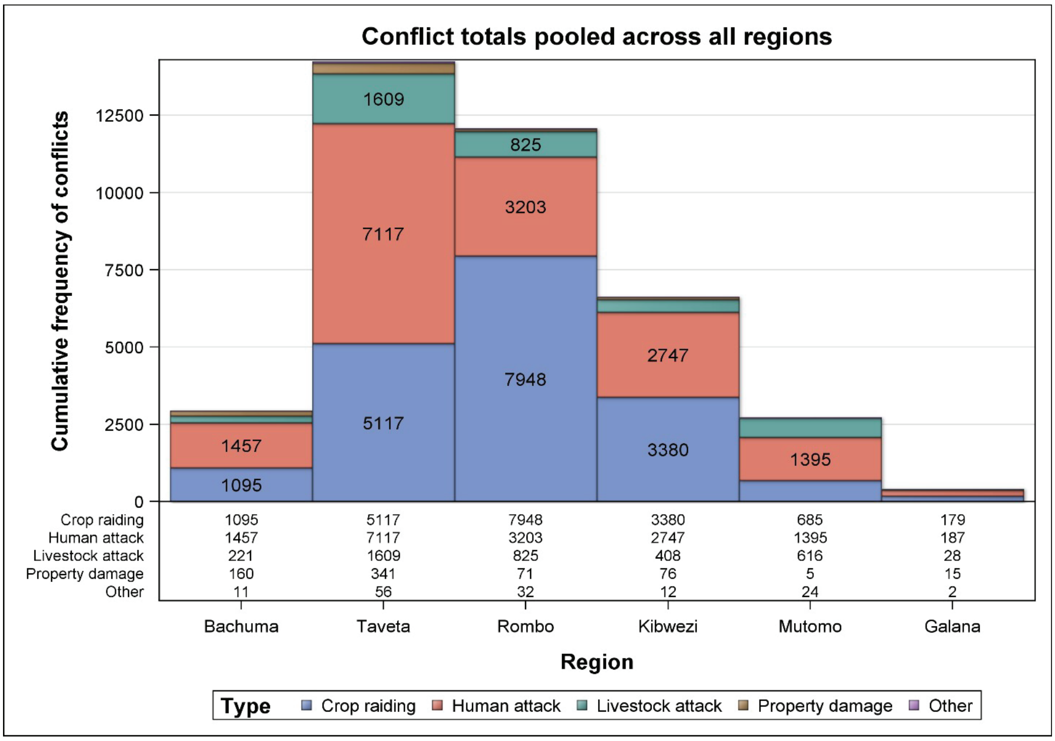

Figure 3: Total frequency of conflict types per region

Frequency of HWC outcomes by region.

HWC incidents can have various physical or psychological consequences. Although the majority of people involved in HWC were neither injured nor killed, a sizable number felt threatened (Table 5). People were more likely to be threatened, injured or killed during conflicts in Taveta, Bachuma and Mutomo than in the other regions. Elephants caused most human threats, injuries and deaths in Taveta and Bachuma but buffaloes, snakes and pythons also caused a few threats, injuries and deaths in Taveta. In contrast, snakes and pythons caused most, while crocodiles caused few, human injuries and deaths in Mutomo (Figure 4). More details of the frequency of HWC outcomes by region are provided in Table A. 4 in the associated files.

Table 5:

Chi-squared goodness-of-fit tests of the null hypothesis that the percentage contribution of each conflict outcome to the total does not differ across the six regions in the Greater Tsavo Ecosystem, df = 5 for all the chi-square tests.

Human-related conflict outcome	Percentage of conflict outcome within region							Chi-square test		
	Bachuma	Taveta	Rombo	Kibwezi	Mutomo	Galana	Total	%†	χ^2_5	P-value
Nothing happened	50.34	49.93	73.47	58.80	50.35	54.50	22957	58.83	1707.0	<0.001
Human felt threatened	44.06	45.28	24.42	39.54	14.35	41.12	13874	35.55	1920.4	<0.001
Human were injured	4.48	3.76	1.62	1.27	31.85	3.16	1828	4.68	4961.3	<0.001
Human were killed	1.12	1.03	0.48	0.39	3.45	1.22	363	0.93	238.1	<0.001

†Percentage contribution to the overall conflict outcome. All the P-values are statistically significant at P<0.01.

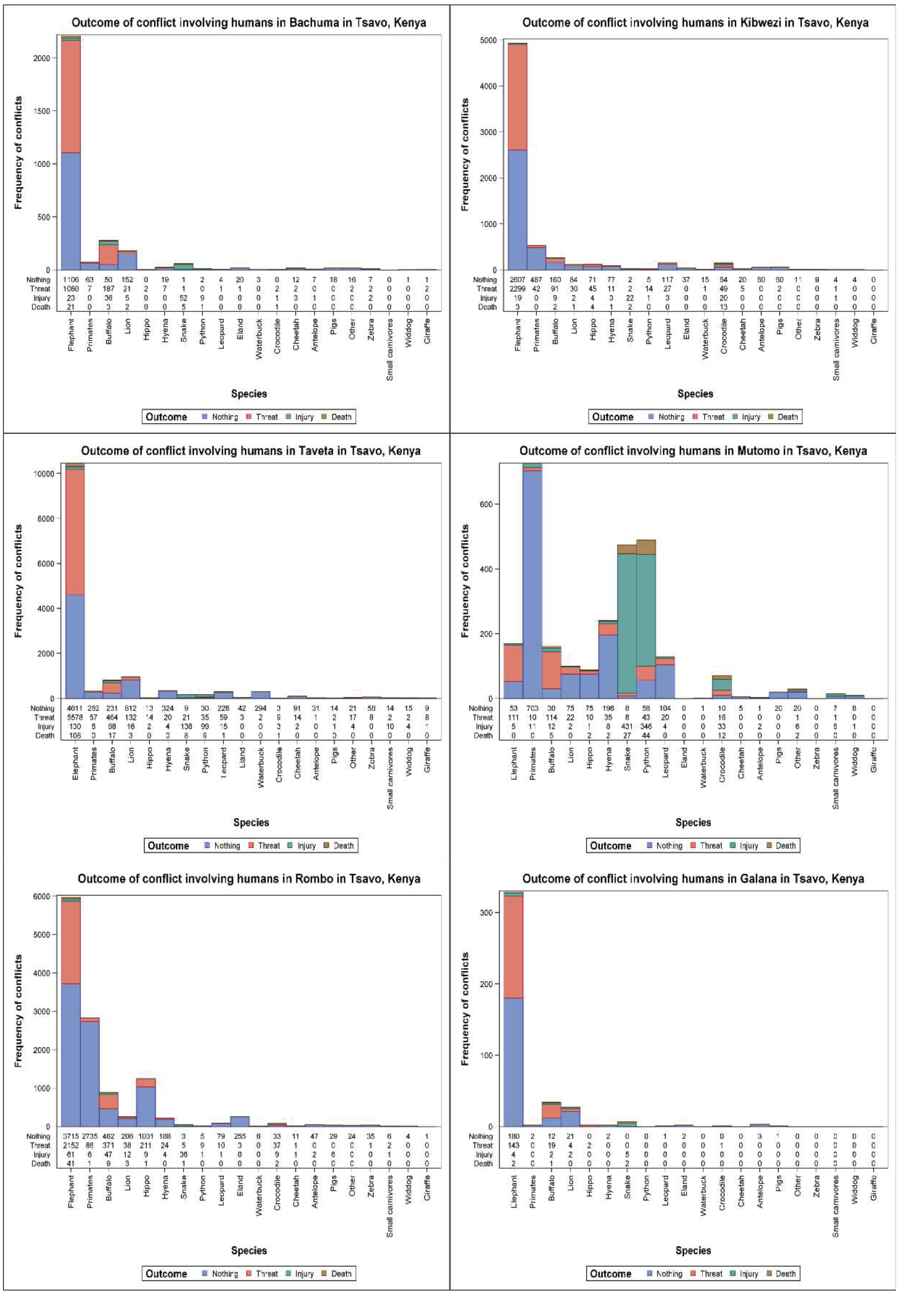

Figure 4: Frequency distribution of conflict outcome incidents experienced around Tsavo PA during 1995-2017.

Variation in Elephant conflicts with human and elephant population sizes

Conflicts involving elephants were positively and linearly correlated with human population size (r_s = 0.80, P = 0.001, df = 23) and elephant population density (Figure 5 a, r_s = 0.80, P = 0.001, df = 23, two tailed). Univariate linear regression models showed that variation in human population size explained 76.6% ($F_{1,21}$ = 68.56, P = 0.001) whereas variation in elephant population size accounted for 70.9% ($F_{1,21}$ = 51.26, P = 0.001) of the total variation in elephant conflicts. The interaction between human and elephant populations may exacerbate elephant conflicts. Indeed, a negative binomial regression model showed that HEC increases with increasing elephant and human population size. But a unit increase in elephant population size ($F_{1,19}$ = 6.49, P = 0.0197) had a stronger impact on HEC than a unit increase in human population size ($F_{1,1\ 9}$ = 6.44, P = 0.0201) though both had a positive and significant interactive effect ($F_{1,19}$ = 4.82, P = 0.0408). The dependence of HEC on elephant and human population sizes and their interaction is given by: HEC = exp (0.10011651× elephant population size + 0.00075125 × human population size- 0.00000005 ×elephant population size × human population size) (Figure 5 a).

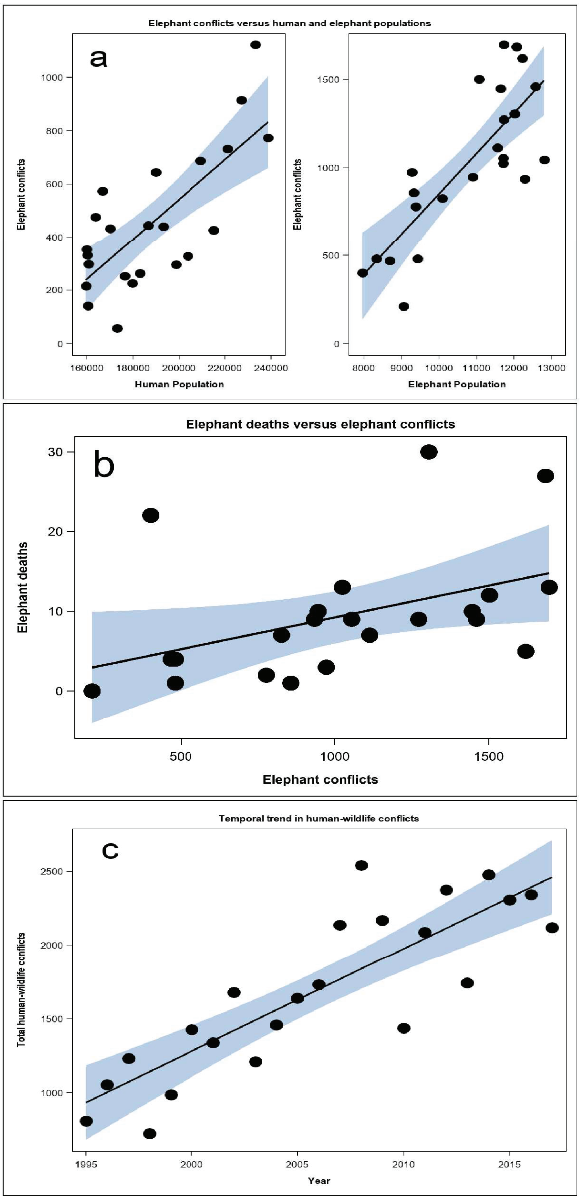

Figure 5: Total human-wildlife and elephant conflicts Tsavo 1995-2017

HEC and Elephant mortalities

Problem animal control or retaliatory killings of elephants results from HEC. We therefore expected elephant fatalities to increase with increasing human elephant conflicts. Elephant deaths were moderately, positively and linearly related to elephant conflicts (Figure 5 b, $r_s = 0.57$, P = 0.006, df = 23). A univariate linear regression model showed that variation in elephant conflicts explained 19.3% ($F_{1,20} = 4.79$, $P = 0.04$) of elephant mortalities in Tsavo Ecosystem.

HEC and Livestock numbers

We expected human-elephant conflicts to increase with increasing livestock numbers because of intensifying competition for limiting resources. Our results showed a strong positive relationship between HEC and the number of shoats (sheep and goats; $t = 4.74$, df = 18, $P = 0.001$) and cattle ($t = 5.43$, df = 18, $P = 0.001$) in the Greater Tsavo Ecosystem.

Temporal variation in HWC in the Greater Tsavo ecosystem

Overall HWC trends by year for Greater Tsavo ecosystem.

The Greater Tsavo Ecosystem experienced markedly high HWC incidents annually during 1995 - 2017. The annual conflict totals averaged 1,696.6 ± 553.8 (range 724 - 2,008). Reported conflicts were the fewest ($n = 724$) in 1998, the highest ($n = 2541$) in 2008 and increased strongly linearly from 1995 to 2017 ($r^2 = 0.716$, $P = 0.001$, Figure 5 c).

Seasonal variation in HWC incidents.

We expected conflicts to mirror rainfall seasonality because rainfall is the principal climatic component governing variation in food and water availability and quality for herbivores in savannas (Deshmukh 1984, Boutton et al. 1988, Ogutu et al. 2010, 2014a). As expected, conflicts displayed strong monthly seasonality besides a strong positive average trend during 1995 - 2017 (Figures A. 5, A.6, associated files).

The Unobserved Components Model (UCM) fitted the data well (r^2 = 0.56597, Table A. 5, associated files) and indicated a strong and significant seasonal variation in HWC in the Greater Tsavo Ecosystem. Further, the model showed four other important features of HWC trends: (1) a significant systematic increase in the average level (level) of conflicts over time, (2) a strong positive trend in the conflicts during 1995 - 2017 (Figure 6 a, b and c), (3) a pronounced, non-random and sustained seasonality in the conflicts (Figure 6 d and Tables A.6 and A.7 associated files) and, (4) that the conflicts showed two significant but stochastic or transient cyclical patterns. The cycles had fixed periods but time-varying amplitudes and phases. The primary cycle had a period of 6 months (Figure 6 e) and the secondary cycle had a period of 44.8 months, meaning that the latter patterns recurred after approximately 4-years (Figure 6 f).

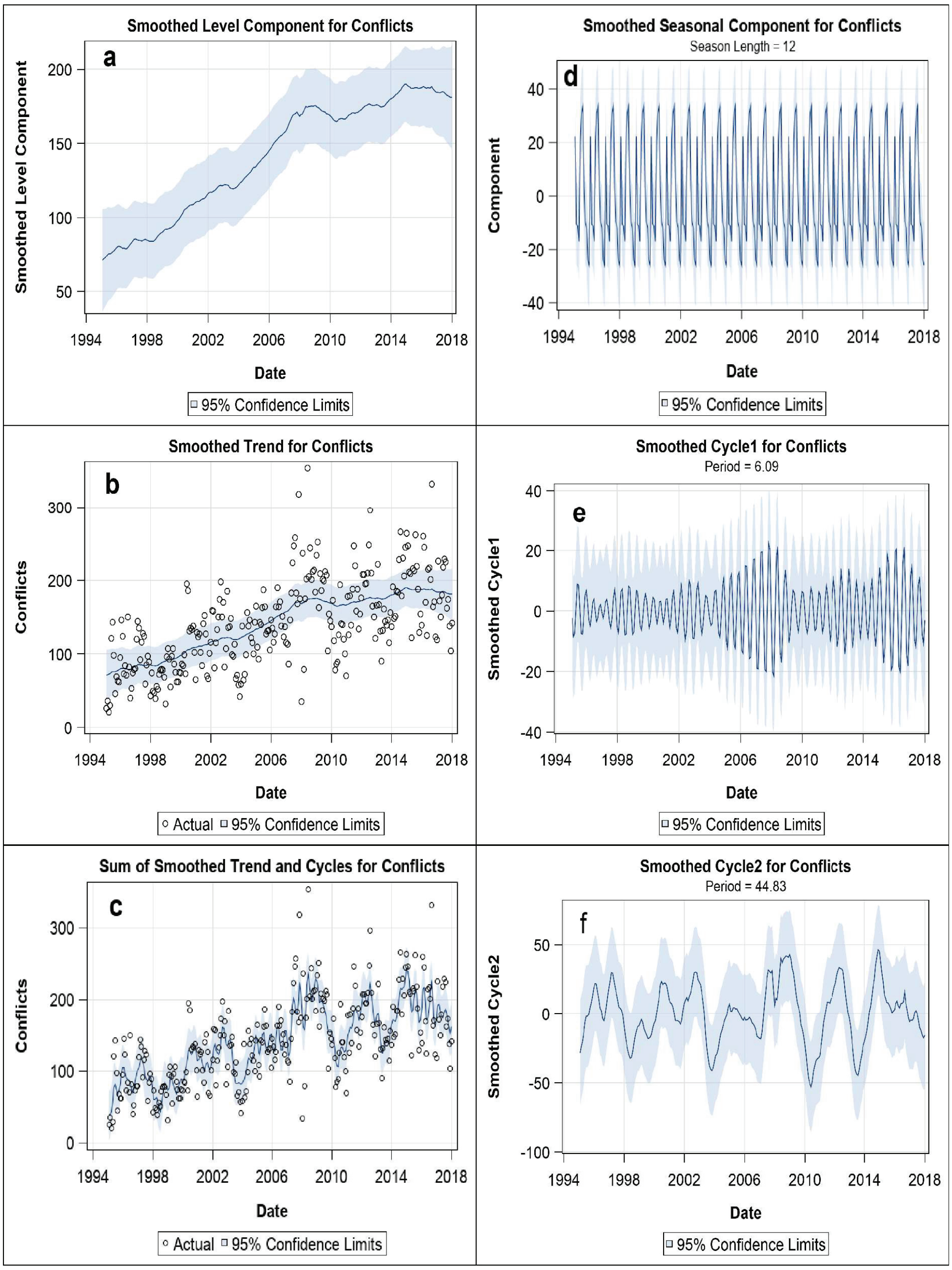

Figure 6: The UCM outputs for HWC series in GTE (1995-2017).

Responses to HWC in the Greater Tsavo Ecosystem

During the 23 years spanning 1995 - 2017, KWS attended to 81.9% of the reported conflict cases (n = 31,976). Of the remaining cases, KWS did not attend to 14.9% (n = 5,812) while the status of the remaining cases (3.2%, n = 1,234) could not be determined from the data. The frequency of cases KWS attended to varied across years and was the lowest (53.9%) for 2003 and the highest (95.1%) for 2008. However the cumulative frequency of conflicts was the lowest in 1998 (Figure 7).

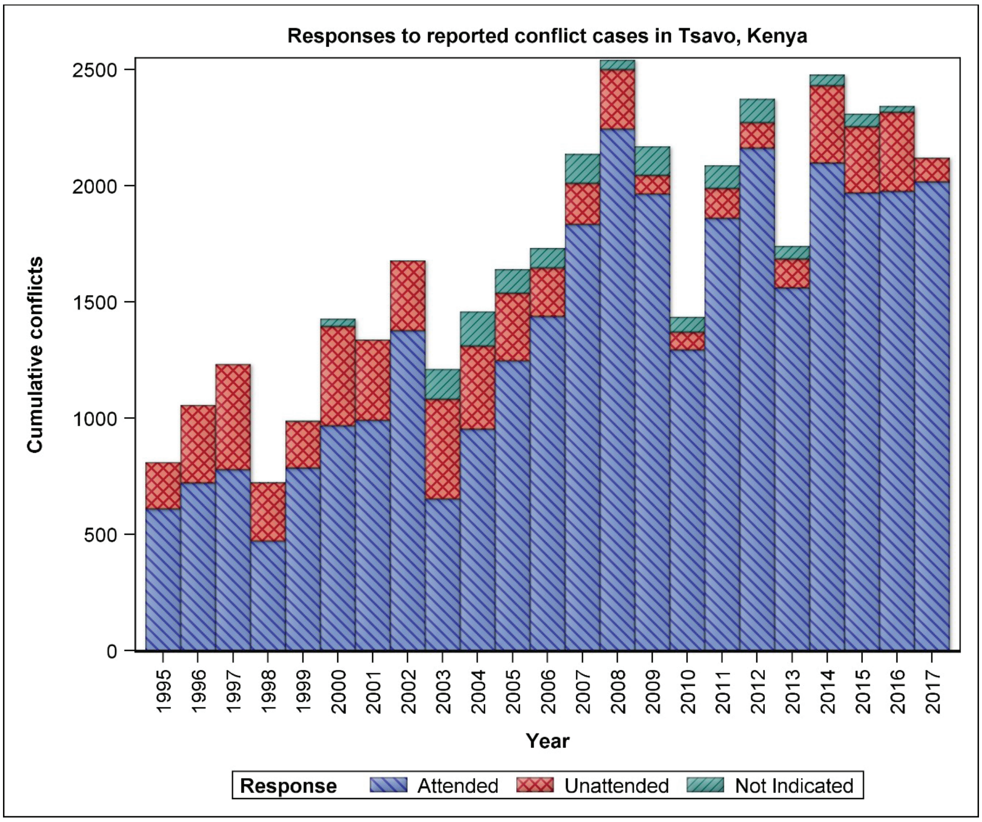

Figure 7: Kenya Wildlife Service responses to HWC cases in the Greater Tsavo Ecosystem during 1995-2017.

Discussion

Frequency and spatial variation in HWC in the Greater Tsavo ecosystem

The Greater Tsavo Ecosystem experienced a myriad of HWC caused by different species at varying intensities (H.1) that were not simply proportional to the areal size of the regions. This implies that factors other than the size of a region determined the occurrence frequency of HWC and the species causing the conflicts. Elephants were responsible for most conflicts in the GTE. Taveta (third smallest region) followed by Rombo (second smallest region) reported most of the cases attributed to the elephant. Thus, the Taveta region is an HEC hotspot (H1.1) in Tsavo. HWC thus reflect the rich wildlife diversity and the large number and activities of humans in the Greater Tsavo Ecosystem.

Two important developments appear responsible for increased conflicts involving the elephant and other large herbivores such as buffalo, hippo, zebra and giraffe in Tsavo. First, human population growth in Taveta, Rombo and Kibwezi may be responsible for the high HEC conflicts in these regions. Between 1989 and 2017, human population size in the Greater Tsavo Ecosystem grew by 62.3%, greatly increasing the pressure on natural resources, agricultural intensification and land fragmentation. The changes degrade and reduce wildlife habitats (Ogutu et al. 2014a, Messmer 2000), thus accentuating the frequency and intensity of human-wildlife conflicts. In similar studies in Nepal (Acharya, Paudel, Neupane, and Köhl 2016) and India (Gubbi, Swaminath, Poornesha, Bhat, and Raghunath 2014), conflicts were higher in settled areas where human population was high.

Second, increasing elephant population size in the Greater Tsavo Ecosystem is partly responsible for the increase in HEC in Tsavo. Tsavo is a water-deficient region (Patterson et al. 2004) and often experiences prolonged droughts that are increasing in frequency and intensity due to climate change (Ogutu et al. 2016). The trend of increasing elephant population size and contemporaneous decrease in food and water resources increases the pressure falling on these resources, forcing elephants to wander more frequently outside the PA. Besides, the large sisal plantations and irrigated schemes bordering the Tsavo PA provide nutritive food that attracts wildlife (Røskaft et al. 2014, Kumar, Bargali, David, and Edgaonkar 2017), accentuating conflicts. Reduced rains may also have led to reduced agriculture in the Taveta region, leading, in turn, to fewer crop raiding than human attack incidents. Thus, these two factors (increasing human and elephant population size) seem to be exerting immense pressures on resources in the smaller regions, including Taveta and Rombo.

We expected the construction of fences in the Taveta and Rombo regions (Figure 1) to be accompanied by a corresponding reduction in HEC but this was not the case. One plausible explanation for this is fence-breaking by elephants (Thouless and Sakwa 1995). The fences were apparently effective in preventing crop raiding but not in protecting humans from attacks by elephants, which have been on the rise in Taveta and Bachuma regions. Further, some of the fences were only recently constructed and hence their impact may not yet be evident. Herders also vandalize fences to illegally access pasture and graze their livestock in the parks and this means that maintenance (Gubbi et al. 2014) of fences is important. Increased livestock numbers in the GTE have resulted in increased HWC due to competition for water and forage (Ogutu et al. 2016). The elephant corridors in the Taveta region may not have been completely blocked, allowing elephants to still find their way through this region. Future work should thus evaluate the effectiveness of the fences put up by KWS in reducing HWC.

HWC conflicts cause immense socio-economic (Kanga et al. 2012), physical, and psychological losses. In the Greater Tsavo Ecosystem, the small-scale farmers suffer considerable losses to crop raiding (H1.2) by elephants, the most frequent conflict type. Further, it is not uncommon to lose a family member, entire livestock herd or other property through HWC. This explains why higher number of people felt threatened in four of the six regions of the GTE including Taveta, Bachuma, Galana, and Kibwezi regions. Thus, due to high species diversity in the GTE, conflicts caused by other species like primates, carnivores and herbivores (buffalo and hippopotamus) consistent with other studies (Kanga et al. 2012, Patterson et al. 2004, Smith and Kasiki 2000) are quite significant (H2). The local communities are vulnerable to HWC because they are too poor to afford expensive HWC prevention methods, such as effective fencing.

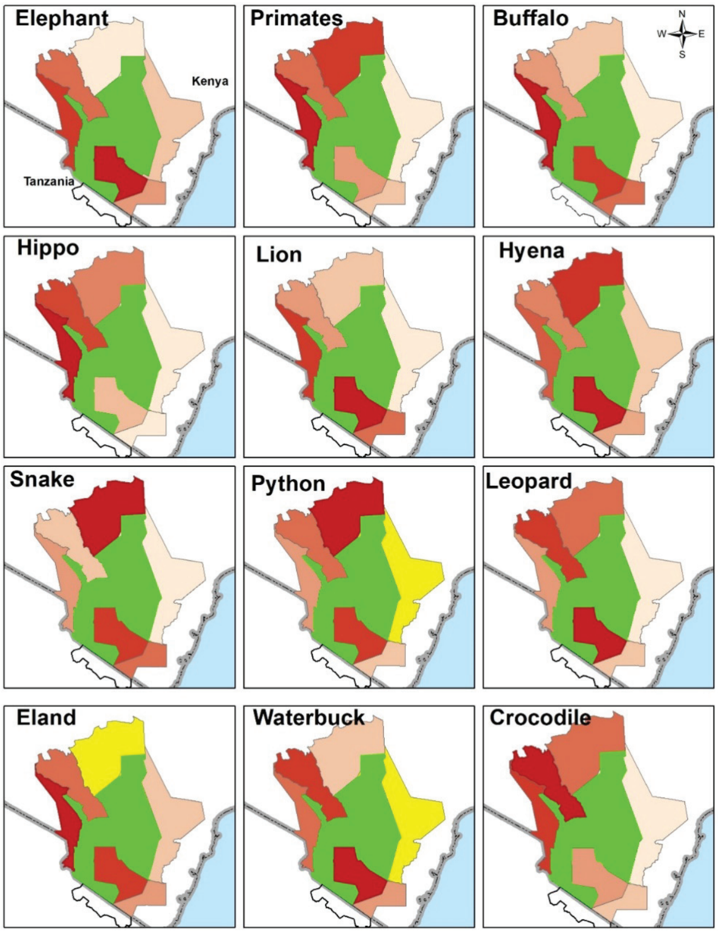

Figure 8: Map showing the conflict incidents for the first 12 species in the six regions of the Greater Tsavo Ecosystem in decreasing order (top left to top right) of contribution to the overall HWC. Darker red colors mean higher incidents and lighter shades indicate fewer HWC incidents. Yellow regions had no reported conflict incidents for the species, while the green region is Tsavo PA and the light blue region is the Indian Ocean.

There were evident spatial distinctions in the distribution of wildlife species causing HWC around the Greater Tsavo Ecosystem, including large carnivores. That Taveta and Rombo regions accounted for close to 70% (n = 26,319) of all the conflicts in the GTE can be attributed to the major land uses in both regions. Large mixed livestock-wildlife ranches are the major land use in the Taveta region. As a result, livestock depredation is common in this region because wild prey are more difficult to hunt than domestic animals (Patterson et al. 2004), and its proximity to the PA may be contributing to increased conflicts. Even though, our results showed weak relationship between PA boundary length and region consistent with other Gubbi et al. (2014). Thus, whilst pastoralism was largely compatible with conservation, large livestock numbers or reduction of the natural prey base can lead to more frequent HWC incidents, making predator killing unsustainable. Nonhuman primates are a major source of conflict (Hill 1997, Syombua 2013 - PhD Thesis unpublished, Gross et al. 2018) and were a common cause in the Rombo region where horticulture provides succulent food for primates. Serious snake and python conflicts threaten human life and livelihoods in the arid Mutomo region with very scarce water supply. This region still contains more intact and less developed wilderness areas and hosts some of the most poisonous and large snakes in Kenya. Thus, the nature of conflict species may indicate conflict outcome, such as fewer human threats in Rombo, but higher human injuries in Mutomo regions.

Human-elephants conflicts and elephant mortalities

HWC conflicts pose serious threats to the survival and conservation of many wildlife species, including the vulnerable African savanna elephant (IUCN 2008). Our results show that increased human elephant conflicts lead to more elephant mortalities (H1.3) through statesanctioned problem animal control programs (Wildlife Act 2013) and defense of property and human livelihood by communities. Both these actions serve to pacify aggrieved communities as well as eliminate habitual human killers from the region(s).

Temporal and seasonal dynamics of HWC in the Greater Tsavo Ecosystem

Our trend analysis indicates that human-wildlife conflict in the Greater Tsavo Ecosystem and its environs is a perennial problem and has steadily increased from 1995 to 2017. Further, HWC in the Greater Tsavo Ecosystem shows strong seasonality, consistent with the prediction of H3 that the number, type and location of HWC exhibit strong seasonal fluctuations in the Greater Tsavo Ecosystem. Reliable knowledge of seasonality in HWC can thus aid the development of HWC mitigation measures. For instance, control of conflicts caused by primates can target the period when crops ripen and conflicts peak (Hill 2000, Gross et al. 2018). HWC decreased during 1997 - 1998 and for a period thereafter likely because of high food and water availability associated with the exceptional rains during the striking El Niño Southern Oscillation events (Saji et al. 1999, Ogutu et al. 2008). HWC peaked in the Tsavo region in 2008 - 2009 characterized by a severe drought in Kenya (Ogutu et al. 2014b). The trend of declining rainfall in the ecosystem is likely forcing animals to wander more widely in search of food and water and to come into more frequent contacts with people and livestock, resulting in more frequent conflicts.

Human-wildlife conflict resolution and responses by KWS

The majority of HWC incidents were attended to by KWS staff. Such responses by KWS include visiting the area to drive the wildlife back to the park, e.g., scaring by use of vehicles and thunder flashes, laying traps to catch elusive carnivores or camping over night to keep watch. This is in addition to preventive measures including the construction of fences that separate wildlife from human-inhabited areas. This is consistent with the expectation of H4 of an increasing trend in responses to HWC incidents over time. Nevertheless, there was considerable inter-annual variation in the frequency of responses to HWC, possibly indicating temporal variability in the availability of such resources as vehicles which are necessary for effectively responding to HWC. Over time, KWS has been actively expanding its ranger force to effectively deal with wildlife issues, including HWC and poaching. Timely response to HWC is essential to sustaining the goodwill and support of local communities for conservation but is becoming increasingly more expensive as conflicts increase over time.

Management implications

1. Increasing human population, livestock numbers and infrastructure are leading to habitat degradation and loss for wildlife. Sustainable HWC conflict resolution in the Greater Tsavo Ecosystem and possibly elsewhere would thus require developing and implementing measures that seek to enhance wildlife conservation benefits to the local communities. Such measures may include re-introduction of consumptive utilization of wildlife that was abolished in Kenya in 2002 (Kameri-Mbote 2005). Elsewhere, community based conservancies are proving to be effective tools of biodiversity conservation in Maasai Mara and other parts of Kenya (Msoffe et al. 2019).

2. Multiple wildlife species are responsible for HWC involving people, their livestock, crops and property in the Greater Tsavo Ecosystem. This complicates mitigation of HWC, but spatial stratification should be used when developing mitigation measures to account for regional

distinctions in conflict intensity, types and outcomes. This would enable the development of targeted mitigation measures focusing, for instance, on HWC involving snakes and pythons in the remote Mutomo region, such as provision of adequate antivenom drugs in local dispensaries

3. Multiple mitigation strategies are needed to address the multiplicity of species, types and outcomes of HWC. Conventional HWC mitigation strategies, such as problem animal control (PAC), scaring, keeping guard dogs, etc., are preventive strategies and cannot effectively address certain types of conflicts such as those involving nonhuman primates that need a combination of many of these methods at any given time.

4. Carefully planned and managed provision of artificial watering points for wildlife during dry periods and managing protected areas to sustain functional heterogeneity may help reduce the probability of wildlife wandering to areas outside of the PA and therefore limit interactions between wildlife and people in the dry season. These artificial water points should be sufficiently widely separated spatially to minimize potential deleterious effects on vegetation as documented for the Kruger National Park in South Africa (Owen-Smith 1996, Owen-Smith, Chirima, Macandza, and Le Roux 2012). This can allow wildlife to use the PA habitat in a way that promotes functional heterogeneity and therefore retain more wildlife inside the PA. Further, and as a complement, land use zone planning is important to minimize habitat fragmentation outside the protected areas and to allow continuing movement of wildlife between the PA and adjacent conservancies, whilst minimizing interactions with farming regions that contain attractive forage.

5. The Taveta region will almost certainly continue to experience more HEC than the other regions adjoining the PA of Tsavo Ecosystem because of its proximity to the Tsavo PA, large and growing elephant population and wildlife ranches (Graham et al. 2012). Therefore

wildlife management, e.g. by KWS, and conservation non-governmental organizations (NGO) should consider channeling more resources to this important region.

6. Finally, HWC monitoring databases should be enhanced to capture more useful details such as by specifying why an animal was killed during conflicts, e.g., as part of problem animal control, retaliatory killing by local communities, or to make a political statement to help guide the development of targeted response strategies. Further, the databases should provide a breakdown of the nature and timeliness of responses undertaken by wildlife managers in response to complaints about human-wildlife conflicts.

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Associated files

Article title
Spatial and temporal dynamics of human-wildlife conflicts in the Greater Tsavo Ecosystem, Kenya.

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Table A. 1. The composition of the six groups of species of conflict animals used in this study.

No	Species or group	Composition	†*n*
1	Primates	Baboons	3813
		Monkeys	667
2	Snakes	Snakes	788
		Puff adder	1
3	Antelopes	Antelope	3
		Bush buck	35
		Kirk's dik-dik	5
		Common duiker	1
		Grant's gazelle	9
		Hartebeest	2
		Impala	68
		Lesser kudu	3
		Reedbuck	3
		Thomson's gazelle	1
		Wildebeest	25
4	Pigs	Bush pig	110
		Giant forest hog	2
		Warthog	28
		Wild pig	13
5	Small carnivores	Civet	1
		Honey badger	19
		Jackal	4
		Mongoose	8
		Serval cat	23
6	Others	Bees	5
		Birds	24

No	Species or group	Composition	†*n*
		Frog	1
		Monitor lizard	1
		Porcupine	1
		Scorpion	10
		Tortoise	2
		squirrel	3
		Automobile	7
		Unknown	70

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Table A. 2. Common English names and scientific names of species involved in conflicts in Greater Tsavo Ecosystem(GTE).

Where it was not possible to reliably identify individuals to species, the lowest possible taxonomic grouping was used.

No	Common English name of species	*Scientific name of species*
1	Antelope (assorted)	*Bovidae family*
2	Baboons	*Papio spp.*
3	Bees	*Apis mellifera scutellata*
4	Birds	Class: Aves
5	Buffalo	*Syncerus caffer*
6	Bushbuck	*Tragelaphus scriptus*
7	Bush pig	*Potamochoerus larvatus*
8	Cheetah	*Acinonyx jubatus*
9	Civet	family *Viverridae*
10	Common duiker	*Sylvicapra grimmia*
11	Crocodile	*Crocodylus niloticus*
12	Eland	*Taurotragus oryx*
13	Elephant	*Loxodonta africana*
14	Frog	Order Anura
15	Giant Forest hog	Family Suidae
16	Giraffe	*Giraffa camelopardalis*
17	Grant's gazelle	*Gazella granti*
18	Hartebeest	*Alcelaphus buselaphus*
19	Hippopotamus	*Hippopotamus amphibius*
20	Honey badger	*mellivora capensis*
21	Impala	*Aepyceros melampus*

No	Common English name of species	*Scientific name of species*
22	Jackal	genus *canis*
23	Kirk's dik-dik	*Madoqua kirkii*
24	Leopard	*Panthera pardus*
25	Lesser kudu	*Tragelaphus imberbis*
26	Lion	*Panthera leo*
27	Mongoose	family *herpestidae*
28	Monitor lizard	Genus: Varanus
29	Monkeys	*Cercopithecus spp.*
30	Pigs (assorted)	*Suidae family*
31	Porcupine	*Apis mellifera scutellata*
32	Primates	*Family cercopithecidae*
33	Puff adder	*Bitis arietans*
34	Python	*Python sebae*
35	Reedbuck	*Redunca fulvorufula*
36	Scorpion	bothrirurids
37	Serval cat	*Leptailurus serval*
38	Snake	*Serpentes suborder*
39	Spotted hyena	*Crocuta crocuta*
40	squirrel	sciurids
41	Thomson's gazelle	*Gazella thomsonii*
42	Tortoise	Family Testudinidae
43	Warthog	*Phacochoerus africanus*
44	Waterbuck	*Kobus ellipsiprymnus*
45	Wild dog	*Lycaon pictus*
46	Wild pig	*Sus scrofa*
47	Wildebeest	*Connochaetes taurinus*
48	Zebra	*Equus quagga*

Table A. 3. Chi-squared tests of the null hypothesis that the percentage contribution of each species or species group to the total conflicts does not differ among the six regions of the Greater Tsavo Ecosystem, DF = 5 for all the chi-square tests.

Rank	Species	Percentage contribution by region						Overall contribution (%)	Chi-square test	
		Bachuna	Taveta	Rombo	Kibwezi	Mutomo	Galana		χ^2_5	P-value
1	Elephant	75.1	73.2	49.4	74.4	6.2	80.0	61.6	5850.1	<0.001
2	Primates	2.4	2.3	23.4	8.0	26.6	0.5	11.5	3853	<0.001
3	Buffalo	9.4	5.7	7.4	4.0	5.9	8.3	6.2	145.4	<0.001
4	Lion	6.1	6.8	2.1	1.8	3.6	6.6	4.2	489.7	<0.001
5	Hippo	0.1	0.2	10.4	1.9	3.2	0.5	3.8	2102.8	<0.001
6	Hyena	0.9	2.4	1.8	1.4	8.8	0.5	2.4	573.5	<0.001
7	Snake	2.0	1.2	0.4	0.4	17.4	1.7	2.0	3546.6	<0.001
8	Python	0.4	1.2	0.1	0.3	17.9	0.0	1.8	4321.9	<0.001
9	Leopard	0.2	2.1	0.7	2.2	4.7	0.2	1.7	280.5	<0.001
10	Eland	0.7	0.3	2.1	0.6	0.0	0.5	0.9	286.7	<0.001
11	Waterbuck*[1]	0.1	2.1	0.0	0.2	0.0	0.0	0.8	432.7	<0.001
11	Crocodile*[1]	0.1	0.1	0.7	2.2	2.6	0.2	0.8	373.7	<0.001
13	Cheetah*[2]	0.6	0.8	0.1	0.4	0.2	0.0	0.4	71.6	<0.001
13	Antelope*[2]	0.3	0.2	0.4	0.9	0.1	0.7	0.4	62.1	<0.001
13	Pigs*[2]	0.6	0.1	0.3	0.9	0.7	0.2	0.4	92.6	<0.001
16	Others*[3]	0.6	0.3	0.2	0.2	1.1	0.0	0.3	67.7	<0.001
16	Zebra*[3]	0.4	0.5	0.3	0.1	0.0	0.0	0.3	27.3	<0.001
18	Small carnivores*[4]	0.0	0.2	0.1	0.1	0.5	0.0	0.1	38.4	<0.001
18	Wild dog*[4]	0.0	0.1	0.0	0.1	0.3	0.0	0.1	25.9	<0.001
18	Giraffe*[4]	0.1	0.1	0.0	0.0	0.0	0.0	0.1	23.9	<0.001

*[1-4]Overall percentage contribution to human-wildlife conflicts was equal for these species or species groups.

Table A. 4. Human wildlife conflicts by species or species groups, conflict outcomes and regions of the Greater Tsavo Ecosystem. Human wildlife conflicts (crop raiding, attacks on humans, livestock attacks and property damage) and their four outcomes (nothing happened to humans, humans felt threatened, were injured or killed) during 1995-2017 are summarized for the Greater Tsavo Ecosystem. n is the number of incidents, % is the percentage contribution of each species or species group to the outcome per region.

	Region	**Bachuma**		**Taveta**		**Rombo**		**Kibwezi**		**Mutomo**		**Galana**		**Total**	
Species	Conflict outcome	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Antelope	Nothing happened to human	7	87.50	31	96.88	47	95.92	60	100.00	1	33.33	3	100.00	149	96.13
	Human felt threatened	0	0.00	1	3.13	0	0.00	0	0.00	0	0.00	0	0.00	1	0.65
	Human were injured	1	12.50	0	0.00	2	4.08	0	0.00	2	66.67	0	0.00	5	3.23
		8	**100.00**	**32**	**100.00**	**49**	**100.00**	**60**	**100.00**	**3**	**100.00**	**3**	**100.00**	**155**	**100.00**
Primates	Nothing happened to human	63	90.00	262	80.12	2735	96.71	487	92.06	703	97.10	2	100.00	4252	94.91
	Human felt threatened	7	10.00	57	17.43	86	3.04	42	7.94	10	1.38	0	0.00	202	4.51
	Human were injured	0	0.00	8	2.45	6	0.21	0	0.00	11	1.52	0	0.00	25	0.56
	Human were killed	0	0.00	0	0.00	1	0.04	0	0.00	0	0.00	0	0.00	1	0.02
		70	**100.00**	**327**	**100.00**	**2828**	**100.00**	**529**	**100.00**	**724**	**100.00**	**2**	**100.00**	**4480**	**100.00**
Buffalo	Nothing happened to human	50	18.12	231	28.52	462	51.97	160	61.07	30	18.63	12	35.29	945	38.86
	Human felt threatened	187	67.75	464	57.28	371	41.73	91	34.73	114	70.81	19	55.88	1246	51.23
	Human were injured	36	13.04	98	12.10	47	5.29	9	3.44	12	7.45	2	5.88	204	8.39
	Human were killed	3	1.09	17	2.10	9	1.01	2	0.76	5	3.11	1	2.94	37	1.52
		276	**100.00**	**810**	**100.00**	**889**	**100.00**	**262**	**100.00**	**161**	**100.00**	**34**	**100.00**	**2432**	**100.00**
Pigs	Nothing happened to human	18	100.00	14	82.35	29	82.86	60	96.77	20	100.00	1	100.00	142	92.81
	Human felt threatened	0	0.00	2	11.76	0	0.00	2	3.23	0	0.00	0	0.00	4	2.61
	Human were injured	0	0.00	1	5.88	6	17.14	0	0.00	0	0.00	0	0.00	7	4.58
		18	**100.00**	**17**	**100.00**	**35**	**100.00**	**62**	**100.00**	**20**	**100.00**	**1**	**100.00**	**153**	**100.00**
Cheetah	Nothing happened to human	12	70.59	91	85.05	11	84.62	20	80.00	5	100.00		0.00	139	83.23

	Region	Bachuma		Taveta		Rombo		Kibwezi		Mutomo		Galana		Total	
	Human felt threatened	2	11.76	14	13.08	1	7.69	5	20.00	0	0.00		0.00	22	13.17
	Human were injured	3	17.65	2	1.87	1	7.69	0	0.00	0	0.00		0.00	6	3.59
		17	**100.00**	**107**	**100.00**	**13**	**100.00**	**25**	**100.00**	**5**	**100.00**		**0.00**	**167**	**100.00**
Crocodile	Nothing happened to human	0	0.00	3	18.75	33	40.74	64	43.84	10	14.08	0	0.00	110	34.48
	Human felt threatened	2	50.00	9	56.25	37	45.68	49	33.56	16	22.54	1	100.00	114	35.74
	Human were injured	1	25.00	3	18.75	9	11.11	20	13.70	33	46.48	0	0.00	66	20.69
	Human were killed	1	25.00	1	6.25	2	2.47	13	8.90	12	16.90	0	0.00	29	9.09
		4	**100.00**	**16**	**100.00**	**81**	**100.00**	**146**	**100.00**	**71**	**100.00**	**1**	**100.00**	**319**	**100.00**
Eland	Nothing happened to human	20	95.24	42	93.33	255	98.84	37	100.00		0.00	2	100.00	356	98.07
	Human felt threatened	1	4.76	3	6.67	3	1.16	0	0.00		0.00	0	0.00	7	1.93
		21	**100.00**	**45**	**100.00**	**258**	**100.00**	**37**	**100.00**		**0.00**	**2**	**100.00**	**363**	**100.00**
Elephant	Nothing happened to human	1106	50.05	4611	44.22	3715	62.24	2607	52.90	53	31.36	180	54.71	12272	51.07
	Human felt threatened	1060	47.96	5578	53.50	2152	36.05	2299	46.65	111	65.68	143	43.47	11343	47.20
	Human were injured	23	1.04	130	1.25	61	1.02	19	0.39	5	2.96	4	1.22	242	1.01
	Human were killed	21	0.95	108	1.04	41	0.69	3	0.06	0	0.00	2	0.61	175	0.73
		2210	**100.00**	**10427**	**100.00**	**5969**	**100.00**	**4928**	**100.00**	**169**	**100.00**	**329**	**100.00**	**24032**	**100.00**
Giraffe	Nothing happened to human	1	33.33	9	50.00	1	100.00		0.00		0.00		0.00	11	50.00
	Human felt threatened	2	66.67	8	44.44	0	0.00		0.00		0.00		0.00	10	45.45
	Human were injured	0	0.00	1	5.56	0	0.00		0.00		0.00		0.00	1	4.55
		3	**100.00**	**18**	**100.00**	**1**	**100.00**		**0.00**		**0.00**		**0.00**	**22**	**100.00**
Hippo	Nothing happened to human	0	0.00	13	44.83	1031	82.35	71	57.26	75	85.23	0	0.00	1190	79.49
	Human felt threatened	2	100.00	14	48.28	211	16.85	45	36.29	10	11.36	2	100.00	284	18.97
	Human were injured	0	0.00	2	6.90	9	0.72	4	3.23	1	1.14	0	0.00	16	1.07
	Human were killed	0	0.00	0	0.00	1	0.08	4	3.23	2	2.27	0	0.00	7	0.47
		2	**100.00**	**29**	**100.00**	**1252**	**100.00**	**124**	**100.00**	**88**	**100.00**	**2**	**100.00**	**1497**	**100.00**
Hyena	Nothing happened to human	19	73.08	324	93.10	188	87.04	77	83.70	196	81.33	2	100.00	806	87.14
	Human felt threatened	7	26.92	20	5.75	24	11.11	11	11.96	35	14.52	0	0.00	97	10.49
	Human were injured	0	0.00	4	1.15	4	1.85	3	3.26	8	3.32	0	0.00	19	2.05

	Region	Bachuma		Taveta		Rombo		Kibwezi		Mutomo		Galana		Total	
	Human were killed	0	0.00	0	0.00	0	0.00	1	1.09	2	0.83	0	0.00	3	0.32
		26	**100.00**	**348**	**100.00**	**216**	**100.00**	**92**	**100.00**	**241**	**100.00**	**2**	**100.00**	**925**	**100.00**
Leopard	Nothing happened to human	4	80.00	226	75.08	79	87.78	117	79.59	104	81.25	1	100.00	531	79.02
	Human felt threatened	1	20.00	59	19.60	10	11.11	27	18.37	20	15.63	0	0.00	117	17.41
	Human were injured	0	0.00	15	4.98	1	1.11	3	2.04	4	3.13	0	0.00	23	3.42
	Human were killed	0	0.00	1	0.33	0	0.00	0	0.00	0	0.00	0	0.00	1	0.15
		5	**100.00**	**301**	**100.00**	**90**	**100.00**	**147**	**100.00**	**128**	**100.00**	**1**	**100.00**	**672**	**100.00**
Lion	Nothing happened to human	152	84.44	812	84.32	206	79.54	84	71.79	75	75.76	21	77.78	1350	82.07
	Human felt threatened	21	11.67	132	13.71	38	14.67	30	25.64	22	22.22	4	14.81	247	15.02
	Human were injured	5	2.78	16	1.66	12	4.63	2	1.71	2	2.02	2	7.41	39	2.37
	Human were killed	2	1.11	3	0.31	3	1.16	1	0.85	0	0.00	0	0.00	9	0.55
		180	**100.00**	**963**	**100.00**	**259**	**100.00**	**117**	**100.00**	**99**	**100.00**	**27**	**100.00**	**1645**	**100.00**
Python	Nothing happened to human	2	16.67	30	17.34	5	33.33	5	25.00	56	11.45		0.00	98	13.82
	Human felt threatened	0	0.00	35	20.23	9	60.00	14	70.00	43	8.79		0.00	101	14.25
	Human were injured	9	75.00	99	57.23	1	6.67	1	5.00	346	70.76		0.00	456	64.32
	Human were killed	1	8.33	9	5.20	0	0.00	0	0.00	44	9.00		0.00	54	7.62
		12	**100.00**	**173**	**100.00**	**15**	**100.00**	**20**	**100.00**	**489**	**100.00**		**0.00**	**709**	**100.00**
Snake	Nothing happened to human	1	1.69	9	5.11	3	6.67	2	7.14	8	1.69	0	0.00	23	2.92
	Human felt threatened	1	1.69	21	11.93	5	11.11	2	7.14	8	1.69	0	0.00	37	4.69
	Human were injured	52	88.14	138	78.41	36	80.00	22	78.57	431	90.93	5	71.43	684	86.69
	Human were killed	5	8.47	8	4.55	1	2.22	2	7.14	27	5.70	2	28.57	45	5.70
		59	**100.00**	**176**	**100.00**	**45**	**100.00**	**28**	**100.00**	**474**	**100.00**	**7**	**100.00**	**789**	**100.00**
Waterbuck	Nothing happened to human	3	100.00	294	99.32	6	100.00	15	93.75	1	100.00		0.00	319	99.07
	Human felt threatened	0	0.00	2	0.68	0	0.00	1	6.25	0	0.00		0.00	3	0.93
		3	**100.00**	**296**	**100.00**	**6**	**100.00**	**16**	**100.00**	**1**	**100.00**		**0.00**	**322**	**100.00**
Wild dog	Nothing happened to human	1	100.00	15	71.43	4	100.00	4	100.00	8	88.89		0.00	32	82.05
	Human felt threatened	0	0.00	2	9.52	0	0.00	0	0.00	0	0.00		0.00	2	5.13

	Region	Bachuma		Taveta		Rombo		Kibwezi		Mutomo		Galana		Total	
	Human were injured	0	0.00	4	19.05	0	0.00	0	0.00	1	11.11		0.00	5	12.82
		1	**100.00**	**21**	**100.00**	**4**	**100.00**	**4**	**100.00**	**9**	**100.00**		**0.00**	**39**	**100.00**
Zebra	Nothing happened to human	7	63.64	58	87.88	35	97.22	9	100.00		0.00		0.00	109	89.34
	Human felt threatened	2	18.18	8	12.12	1	2.78	0	0.00		0.00		0.00	11	9.02
	Human were injured	2	18.18	0	0.00	0	0.00	0	0.00		0.00		0.00	2	1.64
		11	**100.00**	**66**	**100.00**	**36**	**100.00**	**9**	**100.00**		**0.00**		**0.00**	**122**	**100.00**
Small carnivores	Nothing happened to human		0.00	14	53.85	6	66.67	4	66.67	7	50.00		0.00	31	56.36
	Human felt threatened		0.00	2	7.69	2	22.22	1	16.67	1	7.14		0.00	6	10.91
	Human were injured		0.00	10	38.46	1	11.11	1	16.67	6	42.86		0.00	18	32.73
			0.00	**26**	**100.00**	**9**	**100.00**	**6**	**100.00**	**14**	**100.00**		**0.00**	**55**	**100.00**
Others	Nothing happened to human	16	88.89	21	50.00	24	100.00	11	100.00	20	68.97		0.00	92	74.19
	Human felt threatened	2	11.11	17	40.48	0	0.00	0	0.00	1	3.45		0.00	20	16.13
	Human were injured	0	0.00	4	9.52	0	0.00	0	0.00	6	20.69		0.00	10	8.06
	Human were killed	0	0.00	0	0.00	0	0.00	0	0.00	2	6.90		0.00	2	1.61
		18	**100.00**	**42**	**100.00**	**24**	**100.00**	**11**	**100.00**	**29**	**100.00**		**0.00**	**124**	**100.00**
Total	Nothing happened to human	1482	50.34	7110	49.93	8875	73.47	3894	58.80	1372	50.35	224	54.50	22957	58.83
	Human felt threatened	1297	44.06	6448	45.28	2950	24.42	2619	39.54	391	14.35	169	41.12	13874	35.55
	Human were injured	132	4.48	535	3.76	196	1.62	84	1.27	868	31.85	13	3.16	1828	4.68
	Human were killed	33	1.12	147	1.03	58	0.48	26	0.39	94	3.45	5	1.22	363	0.93
	Grand Total	**2944**	**100.00**	**14240**	**100.00**	**12079**	**100.00**	**6623**	**100.00**	**2725**	**100.00**	**411**	**100.00**	**39022**	**100.00**

Table A. 5. Fit statistics for the Unobserved Components Model (UCM) fitted to the total monthly human-wildlife conflict data spanning 1995-2017.

Fit Statistic	Value
Mean Squared Error	1499.20871
Root Mean Squared Error	38.71962
Mean Absolute Percentage Error	24.20202
Maximum Percent Error	88.7184
R-Square	0.56597
Adjusted R-Square	0.5523
Random Walk R-Square	0.36005
Amemiya's Adjusted R-Square	0.53521

Table A. 6. The estimated variances of the disturbance terms, the variances of the irregular component, damping factor and period of the cycles in the human-wildlife conflict series for the Greater Tsavo Ecosystem during 1995-2017.

Component	Parameter	Estimate	Standard Error	t Value	Approx Pr >|t|
Irregular	Error Variance	797.03062	110.171188	7.23	<0.0001
Level	Error Variance	19.12666	14.4977898	1.32	0.1871
Season	Error Variance	0.00001108	0.00363701	0	0.9976
Cycle_1	Damping Factor	0.96382	0.03711192	25.97	<0.0001
Cycle_1	Period	6.09393	0.18853471	32.32	<0.0001
Cycle_1	Error Variance	11.80217	6.38666202	1.85	0.0646
Cycle_2	Damping Factor	0.92624	0.04348281	21.3	<0.0001
Cycle_2	Period	44.83071	14.1169336	3.18	0.0015
Cycle_2	Error Variance	104.84721	41.5657282	2.52	0.0117

Table A. 7. Significance analysis of components (based on the final state) of the human-wildlife conflicts series for the Greater Tsavo Ecosystem during 1995-2017.

Component	Degrees of Freedom	Chi-Square	Approx Pr >Chi-Square
Irregular	1	1.49	0.2219
Level	1	103	<0.0001
Cycle_1	2	1.18	0.5531
Cycle_2	2	0.94	0.6241
Season	11	77.45	<0.0001

Article title

Spatial and temporal dynamics of human-wildlife conflicts in the Greater Tsavo Ecosystem, Kenya.

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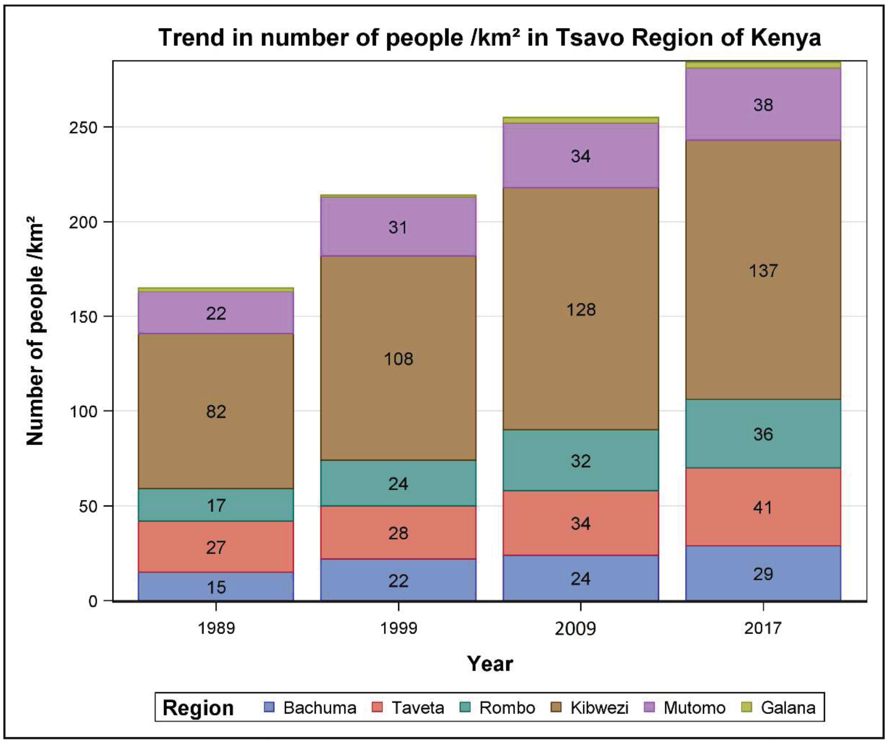

Fig. A. 1: Human population trends in the six regions of the Greater Tsavo Ecosystem

Temporal trend in human population density in each of the six regions around the Tsavo PA from 1989 to 2017 are provided. The corresponding densities for Galana are too small to display (2, 1, 3, 3 people /km^2 for 1989, 1999, 2009 and 2017, respectively) but show that Galana had the lowest human population growth rate and density. Densities for 1989, 1999 and 2009 were derived from actual decadal national censuses but those for 2017 were extrapolated using population growth rates obtained from KNBS (2017).

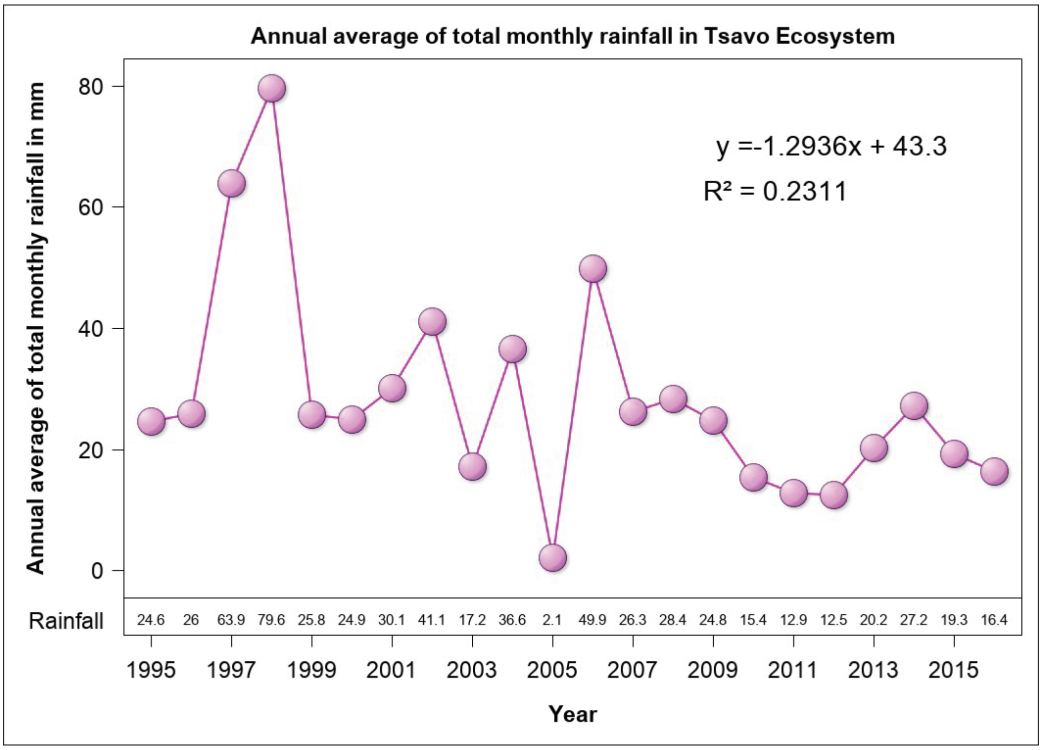

Fig. A. 2: Average total monthly rainfall received in Tsavo (1995-2016). There is a generally decreasing trend in rainfall (Annual average of total monthly rainfall = -1.23 × year + 2624.8, $\boldsymbol{r}^2$ =0.23) during 1995-2016. Notice the exceptionally high El Niño rainfall in 1997-1998.

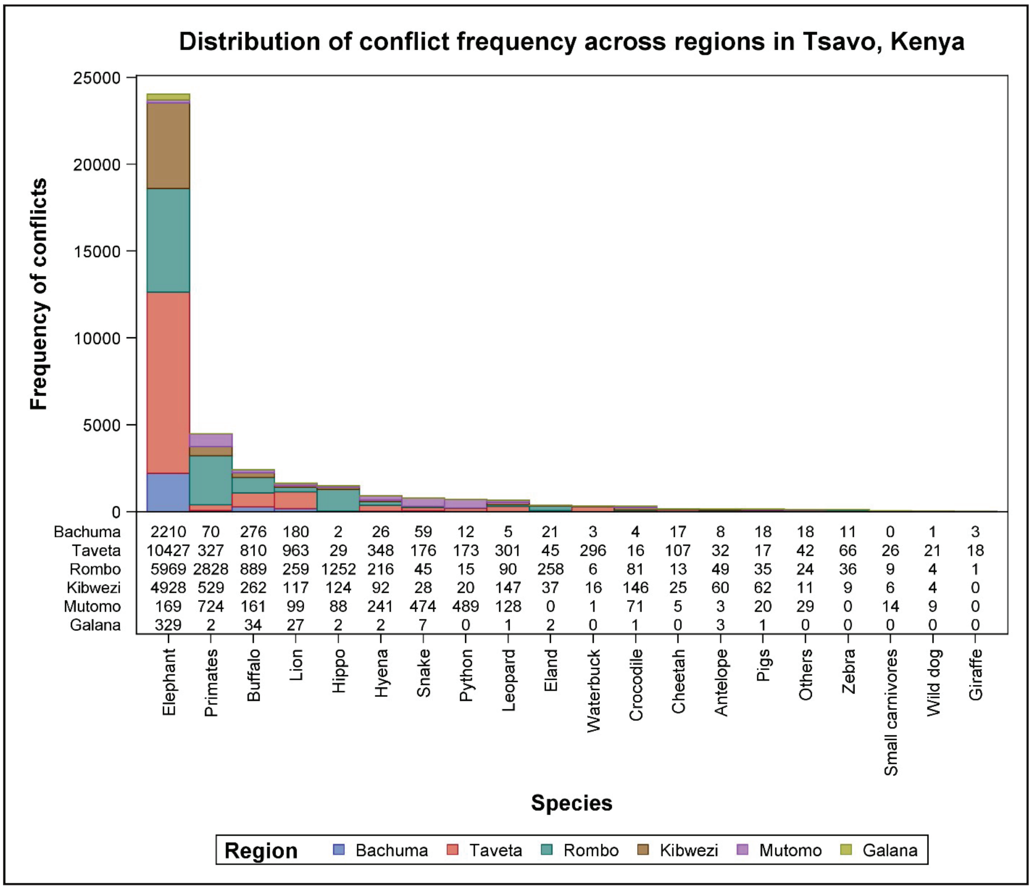

Fig. A. 3: Distribution of human-wildlife conflict incidents for each species or species group across the six regions of the Greater Tsavo Ecosystem (1995-2017).

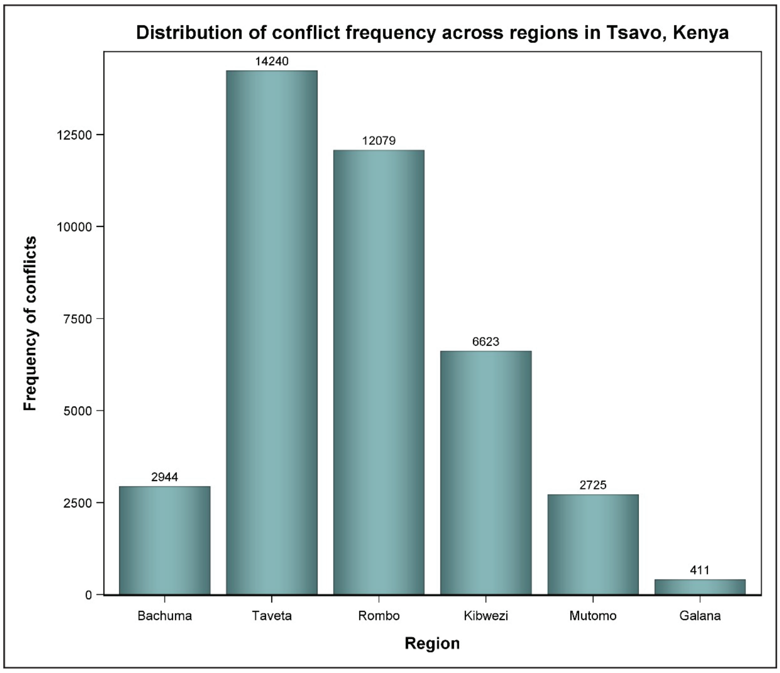

Fig. A. 4: Total number of all human-wildlife conflict incidents for all species in each of the six study regions during 1995-2017.

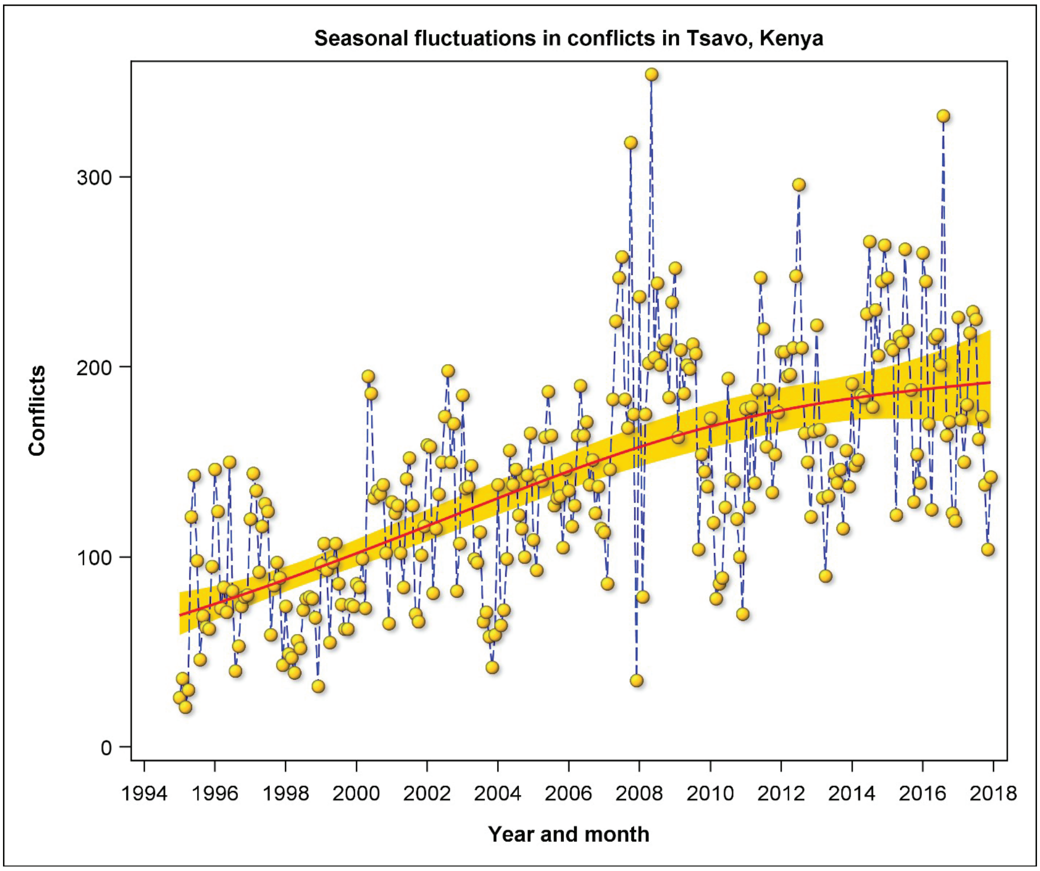

Fig. A. 3: Temporal trend in total monthly conflicts (filled circles), the fitted trend line (red line) and the associated 95% pointwise confidence band for the Greater Tsavo ecosystem during 1995-2017.

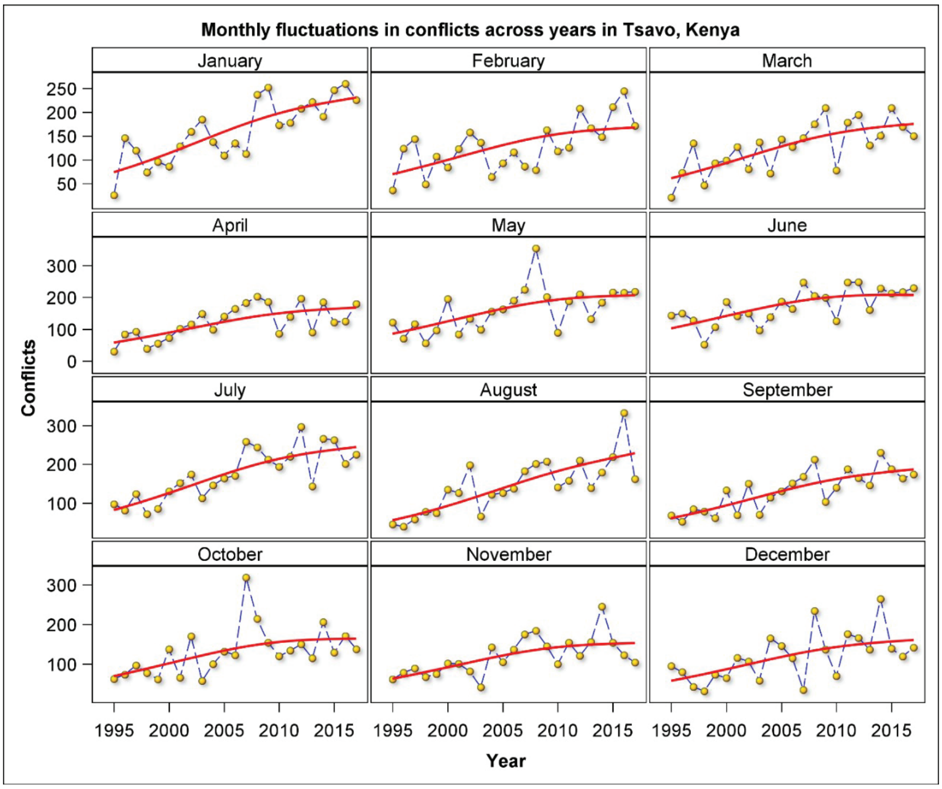

Fig. A. 4: Monthly human wildlife conflict trend for each calendar month for the Tsavo Ecosystem during the period 1995-2017

Paper III

This paper is awaiting publication and is not included in NTNU Open

Paper IV

Trends in compensation for human-wildlife conflict losses in Kenya

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Abstract

Human-wildlife conflicts (HWC) can cause substantial losses. Compensation for such losses is essential to foster positive community attitudes toward wildlife conservation. Monetary compensation for the loss of human life, injury, crop and property damage, or livestock depredation by wildlife is a common strategy for mitigating HWC. We analyzed inter-specific, spatial, inter-annual and seasonal variation in human-wildlife conflicts, conflict outcome and the associated monetary costs of compensation in Kenya during 2007-2016. A total of 18,794 compensation claims were filed with the Kenya National Compensation Scheme (KNCS) during 2007 - 2016. Snakes made the greatest contribution to the total cases (44.8%, n = 8,423), human fatalities (43.1%, n = 614) and human injuries (76.9%, n = 7,772). The elephant was the second leading conflict species (22.3%, n = 4,181) and was responsible for 18.8% (n = 266) of human deaths and over 75% of crop and property damage. The spotted hyena, leopard and lion, caused 85% of livestock predation cases. The intensity and outcome of conflicts varied across counties such that most human fatalities occurred in arid Tana River and Wajir counties, whereas most human injuries occurred in Kitui and Wajir counties. The intensity of conflicts was strongly influenced by the agro-climatic potential and the percentage of a county under protection, rainfall and temperature and their interactions. In consequence, crop damage was highest in counties with high agricultural potential (Meru and Taita Taveta) but livestock predation was highest in counties with large protected areas (Samburu and Taita Taveta). Human fatality and injury were higher among males than females and adults than children. Over the 10-year period, the Kenya government spent about 3 billion Kenya shillings on compensation of about 30% of all filed claims. Compensation schemes require sustainable funding mechanisms and effective administration to minimize negative unintended consequences.

Keywords

Human-wildlife conflicts, compensation, snake bites, attack on humans, livestock predation, crop raiding, rainfall, temperature, human population growth

INTRODUCTION

Human-wildlife conflicts (HWC) cause considerable losses to many communities, the compensation for which makes wildlife conservation an expensive undertaking globally (Nyhus et al., 2005; Ravenelle and Nyhus, 2017). The four main conflict types are, attack on human, livestock depredation, crop raiding, and property destruction (Conover, 2001; Messmer, 2000). Attack on humans can result into different outcomes ranging from death, injury, and general insecurity. Livestock depredation is attack on domesticated animals such as cattle, donkeys, sheep, goats, and poultry. Crop raiding is varied, however it leads to destruction of farmed crops for human consumption, while property damage could be damage to fences, water pipes, and houses (Distefano, 2005; Messmer, 2009). Occurrence of HWC is attributed to a number of factors including but not limited to the following: exponential human population growth, land use change that results in habitat loss, degradation and fragmentation, climatic change, and livestock and wildlife population increase (Distefano, 2005; Thirgood et al., 2005). These factors reduce food, water and other resources that wildlife require for survival, increase competition and therefore HWC occurrences.

Thus, compensation is a monetary payment (Distefano, 2005; Woodroffe et al., 2005; Tveraa et al., 2014) used by governments and conservation organizations to appease communities that live with wildlife when people are killed, injured or lose property to wild animals (Madhusudan, 2003). Access to compensation is critical to ensure that communities that bear the brunt of HWC continue to support wildlife conservation. As a result, such payments can constitute a significant expenditure portfolio for governments or conservation organizations (Nemtzov, 2003; Treves et al., 2006; Karanthet al., 2018). Unsurpisingly, most compensation schemes (88%) have been ex-post and instituted mostly in Europe and North America, with very few in Africa (Ravenelle and Nyhus, 2017). This is because compensation is costly and competes with other state priorities for limited revenues in developing countries. Even so, it is often presumed that implementing compensation programs should be easier and cheaper in rural areas of developing countries where people are generally poor (Bulte and Rondeau, 2007). Yet, experience shows that compensation for losses arising from HWC can be both difficult and expensive to implement, even among poor rural communities in developing countries. For example, a carnivore protection program operated by the Friends of Nairobi National Park (FoNNP) made consolation payments to families that lost their livestock to prevent retaliatory killings of carnivores in the Athi-Kaputiei Ecosystem, encompassing the Nairobi National Park in Kenya, from 2000 to 2012 (Lesilau et al., 2018; Ogutu et al., 2013; Mutuga, 2009), but stopped operating due to financial constraints. However, two other community-based compensation schemes, the Mbirikani Predator Compensation Fund (Hazzah et al., 2014; Maclennan et al., 2009) and the Maasai Wilderness Conservation Trust (Bauer et al., 2017) have been making similar payments to reduce retributive killings of lions (*Panthera leo)* in the Amboseli-Tsavo West Ecosystem of Kenya since 2003. But both programmes focus solely on livestock depredation and cover relatively small areas and the conservation trust program focuses only on the lion. More precisely, the Maasai Wilderness Conservation Trust was started in 2010, is funded by conservation fees, covers only 1,133 km^2 and supports about 17,000 people (Bauer et al., 2017). The Mbirikani programme was started earlier in 2003, is funded by conservation non-governmental organizations, covers 1,229 km^2 and caters for about 10,000 people (Groom, 2007; Maclennan et al., 2009).

Compensation can increase tolerance of wildlife by communities, leading to peaceful co-existence between humans and wildlife, but not necessarily always (Maclennan et al., 2009; Karanth et al., 2018). For instance, in India, compensation is faulted as failing because of focusing on charismatic animals and ignoring conflicts caused by other species (Johnson et al., 2018). Thus, reducing retaliatory killings of wildlife should be a key priority of sustainable biodiversity conservation. To this end, many compensation schemes have been established worldwide. But, many compensation schemes often focus on single wildlife species that are of conservation concern (i.e. threatened), such as the Indian tiger (*Panthera tigris*, Karanth et al., 2012), or the African lion (Maclennan et al., 2009), and hardly on multiple species. This is a major shortcoming of most schemes because multiple species often contribute to human-wildlife conflicts and therefore focusing on a single species overlooks others is not advisable.

Hence, a compensation scheme that targets a specific wild animal species ignores others which can result in less attention, persecution killings and decline in species population or extinction.

Whereas compensation has long been practiced in many countries, including USA (Treves et al., 2006), India (Karanth et al., 2018), Sweden (Zabel and HOLM-MÜLLER, 2008), Norway (Swenson and Andrén, 2005) and Israel (Nemtzov, 2003), relatively few studies have thus far evaluated the performance of National Compensation Schemes such as the Kenyan National Compensation Scheme (KNCS). However, such an evaluation can furnish valuable feedback and insights for improving the effectiveness of decision making in sustainable biodiversity conservation. Moreover, evaluating National Compensation Schemes (NCS) that target multiple wildlife species can provide understanding and insights into the outcomes and costs of human-wildlife conflicts beyond those obtainable only from the prevalent single species schemes.

Here, we evaluate a national compensation scheme that has been in existence in Kenya since 1976. The scheme pays out compensation for human fatality, injury or property damage (e.g., depredation of crops and livestock). Kenya's national government allocates funds for the compensation payments in its yearly budgets through the national treasury. This is because wildlife is a national resource owned by the state in Kenya. The Kenyan state therefore bears responsibility for wildlife conservation, management and compensation for losses caused by human-wildlife conflicts. The Wildlife Act defines what qualifies for compensation and provides elaborate procedures that all compensation claims must follow before the government can make compensation payments. The national compensation scheme regulates compensation for losses caused by HWC in Kenya and has been anchored in two Acts of Parliament since 1976, namely the Wildlife (Conservation and Management) Act, Chapter 376 (hereafter Cap 376, Kenya Wildlife Service, n.d.) and The Wildlife Conservation and Management Act 2013 (Kenya Law, 2013). Cap 376 was in force from 1976 to 2013 but underwent multiple revisions during this period. Under this Act, human injury or death caused by wildlife was eligible for a meager compensation, of Kenya Shillings

(KES) 15,000 or 30,000, respectively, while crop damage and livestock depredation were assessed at the prevailing market values. However, compensation for all types of losses but human death or injury was suspended in 1989 through an amendment to Cap 376.

The amounts paid for compensation by the KNCS were not only too meager but the process of getting compensated was too slow and cumbersome (Sindiga, 1995). This was mainly because of elaborate procedures for launching and processing compensation claims for losses linked to human-wildlife conflicts. Consequently, an amendment to the Act that came into effect on 1st July 2006 increased the amounts payable as compensation for human injury or death to KES 50,000 or 200,000, respectively. Cap 376 was repealed and replaced with The Wildlife Conservation and Management Act, 2013 (hereafter Act 2013) that came into force on 10th January 2014 (Kenya Law, 2013).

Act 2013 introduced two major changes relative to Cap 376, namely that it reinstated compensation for property damage caused by wildlife and substantially raised compensation payments. Specifically, Act 2013 expanded the types of losses caused by human-wildlife conflicts eligible for compensation to include human injury and its severity, human fatality and damage to private property (e.g. crops and livestock). Moreover, the compensation payments for human injury or fatality were increased almost 100-fold relative to the 2006 levels. In contrast, compensation for property damage was pegged at the prevailing market value of the damaged property, subject to the caveat that payment can only be made if, carelessness or laxity by the property owner, is not proven to have facilitated the loss. Act 2013 also provides an elaborate list of wildlife species in respect of which compensation payments may be made, if they cause human injury, death or property damage. The large number of wildlife species in this list is a clear recognition that HWC are caused by multiple species (Mukeka et al., 2018), and that it is therefore not logically or legally tenable to consider just a small subset of species for compensation.

Our prime aim is to evaluate the performance of the KNCS by seeking answers to the following seven research questions by analyzing data collected by the Kenya Wildlife Service (KWS) from 2007 to 2016: 1) What is the inter-annual and seasonal pattern of HWC compensation claims? 2) What are the common human-wildlife conflict causing species, the types and number of conflicts they cause? 3) How are wildlife attacks on humans spread across the two key demographic attributes of gender and age? 4) How are HWC incidents distributed across Kenya's administrative counties? 5) How do HWC vary with the proportion of a county under protection for conservation, human population density, rainfall, maximum temperature, and predominant agro-climatic zone in each county? 6) What is the monetary cost of HWC compensation payments per wildlife species, conflict type and county and how efficient was the KNCS during 2007-2016? 7) How did the amount of money paid for compensation claims compare with tourism revenue earnings by the Kenyan state during 2007-2016?

MATERIALS AND METHODS

Study Area

Kenya borders Somalia, Ethiopia, Sudan, Uganda, Tanzania, and the Indian Ocean in East Africa (Figure 1). It straddles the equator and lies between longitudes 33°50'E - 41°58' E and latitudes 5°2' N - 4°45' S and has a total area of 582,646 km^2. Kenya's human population has grown exponentially from about 8 million people in 1962 to about 49 million people in 2017 (The World Bank, 2017) distributed across 47 administrative Counties. Altitude ranges between 0 and 5199 m, the highest peak of Mount Kenya. Rainfall in Kenya is mostly bimodal with short rains occurring during November - December and the long rains during March-May (Ogutu et al., 2008). Kenya is divided into seven agro-climatic zones (I to VII), four (IV to VII) of which are hot, dry and receive little and often unreliable rains. The latter four zones have very limited agricultural potential, cover the largest percentage of Kenya (88%) and are often referred to as rangelands. The rangelands are inhabited predominantly by pastoral communities and harbour a wide variety of wildlife species that are adapted to the harsh climatic conditions (Pratt and Gwynne, 1977). Kenya has 63 protected areas, including 23 terrestrial national parks, 26 terrestrial national reserves, four marine national parks, six marine national reserves and four national sanctuaries that account for about 8% of Kenya's total land surface area (Kanga et al., 2013). Most protected areas are not fenced and therefore wildlife move freely to human-dominated landscapes bringing them into frequent interaction with people and their livestock (Figure 1).

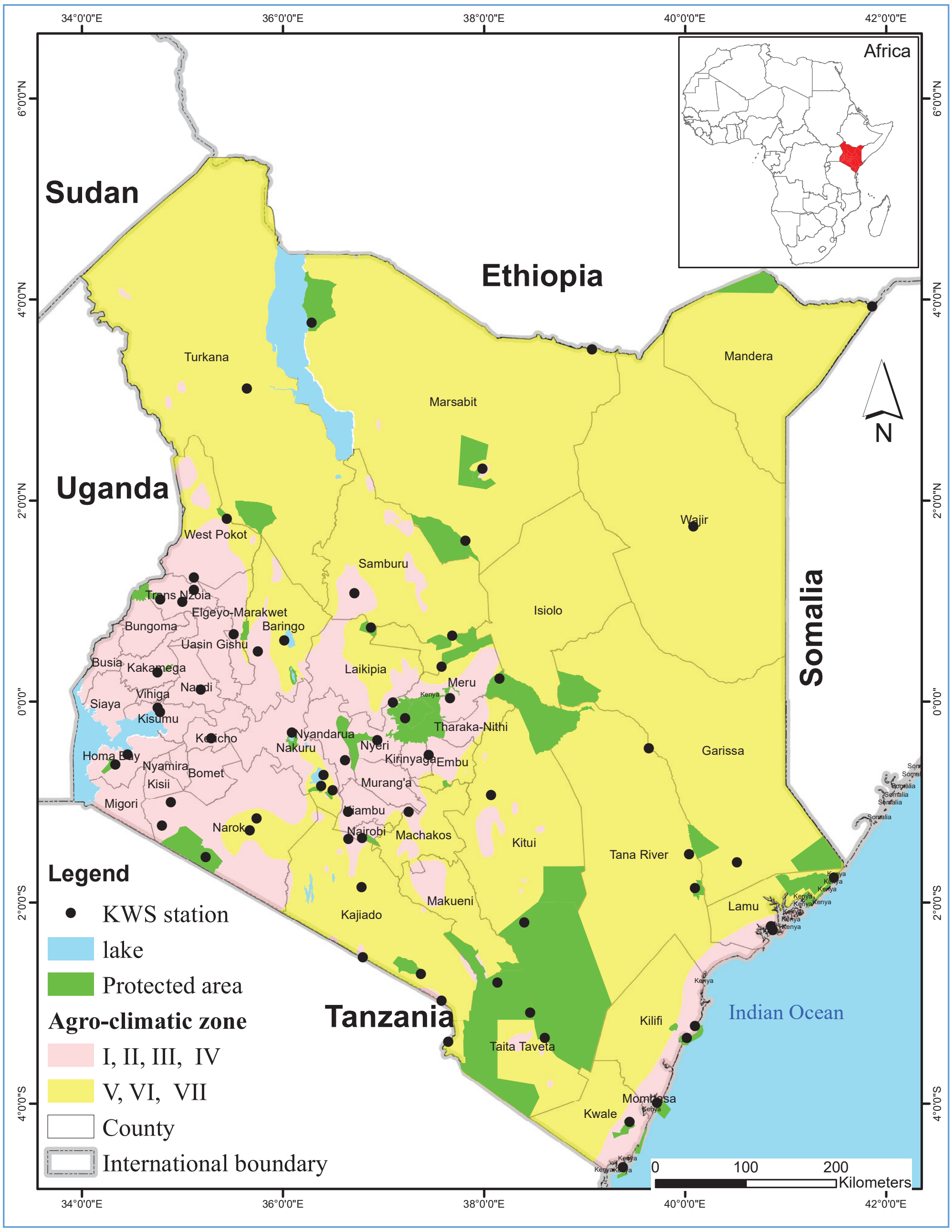


Figure 1: Map of Kenya showing the 47 administrative counties, the seven agro-climatic zones collapsed into two categories, and the various protected terrestrial, freshwater and marine ecosystems distributed

across the country. KWS stations are situated even in counties without protected areas to deal with wildlife-related issues in human-dominated areas, including providing support to victims of HWCs during compensation claims.

METHODS

Processing Human-Wildlife Conflict Compensation Data

The Kenya Wildlife Service (KWS) oversees all matters related to wildlife conservation and management in Kenya. Therefore, KWS maintains a national digital database of all compensation claims at its Headquarters in Nairobi since 2006. This database acts as a repository for all claims on compensation from different parts of the country (Figure 1) and provides timely information to the government. We sourced for and used the data for the 10 years covering 2007-2016. Noteworthy attributes of the compensation database include the date when the conflict incident occurred, the common English name of the wildlife species that caused the conflict, the type of conflict (human injury or death, damage to crops and other properties, livestock depredation), name of county where the conflict incident occurred, gender of the victim (male or female), age of the victim (adult - above 18 years or child - below 18 years), name of claimant (omitted from analysis for confidentiality considerations), whether a loss was compensated (yes or no), amount paid in Kenya shillings (Table I), and the status of the claim (approved, not approved or pending). A claim may be pending or may not be approved due to a number of reasons, including lack of important documents, such as a national identity card of the claimant, missing or incomplete information, for example, the value of the damaged property for which compensation is claimed, or missing signature of the police officer or medical doctor who attended the case.

Prior to analysis, the compensation data were processed with the relevant information extracted. Several conflict species that had only general names in the database or species that caused relatively few conflicts were grouped together. Thus, we use antelopes to group together eland, lesser kudu, impala, bushbuck, wildebeest, and antelope (groups together conflict causing antelope species). We similarly used small carnivores to group together the civet, foxes, genet, honey badger, jackals, mongoose, serval cat and wildcat. Nonhuman primates group together baboons and monkeys, whereas snakes refer to a broad spectrum of mostly poisonous snakes. Moreover, fish refers to stonefish and stingray; pigs to warthog and wild pig and "others" to squirrel, bush baby, monitor lizard, ostrich, porcupine, reptiles, and rock hyrax involved in very few conflicts. Thus, the final list had 12 species, six species groups, and the 'other' species group. A list of the species and their common English and scientific names is provided in Table A.1 in the Appendix.

Table I

Summary of the recommended compensation payments in Kenya shillings (KES) for different conflict types in Kenya during 2007 - 2016.

Conflict type	**Period and amount in KES**	
	2007 - December 2013	After 2014
Loss of human life	200,000	5,000,000
Human injury leading to permanent disability	50,000	3,000,000
Any other human injury	<50,000	≤ 2,000,000
Property damage (crop destruction, livestock loss, etc)	No compensation	Assessed and paid at market value

Kenya Tourism Earnings, Agro-climatic Zones and Protected Areas

We obtained data on Kenya's tourism earnings during 1995 - 2016 from the World Bank (The World Bank, 1995 - 2016, under Creative Commons Attribution 4.0, CC-BY 4.0) to quantify its growth over time, overall contribution of wildlife conservation to the Kenyan economy and assess it relative to the spending on compensation by KNCS. Since compensation is done in Kenya shillings, we obtained average annual US$ to KES exchange rates for comparison from the Central Bank of Kenya (Central Bank of Kenya, 2007 - 2016). We extracted the agro-climatic geo-layer from the UNEP/GRID database, derived from the Exploratory Soil Survey Report number E1, Kenya Soil survey, Nairobi 1982, that classifies Kenya into seven agro-climatic zones (I-VII) based on moisture and temperature. These classes are defined as follows (I) >80-Humid, (II) 65-80-Sub-humid, (III) 50-65-Semi-humid, (IV) 40-50-Semi-humid to Semi-arid, (V) 25-40-Semi-arid, (VI) 15-25-Arid, and (VII) <15-Very arid. We re-classified these zones into two broad classes. Class I included zones I- IV (high agricultural potential), and class II included zones V - VII (low agricultural potential). Further, we calculated the number of HWC by type for each of the two derived classes. We also used Kenya's 63 protected areas (PA) (Kanga, Ogutu, Piepho, & Olff, 2012) to calculate the percentage of each county under protection for conservation.

Human Population Size, Rainfall and Maximum Temperature.

Kenya's human population census data sets for 1962, 1979, 1989, 1999 and 2009 were obtained from the Kenya National Bureau of Statistics (KNBS) (KNBS, n.d). Since these censuses are decadal, we used interpolation to obtain population size estimates for years between censuses and extrapolation to obtain estimates for 2009-2016 for each 5 × 5 km grid cell. The population estimates were summed up across all grid cells in each County for each year to derive the total population size estimate. We used a semi-parametric generalized linear mixed model, assuming a negative binomial error distribution and a log link function. The model allowed for 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 5 × 5 spatial grid unit. The model was implemented in the Glimmix procedure of SAS (SAS Institute 2018). Both total monthly rainfall and average monthly maximum temperature data were obtained from the Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) rainfall data for each 5 × 5 km grid cell for the period 1960 – 2017 (Climate Hazards Group, n.d.). The human population, rainfall and maximum temperature data were obtained for only 21 rangeland counties covering 88% of Kenya's terrestrial land surface and containing most of Kenya's wildlife (Ogutu et al., 2016). For analysis, two counties, Machakos and Makueni are merged to match historical monitoring data.

Statistical Analyses

Descriptive statistics, cross-tabulations, and mostly nonparametric methods since most of the data were counts and not normally distributed after examining histograms and testing using Kolmogorov-Smirnov test (Ghasemi and Zahediasl (2012). Specifically Chi-square goodness of fit tests were used to analyze differences in compensation claims between years, species, conflict types, and across counties. Differences in effects of demographic variables (gender and age), using Chi-square goodness of fit. We tested for significance of the correlation between the percentage of each county under protection and the number of compensation claims made using the Spearman rank two-tailed test (Zar, 1984). We also compared the total number of conflicts in the two derived agro-climatic classes.

We regressed the total number of human deaths or human injuries for each County against the County, human population size, total annual rainfall and average annual maximum temperature and all their possible interactions using a negative binomial regression with a log link. First, we used automatic variable selection, with the forward selection method, to select the best supported covariates from the set of human population, rainfall, and maximum temperature, county and their interactions, considering up to three way interaction effects. The logarithm of the total area of each county was used as an offset to adjust for variation in area across counties. We imposed a strong hierarchy constraint during automatic variable selection, meaning that an interaction term can only be retained in the model if the main effects contributing to the interaction term are also already in the model. Automatic variable selection was carried out using the SAS HPGENSELECT procedure (SAS Institute 2018). The corrected Akaike Information Criterion (AICc) and likelihood ratio test were used to select the subset of the best supported variables and interaction terms to retain in the model. The subset of selected variables and interactions were then used to fit the final model in the SAS Glimmix procedure, assuming a negative binomial error distribution, a log link function and the logarithm of the area of each county as an offset to calculate the number of conflicts per unit area. The total number of human deaths or injuries averaged across all years for each calendar month was similarly related to the county, average total monthly rainfall, average maximum temperature, human population size and their interactions. The variable selection stage did not include human population as an influential predictor of HWC in the 20 rangeland counties in all the models and therefore human population size was omitted from the final model. Thus, county, rainfall and maximum temperature and their interactions were used as the only predictors of both the inter-annual and seasonal variation in the total number of human deaths or human injuries.

Significance was assessed at the 5% level unless otherwise stated. Statistical analyses were carried out using SPSS Version 25.0 (IBM Corp. Release 2017) and SAS Version 9.4, SAS/STAT version 14.3 (SAS Institute 2018).

RESULTS

Annual and Monthly Variation in Compensation Claims in Kenya During 2007 - 2016

A total of 18,794 (1,879.4 ± 1720.1, range 529 - 5,020) compensation claims for losses caused by human-conflicts were filed Kenya-wide during 2007 - 2016. Relative to 2012, the number of claims increased 1.8 fold in 2013, the year Kenya's parliament passed the new Wildlife Conservation and Management Act 2013, and 5.8 fold to a peak in 2014, the year the new Act took effect. Thereafter, the number of claims declined from 2014 to 2016 (Figure 2). Snakes were the leading conflict species (44.8%) followed by the African elephant (*Loxodonta africana,* 22.3%). The next four leading conflict species were the spotted hyena (*Crocuta crocuta,* 6.5%), African buffalo (*Syncerus caffer,* 4.9%), leopard (*Panthera pardus,* 4.6%) and lion (*Panther leo,* 4.0%). Other notable species contributing to conflicts were the crocodile (*Crocodylus niloticus*, 3.5%), hippo (*Hippopotamus amphibius*, 3.0%) and common zebra (*Equus quagga*, 2.5%). Overall, the frequency of conflicts differed between species and across the years (χ^2_{162}= 5104.9, P = 0.001). Ten species caused at least 20 conflicts each year that resulted in compensation claims, and are the main focus of the subsequent sections, even though all the species were included in all the statistical tests (Table II).

There was evident seasonality in conflicts but the nature of seasonality varied among species or species groups. In particular, conflicts caused by snakes peaked during the long (January-May) and short (November-December) wet seasons and were lowest during the long dry season between July-September. In contrast, the large herbivore conflicts peaked during the early dry season month of July. Conflicts caused by the three common carnivores followed a similar pattern to that for the herbivores (Fig. 3).

Table II:

The contribution of each species to the annual total number of conflicts in decreasing order of the total number of cases reported for compensation during 2007-2016.

		Year										Chi-square test		
No	Species	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	n	χ^2_9	P
1	Snakes	218	392	352	367	883	489	1171	1795	1749	1007	8423	1846.5	0.001
2	African elephant	69	56	32	35	71	45	46	1304	943	1580	4181	1916.2	0.001
3	Spotted hyena	14	21	4	12	13	23	27	469	377	270	1230	325.7	0.001
4	Buffalo	53	56	68	19	99	80	69	185	146	149	924	213.4	0.001
5	Leopard	19	7	13	4	22	13	22	268	320	167	855	220.9	0.001
6	Lion	38	25	10	12	21	26	19	249	212	141	754	99.5	0.001
7	Crocodile	66	53	34	45	66	86	79	63	100	61	653	474.4	0.001
8	Hippopotamus	23	26	14	15	40	34	33	141	101	136	564	24.2	0.004
9	Common zebra	0	1	0	0	1	0	1	393	67	16	479	793.5	0.001
10	Wild dog	8	10	3	9	5	0	5	77	81	38	236	53.1	0.001
11	Small carnivores	9	8	5	13	26	34	26	9	7	13	150	227.4	0.001
12	Pigs	2	1	4	1	2	8	3	19	23	27	90	19.2	0.024
13	Nonhuman primate	8	5	4	7	15	12	18	4	3	3	79	121.6	0.001
14	Cheetah	1	2	2	1	3	0	2	22	14	30	77	24.8	0.003
15	Antelopes	0	2	1	1	4	3	3	7	19	7	47	12.3	0.195
16	Other	1	2	1	1	6	3	7	1	0	0	22	48.4	0.001
17	Fish	0	0	0	0	0	0	0	10	7	4	21	11.3	0.257
18	Rhino	0	1	0	0	0	1	0	2	1	0	5	8.9	0.445
19	Giraffe	0	0	0	0	0	0	1	2	1	0	4	3.9	0.916

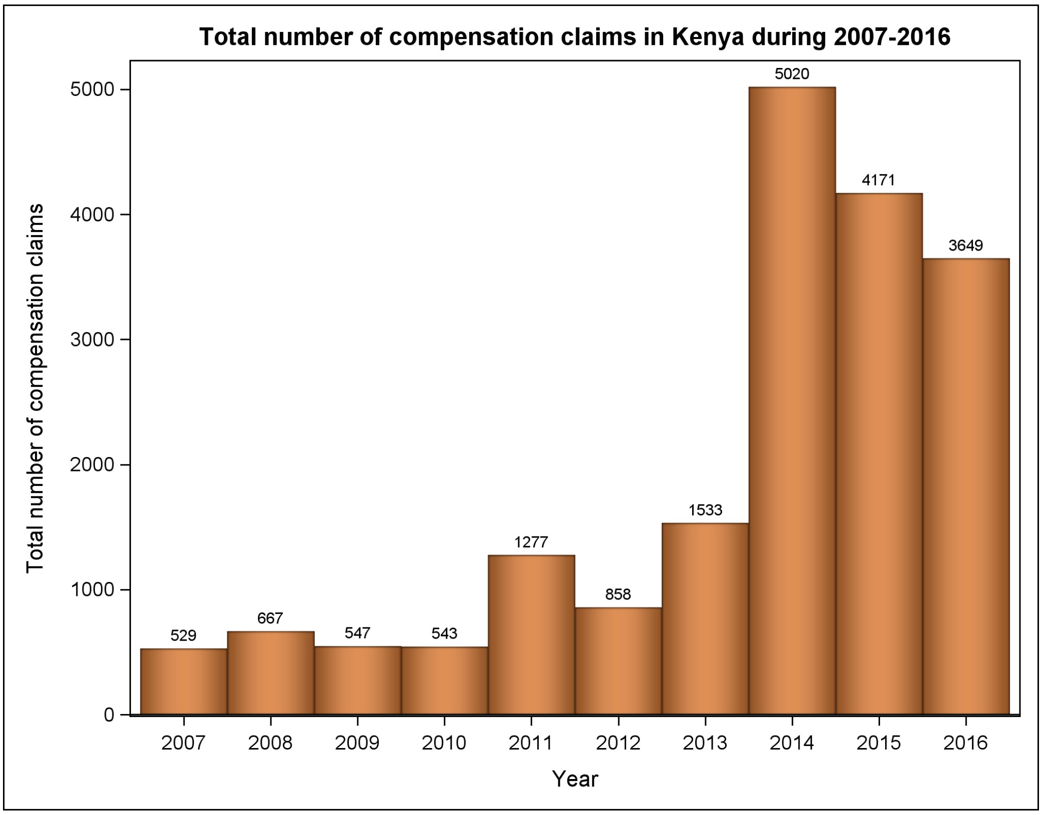


Figure 2: Yearly compensation claims for losses caused by human-wildlife conflicts filed in Kenya during 2007-2016.

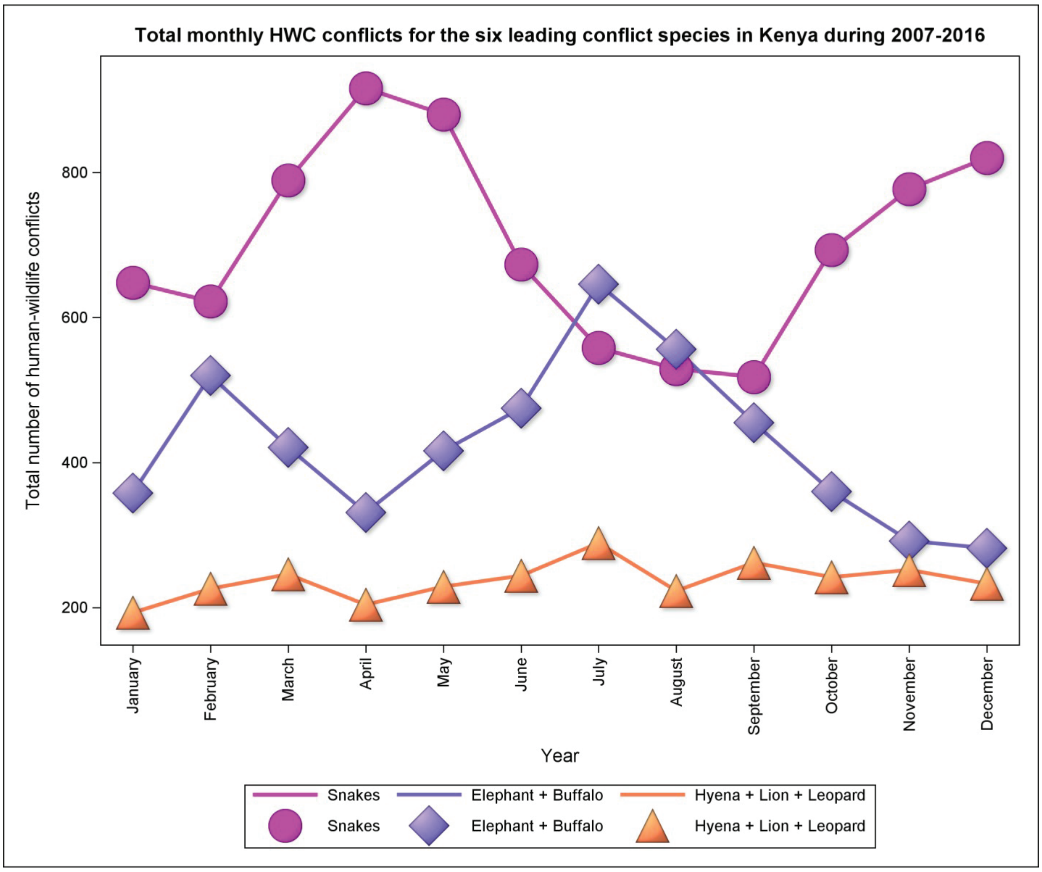
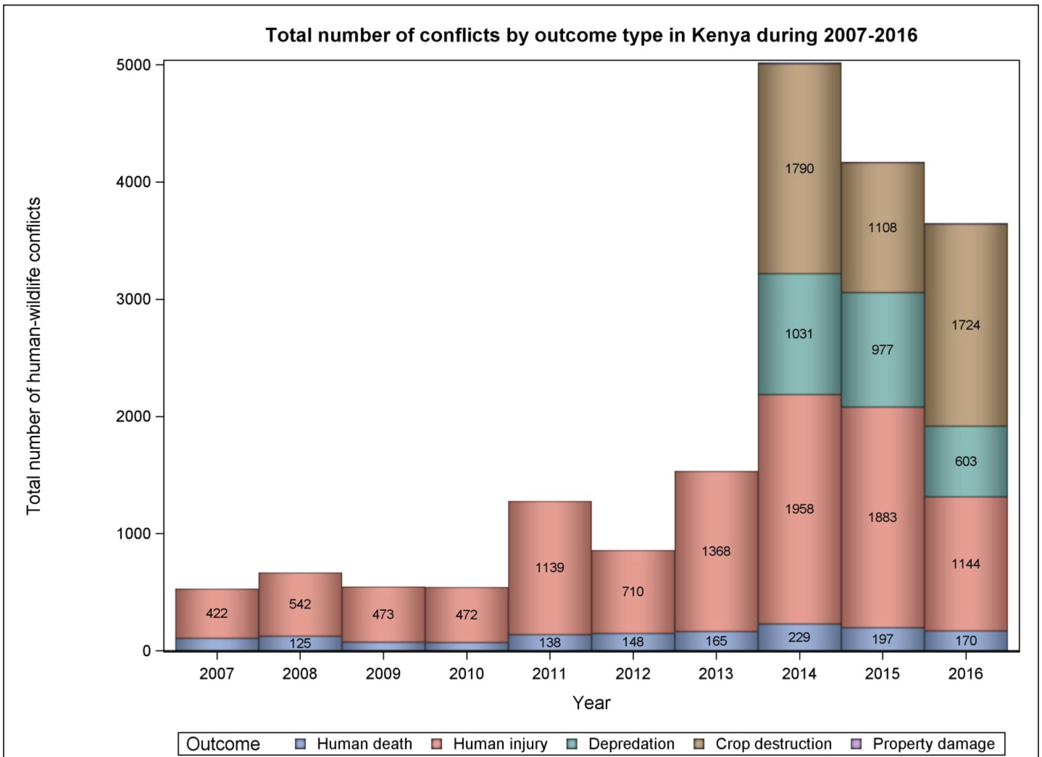


Figure 3: Total monthly HWC conflicts for the six leading conflict species in Kenya 2007-2016

Frequency of Compensation Claims by Conflict Type During 2007-2016

Human-wildlife conflicts resulted in five different types of reported outcomes during the 10 years (Table III). Conflicts were seven times more likely to result in human injury (1011.1 ± 582.7) rather than death (142.4 ± 50.7). Crop destruction (1540.7 ± 376.2 SD) was nearly twice as likely to occur as livestock depredation events (870.3±233.1), and property damage (8.6 ± 3.1) was the least likely conflict type to occur in this period (Figure 4). The total number of conflict types varied significantly between years (χ^2_{36}= 6104.4, P < 0.001).



	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Human death	107	125	74	71	138	148	165	229	197	170
Human injury	422	542	473	472	1139	710	1368	1958	1883	1144
Depredation								1031	977	603
Crop destruction								1790	1108	1724
Property damage								12	6	8

Figure 4: Reported conflicts by type in Kenya during 2007 - 2016

The Total Number of Compensation Claims for Losses by Species and Conflict Type

The number of compensation claims varied widely among species and conflict type, reflecting a marked disparity in the distribution of the total number of conflicts among conflict causing species and conflict type. Only five of the 19 wildlife species and species groups were responsible for over 90% of human deaths. They included snakes (43.1%, n = 614), elephant (18.8%, n = 268), crocodile (14.7%, n = 210), hippo (8.4%, n = 119) and the buffalo (7.4%, n = 106). Snakes (76.9%), buffalo (6.0%) and crocodile (3.8) caused the highest number of human injuries. The elephant caused most of the damage to crops (77.7%) and other properties (80.8%). Three large carnivores comprising the hyena, leopard, and lion were responsible for 85.6% of all the livestock depredation cases, whereas the wild dog caused a mere 6.0% (Table III). Overall, comparisons of HWC between species and conflict types showed significant differences (χ^2_{72} = 28120.57, P < 0.001).

Table III:

The contribution of each species to the total number of conflicts by type, in decreasing order of the total number of cases reported for compensation during 2007-2016

No	**Species**	**Crop destruction**		**Human death**		**Human injury**		**Predation**		**Property damage**		**Pearson Chi-square test**	
		n	%	n	%	n	%	n	%	n	%	χ^2_4	P
1	Snakes	0	0.0	614	43.1	7772	76.9	37	1.4	0	0.0	9964.56	0.001
2	Elephant	3593	77.7	268	18.8	275	2.7	24	1.0	21	80.8	11204.35	0.001
3	Hyena	0	0.0	40	2.8	175	1.7	1015	38.8	0	0.0	5202.88	0.001
4	Buffalo	203	4.4	106	7.4	606	6.0	7	0.3	2	7.7	168.38	0.001
5	Leopard	0	0.0	17	1.2	164	1.6	674	25.8	0	0.0	3176.88	0.001
6	Lion	0	0.0	35	2.5	172	1.7	547	21.	0	0.0	2288.57	0.001

No	Species	Crop destruction		Human death		Human injury		Predation		Property damage		Pearson Chi-square test	
									0				
7	Crocodile	0	0.0	210	14.7	384	3.8	59	2.3	0	0.0	721.50	0.001
8	Hippopotamus	262	5.7	119	8.4	165	1.6	16	0.6	2	7.7	371.54	0.001
9	Zebra	472	10.2	1	0.1	6	0.1	0	0.0	0	0.0	1449.31	0.001
10	Wild dog	0	0.0	2	0.1	77	0.8	157	6.0	0	0.0	569.87	0.001
11	Small carnivores	0	0.0	3	0.2	136	1.3	11	0.4	0	0.0	86.49	0.001
12	Pigs	55	1.2	0	0.0	34	0.3	0	0.0	1	3.8	79.0	0.001
13	Nonhuman primate	2	0.0	1	0.1	76	0.8	0	0.0	0	0.0	57.52	0.001
14	Cheetah	0	0.0	0	0.0	13	0.1	64	2.4	0	0.0	311.25	0.001
15	Antelopes	33	0.7	2	0.1	12	0.1	0	0.0	0	0.0	54.2	0.001
16	Other	0	0.0	5	0.4	17	0.2	0	0.0	0	0.0	17.44	0.002
17	Fish	0	0.0	0	0.0	21	0.2	0	0.0	0	0.0	18.05	0.001
18	Rhino	0	0.0	1	0.1	4	0.0	0	0.0	0	0.0	3.59	0.465*
19	Giraffe	2	0.0	0	0.0	2	0.0	0	0.0	0	0.0	1.93	0.749*

*Not significant

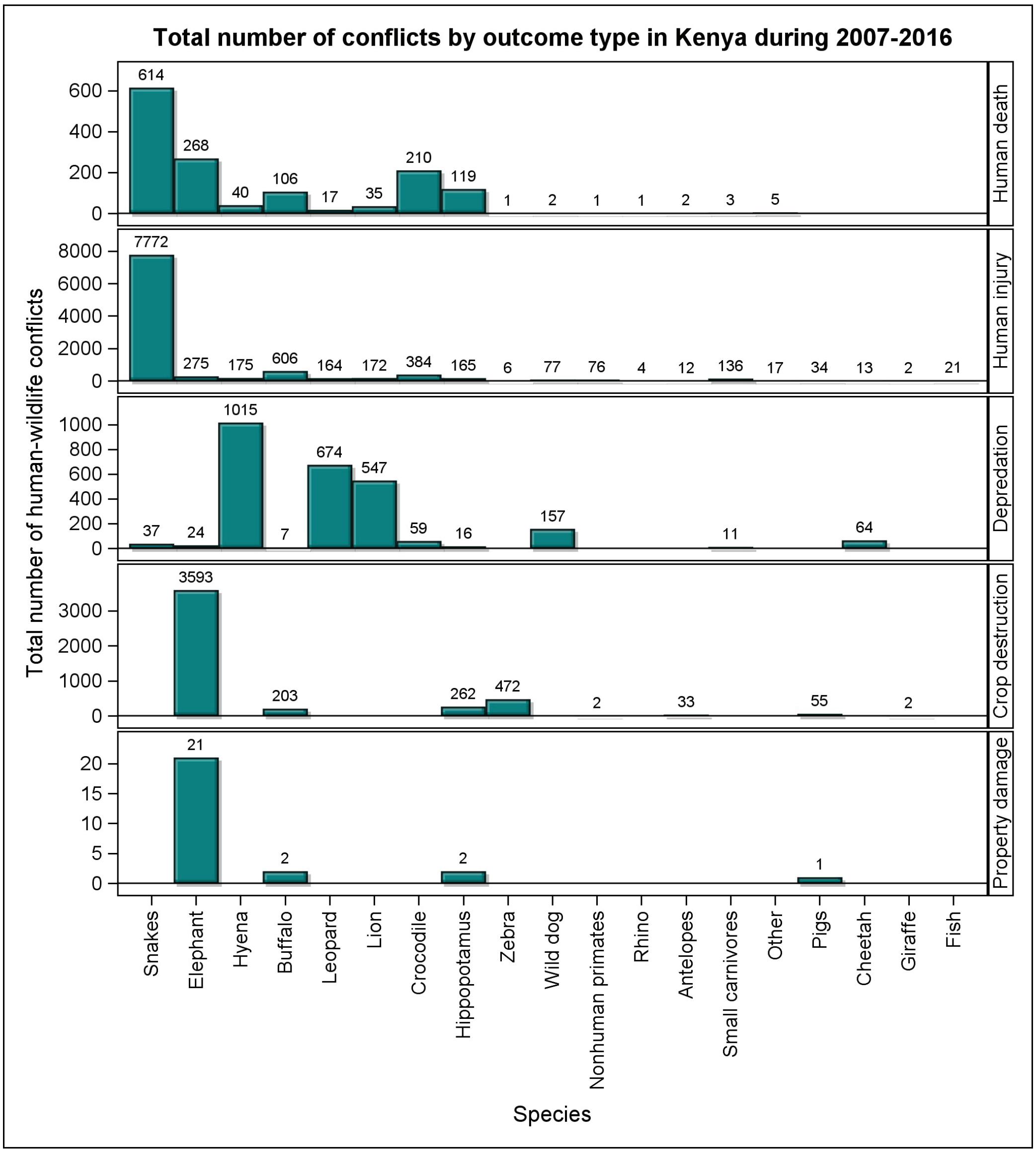


Figure 5: Human-wildlife conflicts grouped by conflict species and outcome type

Human Injuries and Deaths from HWC by Gender and Age

HWC in Kenya resulted in a total of 1,424 compensation claims for loss of human life and 10,111 for human injury between 2007 and 2016. The effect of conflicts was highly unbalanced in favor of females such that males were three times (77.3%, n = 1424) more likely to be killed than females (22.7%). Further, twice as many males (69.4%, n = 10,111) as females (30.6%) were likely to suffer injuries. As a result, significantly more males than females were either killed or injured in the conflicts (χ_1^2 = 37.3, P < 0.001). Moreover, adults were more likely than children to be either killed (61.9%, n = 1424) or injured (65.3%, n = 10,111) in the conflicts. Consequently, significantly more adults than children either died or suffered injuries from the conflicts (χ_1^2 = 6.36, P = 0.012).

Human-Wildlife Conflict Compensation Claims by Conflict Outcome Type and County

HWC occurred country-wide but varied considerably across counties in their intensity and type. Hence, all the 47 counties of Kenya except Nyamira County reported human-wildlife conflict related cases for compensation (Figure 6). As a result, 57.2% of the total of 1,424 (35.6 ± 32.11, n = 40, range = 1 - 112) cases of human deaths reported during 2007 - 2016, were confined to only 10 of the 47 counties. Similarly, only 10 counties accounted for 64.9% of the total of 10,111 (225 ± 289, n = 45, range = 1-1309) cases of human injury reported during 2007 - 2016. Crop damage was concentrated in even fewer counties with 66.6% of the total of 4,622 (165 ± 252, n = 28, range = 1- 992) cases reported by only five counties. Furthermore, the 2,611 (73 ± 124, n = 36, range = 1-670) livestock depredation cases reported were also highly unevenly distributed such that Samburu County was leading with 2.5 times as many cases as the second most affected County - Taita Taveta (Table IV). Although, only 26 property compensation claims were filed during this period, they also showed highly clumped distribution across counties, so that Makueni reported the highest (30.8%) number of cases followed by Samburu (19.2%).

Overall, compensation claims were unevenly distributed across conflict outcome type (χ^2_{180} = 10738.6, P <0.001) over the 46 counties in which they occurred. More details can be found in Table A.2 in the appendix.

Table IV

The first five counties that reported the highest number and percentages (in parentheses) of conflict by outcome type during 2007 - 2016. A subset of 11 Counties ranked among the top five that experienced most conflicts of each type. Missing values in each conflict category means the county was not among the top five for that conflict type.

		Number and percentage frequency of conflicts by type				**Pearson Chi-square test**	
No	County	Death to human	Injury to humans	Crop raiding	Predation	χ^2_4	P
1.	Tana River	112 (7.9)			214 (8.2)	43.8	<0.001
2.	Wajir	107 (7.5)	998 (9.9)			558.2	<0.001
3.	Kitui	101 (7.1)	1309 (12.9)			1022.5	<0.001
4.	Narok	99 (7.0)			255 (9.8)	255.8	<0.001
5.	Mandera	80 (5.6)	653 (6.5)			292.3	<0.001
6.	Marsabit		817 (8.1)			621.0	<0.001
7.	Taita Taveta		534 (5.3)	789 (17.0)	265 (10.1)	583.2	<0.001
8.	Meru			992 (21.5)		2234.3	<0.001
9.	Laikipia			526 (11.4)	139 (5.3)	802.7	<0.001
10.	Samburu			454 (9.8)	670 (25.7)	1776.9	<0.001
11.	Nyeri			316 (6.8)		672.7	<0.001

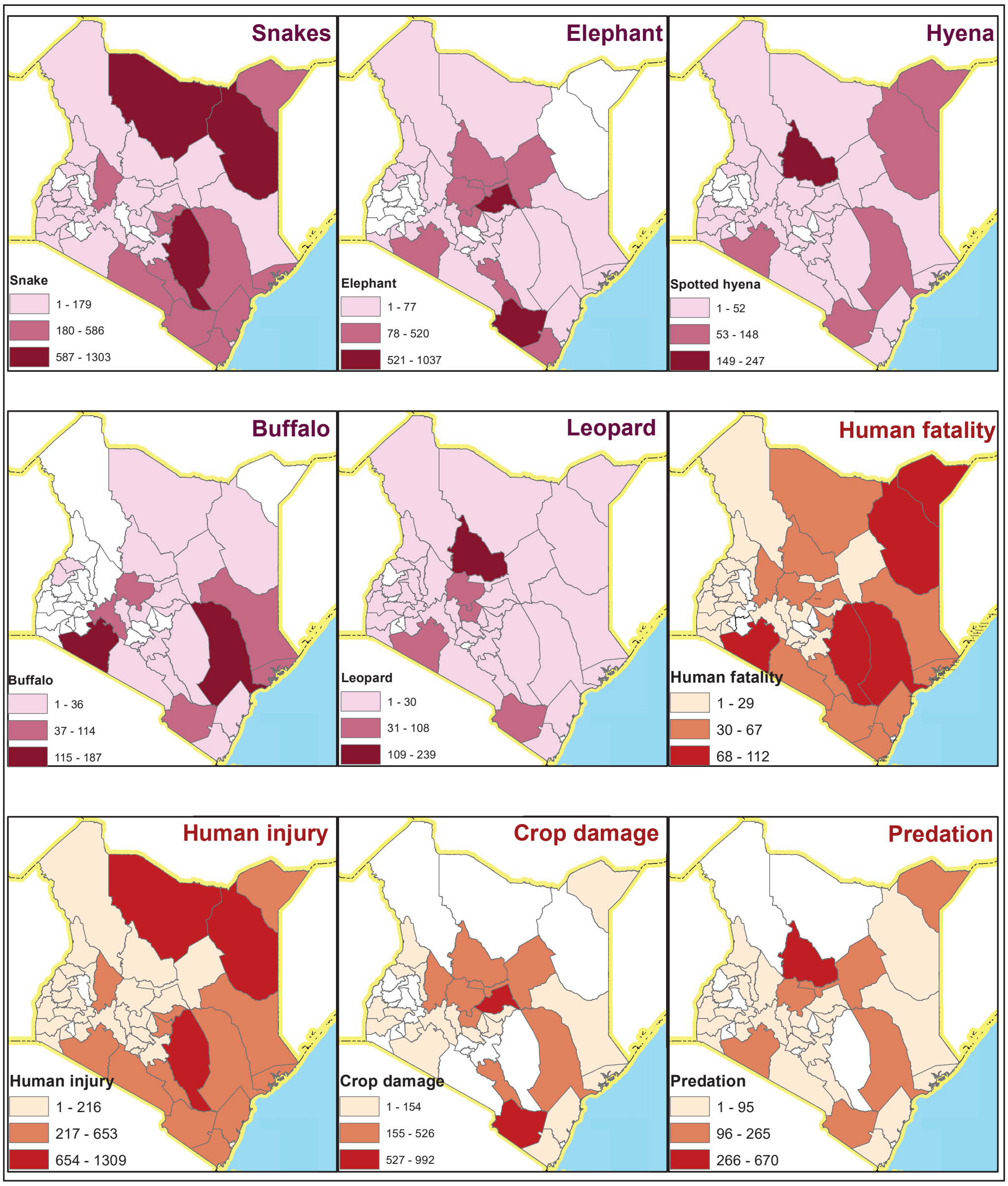


Figure 6: The leading human-wildlife conflict causing species responsible for compensation claims and the four major conflict types associated with them in Kenya (2007-2016). Darker colors indicate highest frequencies of cases. The blue color is the Indian Ocean.

Compensation Claims in Relation to the Percent of a County under Protection and the Predominant Agro-Climatic Zones in a County

The total number of compensation claims was positively and linearly correlated with the percentage of each county under protection (r_s = 0.43, P = 0.002). Similarly, human death (r_s = 0.35, P = 0.016) and injury (r_s = 0.41, P = 0.004), crop damage (r_s = 0.46, P = 0.001) but not livestock depredation (r_s = 0.15, P = 0.33) increased with increase in the percent of each county under protection. After adjusting for the area covered by each agro-climatic zone, crop damage was 1.5 times as likely to occur in the agro-climatic zone with a low (Class II) as in the zone with a high (Class I) agriculture potential. As well, human deaths, human injuries and livestock depredation were 2.5, 3.5, and 2.2 times as likely to occur in the zones with low as in the zones with high agricultural potential, respectively.

HWC in Relation to Human Population Size, Rainfall, and Maximum Temperature in 20 Rangeland Counties of Kenya During 2007 - 2016

Human fatalities and injuries from HWC varied across counties, years and months and this variation was significantly influenced by inter-annual and seasonal variation in rainfall, maximum temperature and their interactions. Across years, the number of human deaths from HWC varied significantly across counties, was higher in drier years and even more pronounced in drier and hotter years, regardless of county. Moreover, the number of people killed in human-wildlife conflicts decreased at higher temperatures in seven counties but increased with temperature in five others (Tables V and A.3). The variation in the number of human deaths across months also displayed very similar relationships to the same set of predictors but increased with the total monthly rainfall. Similar regression relationships to those for human fatalities characterized the inter-annual variation in the number of people injured during human-wildlife conflicts (Tables V and A.3). Seasonal variation in human injuries showed a somewhat different pattern in that it increased with increasing rainfall but at rates that differed across counties and it was not significantly influenced by temperature (Tables V and A.3).

Table V: Results of negative binomial regression of HWC in Kenya during 2007-2016 on County ($\boldsymbol{n}$=20), annual rainfall, maximum temperature and their interactions. Separate models were fitted to the total annual HWC (inter-annual trend) and HWC for each calendar month averaged across all years (seasonal trend)

Type of Trend	HWC Outcome	†Effect	Num DF	Den DF	F Value	Pr > F
Inter-annual	Human Death	County	19	158	5.09	<0.0001
	Human Death	Rainfall	1	158	3.68	0.0569
	Human Death	TMax	1	158	12.09	0.0007
	Human Death	Rainfall*TMax	1	158	4.61	0.0333
	Human Death	TMax*County	19	158	5.01	<0.0001
	Human Injury	County	19	158	10.3	<0.0001
	Human Injury	Rainfall	1	158	5.3	0.0227
	Human Injury	TMax	1	158	6.96	0.0091
	Human Injury	Rainfall*TMax	1	158	7.2	0.0081
	Human Injury	TMaxCounty	19	158	10.19	<0.0001
Seasonal	Human Death	County	19	199	1.89	0.0162
	Human Death	Rainfall	1	199	1.79	0.1821
	Human Death	TMax	1	199	0.17	0.6835
	Human Death	TMax*County	19	199	1.81	0.024
	Human Injury	County	19	200	41.75	<0.0001
	Human Injury	Rainfall	1	200	28.38	<0.0001
	Human Injury	Rainfall*County	19	200	1.89	0.0168

†Tmax is maximum temperature in °C averaged for the year (inter-annual) and month (seasonal)

Trends in Compensation for HWC Cases in Kenya During 2007 - 2016

A total of 18,794 compensation cases were filed during 2007-2016 of which the vast majority (78%) were approved for payment; 17.1% were still being processed by 2016, whereas relatively few were rejected (4.9%). Of the rejected cases, 695 were those involving snake related injury. During the period, the fewest approvals were made in 2010 (1.6%) whereas the highest in 2014 (21.9%). Overall, filed compensation claims were far more likely to be approved than rejected (χ^2_{18}= 1,582.22, P = 0.001) (Table VI).

Table VI

The yearly compensation level ratings and their Chi-square goodness of fit tests. The null hypothesis tested is that the yearly compensation level ratings do not differ between years.

Year	Approved		Pending		Rejected		Pearson Chi-square test	
	n	%	n	%	n	%	χ^2_2	P
2007	455	3.1	65	2.0	9	1.0	23.2	<0.001
2008*	514	3.5	131	4.0	23	2.5	5.3	0.071*
2009	395	2.7	126	3.9	26	2.8	14.0	<0.001
2010	307	2.1	235	7.3	2	0.2	277.0	<0.001
2011	668	4.6	602	18.7	7	0.8	890.8	<0.001
2012	589	4.0	251	7.8	20	2.2	100.1	<0.001
2013	1402	9.5	71	2.1	68	7.4	194.3	<0.001
2014	4112	28.1	628	19.5	280	30.5	104.9	<0.001
2015	3244	22.1	631	19.6	296	32.2	65.7	<0.001
2016	2980	20.3	481	15.0	188	20.5	49. 3	<0.001

*Not significant. The term approved means the case should be paid, pending means the case is yet to be decided, and rejected means the case has been reviewed and a decision made not to pay.

Payments for Human-Wildlife Conflict Compensation by Species and County

Between 2007 and 2016, 5,152 (515.2 ± 326.7, range = 140 -1,341) human-wildlife conflict claims were paid for by the government of Kenya. The number of compensation claims paid for varied strongly between years and was the highest in 2013 (n =1,341) and the lowest in 2016 (n = 140). The total number of claims paid for translates to 35.1% of all the approved (n = 14,666) compensation claims raised with the KNCS during the 10-year period. Consequently, Kenya Shillings 3,047,433,500 (591,505.0 ± 1,476,400.6; range = 2,500 - 5,000,000) were paid out for the total (5,152) HWC compensation claims. Compensation payment varied with the severity of human injury suffered and ranged from a minimum of KES 2,500 to a maximum of KES 3,000,000 whereas compensation for human death ranged from KES 50,000 to KES 5,000,000. However, only eight cases of human death were paid for at the rate of KES 50,000 during this period and were likely long-term pending claims. Human injury and death were the only two conflict claim types compensated during the period even though Act 2013 provides for compensation for property damage. Thus, human death received the bulk of the compensation payments (85.7%) whereas human injury received the rest. Of the total compensation payments, 99% was used to compensate claims related to eight species as follows: snakes (52.6%), elephant (13.6%), crocodile (9.1%), buffalo (8.5%), and hippopotamus (7.8%). The rest was paid out for losses linked to conflicts involving three carnivores comprising the spotted hyena (3.9%), lion (2.2%) and leopard (1.7%).

We further sought to establish if there was a difference in compensation payments between pre - (2007-2013) and post - (2014-2016) Act 2013 periods. Striking differences were apparent with the post-2013 period accounting for 90.2% (KES 2,747,625,000) of all the payments even though the pre-2013 period was twice as long as the post-2013 period.

Trends in Total Tourism Earnings in Kenya During 2007 - 2016

Kenya earned a total of $16.3 billion ($1.6 ± 0.3, range 1.1 - 2.0 per annum) from tourism and the revenue grew by over 50% between 2007 and 2016. Tourism earnings in Kenya took a nose dive from 1998 when the American Embassy in Nairobi was attacked by terrorists to a low in 2002, after which it started increasing. The post-election violence of late 2007 and early 2008 also negatively impacted tourism earnings again, but for a shorter period (Figure 7). In 2013, the Westgate terrorist attack again led to a drop in tourism earnings but its impact was smaller and short-lived (Figure 6). The percentage total amount ($) spent on compensation relative to Kenya's tourism earnings was 0.2 % (annual average: 0.02 ± 0.3%, range 0.01- 0.7) and increased during 2007 - 2016 (r^2 = 0.46, P = 0.037).

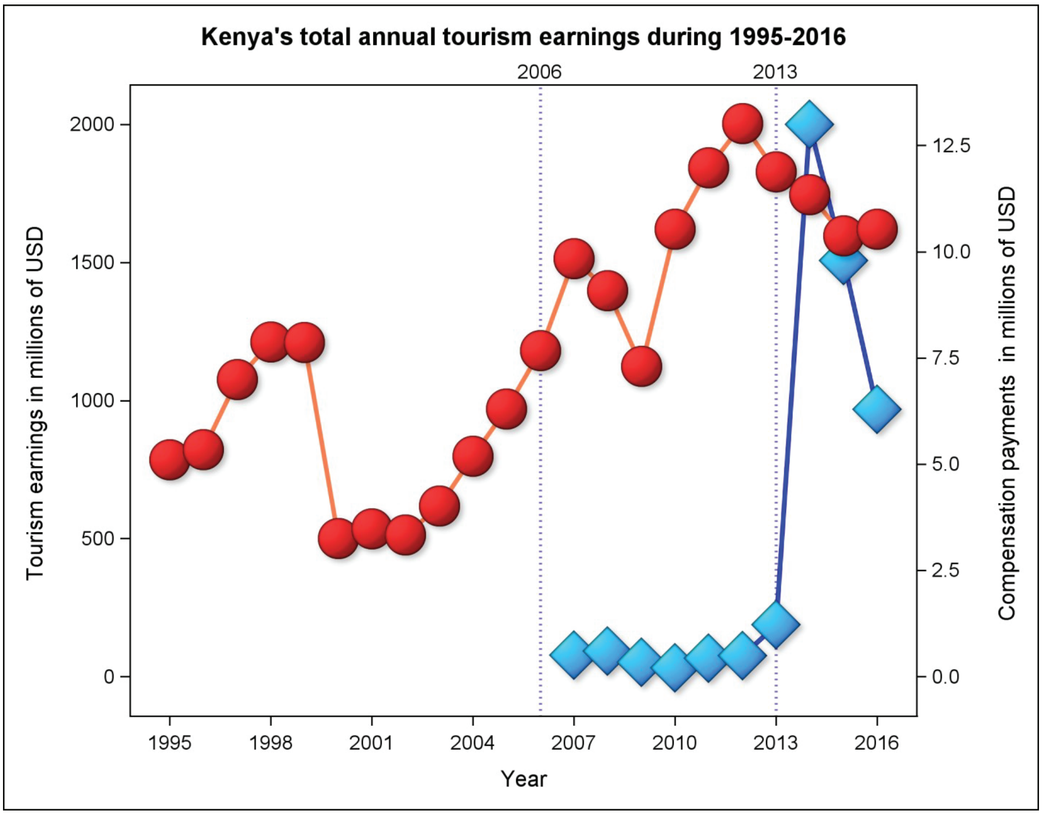


Figure 7: Kenya's international tourism revenue in the period 1995-2016 and KNCS payments 2007-2016.

DISCUSSION

Frequency and Occurrence of Human-Wildlife Conflicts and Compensation Claims in Kenya During 2007-2016

Human-wildlife conflicts were common in various parts of Kenya and were caused by multiple wildlife species during 2007 - 2016. Snakes were a common source of conflicts in Kenya, threatening lives and livelihoods of many people. About 60 people died every year out of snake-related attacks in Kenya during

2007-2016. Further, close to 800 people were injured by snakes, but survived either because the snake was not poisonous or they received timely treatment. These are almost certainly underestimates because many snake-related conflicts go unreported in remote areas or are simply treated using local traditional methods (Kipkore et al., 2014; Owuor and Kisangau, 2006; Coombs et al., 1997). Snake conflicts were especially common in three arid counties, namely Kitui, Wajir, and Marsabit. These counties are found in agro-climatic zones V-VII that are dry, arid and predominantly inhabited by pastoral communities at low human population densities (especially Wajir and Marsabit). Snakes become more active at night when it is cooler and move out in search of water and food (Nhachi and Kasilo, 1994; Duff-Mackay, 1965) and are then more likely to come into contact with people. Further, snake conflicts peaked in the wet season because snakes come out of their shelters to breed at this time (Butler, 1993). Consequently, human injuries, the bulk of which are caused by snake bites, increased with increase in rainfall and peaked in the wet season months of November - December and March - May. Similarly, snake conflicts peaked in the wet season and were the lowest during the short (January - February) and long (July-September) dry seasons. Further, human deaths from HWC were lower at higher temperatures, reflecting reduced activity of snakes. The counties that recorded high snake conflicts during 2005 - 2017 are relatively underdeveloped and have limited access to well-equipped dispensaries to deal with snake bite emergencies. The level of underdevelopment implies that people inhabit houses that render them prone to snake attacks, such as mud walled and grass thatched huts. Furthermore, antivenoms are expensive (Chippaux, 2011) and often beyond the reach of most rural poor. The prevailing situation of limited availability and access to pertinent drugs is made worse by companies stopping the production of these drugs altogether (Theakston and Warrell, 2000; Chippaux et al., 2015). Thus, whereas the problems of snake conflicts will likely persist in Kenya, immediate measures should be taken to address it, especially by making antivenoms more widely accessible. These results reinforce those of Mukeka et al. (2018) who reported snakebites to be a leading issue in the arid Kitui region of Kenya. They also add to the growing body of evidence that snake bites are a major source of human-wildlife conflicts more generally, accounting for over 7,000 human deaths and 10,000 permanent disabilities and requires nearly 300,000 envenomings annually on continental Africa (Chippaux, 2011). Even more alarming are the figures reported for India, where about 49,000 people succumb to snake bites annually (Mohapatra et al., 2011).

The large herbivores, most notably the elephant and buffalo, also caused many conflicts that resulted in costly compensation claims. Specifically, the elephant was the single most important conflict species, contributing about 80% of crop and property damage. Moreover, the elephant and the buffalo caused 268 and 106 human deaths, respectively. Elephant conflicts were most common in Taita Taveta and Meru Counties. Taita Taveta is an elephant conflict hotspot (Smith and Kasiki, 2000) due to the high elephant population density (Ngene et al., 2017) in the adjacent Tsavo East and West National Parks. Meru County hosts the Meru National Park and part of the Mount Kenya National Parks, which contain many elephants and buffaloes. It would thus be interesting to examine how an interaction between species abundance and proximity to PA influence HWC occurrence in details, something we did not fully undertake during this research. The number of crop raiding incidents increased with increase in the percent of each County under national parks or reserves. For instance, about 60% of the total area of Taita Taveta and 36% of Meru Counties are under protection. This finding therefore supports the observation that areas proximal to protected areas have high frequencies of HWC (Sarker and Røskaft, 2014; Johnson et al., 2018). The elephant ranked (over 80%) as the most problematic animal causing conflicts due to crop damages in Northern India (Ogra and Badola, 2008). As well, elephant and buffalo conflicts varied seasonally, with bimodal peaks apparent during the dry season months of February and July, when crops are being harvested. The high food requirements of these large herbivores and the high nutritive content of crops (Conover, 2001) further increase the likelihood of their involvement in conflicts. The buffalo caused notably many conflicts in Tana River and Narok Counties, likely because these counties are inhabited by pastoral communities who are more exposed to buffalo interactions when herding livestock.

Large carnivores including the spotted hyena, leopard, and lion caused over 85% of livestock predation cases during 2005-2016, consistent with findings of other studies in Tsavo (Patterson et al., 2004) and

Maasai Mara (Kolowski and Holekamp, 2006) in Kenya and Serengeti in Tanzania (Holmern et al., 2007; Lyamuya et al., 2016). The spotted hyena and leopard caused more conflicts in the pastoral counties of Laikipia and Narok with large and increasing livestock populations. That the wild dog caused 6.0% of the reported livestock predation cases is noteworthy because it is an endangered species (Woodroffe and Sillero-Zubiri, 2012) and this may thus drive it faster towards extinction through retaliatory killings (Maclennan et al., 2009). Conflicts thus undermine carnivore conservation and call for effective compensation schemes to help ameliorate their impacts on wildlife species.

Temporal and Demographic Variation in Compensation Claims During 2007-2016

The steady increase in the number of HWC cases filed for compensation with the KNCS over the 10-year period was likely due to three factors, two of which are linked to Act 2013. First, as with India (Karanth et al., 2013), HWCs in Kenya have been on the rise as a result of increasing climatic variability (rainfall and temperature), human population, habitat fragmentation and livestock numbers in the rangelands (Ogutu et al., 2016). Rainfall governs the availability and quality of food and water for herbivores (Ogutu and Owen-Smith, 2006), so that reduced rainfall should intensify competition between wildlife and livestock. Second, the sudden spike in HWC between 2013 (n = 1,541) and 2014 (n = 5,020), was likely caused by the increased compensation amounts introduced under Act 2013. Third, livestock predation, crop raiding and other property damage conflict types were reinstated as payable claims under Act 2013, prompting people to launch claims as opposed to the preceding period when compensation for such conflicts was not permitted. This number should therefore stabilize in future under the current Wildlife Act, but at a higher average value than under the repealed Cap 376. Thus, monetary compensation, and in particular an attractive amount as specified in Act 2013, can act as an effective mitigation measure for losses or damages associated with human-wildlife conflicts.

A significant number (about 80%) of the claims filed were approved by the KNCS for payment, while very few were rejected. But, like other compensation programmes, the KNCS suffers from inadequate funding, logistical hurdles and delayed payments (Nyhus et al., 2005; Ogra and Badola, 2008; Johnson et al., 2018). For instance, operationalization of the KNCS as specified in the Act 2013 was delayed, as the various County Wildlife Conservation and Compensation Committees (CWCCC) were being constituted. Even so, the number of cases approved for compensation was more than the number of cases actually paid possibly due to inadequate, and sometimes, delayed release of funds. Also, compensation can be delayed because verification (Nyhus et al., 2005; Ogra and Badola, 2008) is a slow process that involves multiple institutions (Nyhus et al., 2005; Ogra and Badola, 2008) and because of remoteness of some areas experiencing HWCs. Many rejected filed cases were related to snake conflicts, mirroring the difficulty of verifying and ascertaining injuries caused by snake bites, compared with, for example, a large carnivore attack on humans which often leaves clearly observable physical marks on the victim.

More males than females and adults than children were either killed or injured by wildlife, suggesting that more males than females engaged in activities that exposed them to greater risks of wildlife attacks. This may also mean that females and children were less able to file compensation claims than males or adults. For, instance, more males than females are likely to be found herding livestock and fishing where they are more likely to come into contact with wildlife. Further, males will often confront wild animals that threaten their families, livestock, or property (Kaltenborn et al., 2006; Carter and Allendorf, 2016). Thus, gender is an important demographic variable influencing attitude (Kellert and Berry, 1987) and hence predictor of the number of people killed or injured in human-wildlife conflicts. Adults were also more likely to be killed or injured by wildlife than were children probably for similar reasons. Although, the percentage of children killed in HWC was relatively high (38.1%), we did not have data to ascertain the circumstances under which they were killed.

Cost of Compensating for Losses Caused by Human-Wildlife Conflicts in Kenya

The wildlife legislation in Kenya is relatively robust, allowing compensation to be made for multiple wildlife species and conflict outcomes. Over the three years (2014 - 2016) Act 2013 was in operation, a total of about KES 2.7 billion was spent on compensation, which is nine times the amount spent during the seven years spanning 2007 - 2013 under Cap 376. However, only 35% of the filed compensation claims were honored by the KNCS. This is comparable with 31% of the cases that were compensated for Nepal (Karanth et al., 2013), a developing country with similar economic constraints to Kenya. The total compensation claims from 2007 to 2016 translated to about 3 billion Kenya Shillings, half of which was used on snake related conflicts alone. Yet, the Kenya government fell short of the budgetary requirements for compensating all human-wildlife conflicts. This is not unique to Kenya as even a highly developed country, such as the US, spent only $60 million on compensation in 2001 (Treves et al., 2006), which is far less than the cost of total losses in that year estimated by farmers at $2 billion (Messmer, 2000).

Wildlife-based tourism is an important source of revenue (Akama, 2000; Kibara et al., 2012), accounting for about 10% of the Gross Domestic Product (GDP) of Kenya in 2010 (GoK, 2010). Thus, the KNCS spent merely about 0.2% of the total revenue earned from tourism during the 10 years on compensation, translating to about 0.02% annually. This is a paltry amount compared with the contribution of wildlife to the national economy. The government of Kenya should therefore seriously consider allocating more funds for HWC compensation or mitigation strategies to minimize retributive 'killing of the goose that lays the golden egg'. Thus, committing even about 2% of the annual tourism earnings to compensation for HWC can significantly reduce the number of uncompensated claims. This can likely and immensely foster conservation good will from the affected communities and enhance sustainable conservation of biodiversity in Kenya as is happening in the Amboseli region (Hazzah et al., 2014; Maclennan et al., 2009).

An important question is whether the introduction of Act 2013 with higher compensation rates than Cap 376 actually increased compensation claims. The higher amount paid out from 2014 probably incentivized those who were previously likely to be less willing to file for HWC compensation claims. Victims of HWCs are now more likely to launch compensation claims because it is more economically attractive to do so than it was in the period before 2013. Nonetheless, the procedures for filing a compensation claim remain elaborate, long, tedious and often expensive, depending on where one is launching the claim from. A person seeking compensation may have to visit a hospital, meet with the police and the KWS officer(s) in the county. Although this will often require money and time like it did before 2013, victims or their relatives are now more motivated to follow up compensation claims because of the greater expected reward. However, high compensation can have negative unintended consequences, including motivating potential claimants to exaggerate or launch fraudulent claims (Bulte and Rondeau, 2007). Moreover, compensation for crop damage can accelerate habitat destruction, especially in marginalized regions (Bulte and Rondeau, 2007), such as large parts of the Kenya rangelands, if people regard it as an alternative source of income. As a result, the long-term sustainability of compensation schemes, such as KNCS, rests on effective administration to ensure that only deserving cases are promptly compensated.

CONCLUSION AND RECOMMENDATIONS

Human-wildlife conflicts were common across Kenya and involved many wildlife species, with marked inter-specific distinctions in the level of their contributions to the conflicts. The conflicts caused substantial human fatalities, injuries, livestock depredation, crop destruction and damage to other private properties. The intensity of the conflicts varied in space, between years and across months, reflecting underlying rainfall and temperature fluctuations.

Compensation for the losses associated with the conflicts was a negligible fraction (0.2%) of the contemporaneous total annual tourism revenue, driven largely by eco-tourism based on wildlife viewing. Because compensation for losses caused by HWC is essential to fostering positive attitudes towards wildlife conservation, it is strongly advisable to increase the percentage of tourism revenue allocated for compensation.

The bulk of compensation during 2007-2016 went to snake-related fatalities and injuries. Long-term strategies for ameliorating the problem of snake bites could involve making antivenoms more accessible and affordable in hotspots of such conflicts. Further, field studies should investigate why snake conflicts are very frequent and the conditions under which they occur to guide the development of effective mitigation strategies. Furthermore, crop and livestock depredation and damage to private properties should be considered to minimize negative attitudes toward wildlife conservation in human-dominated landscapes.

Compensation for losses caused by human-wildlife conflicts is substantial and expected to increase as increasing human population, land use developments and widening climatic variability reduce the space, food and water for wildlife. Consequently, it is essential to develop sustainable funding mechanisms for compensation schemes such as KNCS.

It is important to evaluate but also to monitor the effectiveness of compensation schemes such as KNCS to establish if compensation is actually targeting the true victims, ameliorating HWC, improving attitudes and thereby promoting biodiversity conservation. Schemes should also be administered effectively and incorporate robust mechanisms for ensuring that filed claims are genuine, are expeditiously processed and concluded, minimize fraudulent claims and other negative unintended consequences.

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APPENDIX

Table A. 1

Common English names and scientific names of species mentioned in the text.

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

No	Common English name of species	*Scientific name of species or closest taxon class*	Frequency
1.	Antelope (various species)	*Bovidae family*	4
2.	Baboons	*Papio spp.*	48
3.	Buffalo	*Syncerus caffer*	624
4.	Bushbaby	*Galago spp.*	1
5.	Bushbuck	*Tragelaphus scriptus*	1
6.	Cheetah	*Acinonyx jubatus*	77
7.	Civet	family *Viverridae*	1
8.	Crocodile	*Crocodylus niloticus*	653
9.	Eland	*Taurotragus oryx*	31
10.	Elephant	*Loxodonta africana*	4141
11.	Fox	*Canidae*	45
12.	Genet	*Reptilia*	1
13.	Giraffe	*Giraffa camelopardalis*	4
14.	Hippopotamus	*Hippopotamus amphibius*	564
15.	Honey badger	*mellivora capensis*	47
16.	Impala	*Aepyceros melampus*	2
17.	Jackal	genus *canis*	16

No	Common English name of species	*Scientific name of species or closest taxon class*	Frequency
18.	Leopard	*Panthera pardus*	855
19.	Lesser kudu	*Tragelaphus imberbis*	5
20.	Lion	*Panthera leo*	755
21.	Mongoose	family *herpestidae*	23
22.	Monitor lizard	Genus: Varanus	2
23.	Monkeys	*Cercopithecus spp.*	31
24.	Ostrich	*Struthio camelus*	3
25.	Porcupine	*Apis mellifera scutellata*	3
26.	Reptile		1
27.	Rock hyrax	*Procavia capensis*	4
28.	Serval cat	*Leptailurus serval*	11
29.	Snake	*Serpentes suborder*	8,423
30.	Spotted hyena	*Crocuta crocuta*	1230
31.	Stingray	*Taeniura meyeni*	15
32.	Stonefish	*Synanceia verrucosa*	6
33.	squirrel	sciurids	8
34.	Warthog	*Phacochoerus africanus*	22
35.	Wild cat	*Felis silvestris*	6
36.	Wild dog	*Lycaon pictus*	236
37.	Wild pig	*Sus scrofa*	68
38.	Wildebeest	*Connochaetes taurinus*	4
39.	Zebra	*Equus quagga*	479

Table A. 2

Human-wildlife conflict compensation cases by county for the period 2007-2016.

No	**County**	**Crop damage**		**Human death**		**Human injury**		**Predation**		**Property damage**		**Pearson test**	**Chi-square**	
		n	%	n	%	n	%	n	%	n	%	χ^2	df	P
1.	Baringo	225	4.9	47	3.3	478	4.7	64	2.4	0	0.0	34.12	4	0.001
2.	Bomet	12	0.3	0	0.0	14	0.1	32	1.2	0	0.0	85.72	4	0.001
3.	Bungoma	0	0.0	2	0.1	1	0.0	0	0.0	0	0.0	15.22	4	0.004
4.	Busia	0	0.0	3	0.2	47	0.5	1	0.0	0	0.0	32.07	4	0.001
5.	Elgeyo Marakwet	44	1.0	25	1.8	164	1.6	32	1.2	0	0.0	12.47	4	0.014
6.	Embu	36	0.8	33	2.3	376	3.7	9	0.3	0	0.0	173.56	4	0.001
7.	Garissa	14	0.3	64	4.5	299	3.0	93	3.6	1	3.8	135.38	4	0.001
8.	Homa Bay	10	0.2	18	1.3	32	0.3	20	0.8	1	3.8	45.00	4	0.001
9.	Isiolo	261	5.6	27	1.9	171	1.7	117	4.5	1	3.8	191.84	4	0.001
10.	Kajiado		0.0	66	4.6	405	4.0	43	1.6	0	0.0	223.00	4	0.001
11.	Kakamega	0	0.0	2	0.1	32	0.3	4	0.2	0	0.0	16.54	4	0.002
12.	Kericho	0	0.0	0	0.0	16	0.2	42	1.6	0	0.0	169.64	4	0.001
13.	Kiambu	0	0.0	15	1.1	9	0.1	11	0.4	0	0.0	79.18	4	0.001
14.	Kilifi	1	0.0	47	3.3	289	2.9	19	0.7	0	0.0	172.56	4	0.001
15.	Kirinyaga	2	0.0	0	0.0	38	0.4	0	0.0	0	0.0	27.57	4	0.001
16.	Kisii*	0	0.0	1	0.1	3	0.0	0	0.0	0	0.0	3.48	4	0.481
17.	Kisumu	21	0.5	17	1.2	52	0.5	25	1.0	0	0.0	16.69	4	0.002
18.	Kitui	0	0.0	101	7.1	1309	12.9	0	0.0	0	0.0	1020.92	4	0.001

No	County	Crop damage		Human death		Human injury		Predation		Property damage		Pearson test	Chi-square	
19.	Kwale	129	2.8	46	3.2	375	3.7	48	1.8	1	3.8	26.70	4	0.001
20.	Laikipia	526	11.4	49	3.4	113	1.1	139	5.3	2	7.7	801.54	4	0.001
21.	Lamu	17	0.4	49	3.4	429	4.2	6	0.2	1	3.8	253.65	4	0.001
22.	Machakos	0	0.0	29	2.0	96	0.9	23	0.9	0	0.0	69.01	4	0.001
23.	Makueni	225	4.9	58	4.1	412	4.1	27	1.0	8	30.8	120.25	4	0.001
24.	Mandera	7	0.2	80	5.6	653	6.5	129	4.9	0	0.0	291.84	4	0.001
25.	Marsabit	0	0.0	61	4.3	817	8.1	0	0.0	0	0.0	620.00	4	0.001
26.	Meru	992	21.5	38	2.7	150	1.5	50	1.9	1	3.8	2230.28	4	0.001
27.	Migori	0	0.0	6	0.4	10	0.1	3	0.1	0	0.0	19.22	4	0.001
28.	Mombasa	0	0.0	0	0.0	13	0.1	0	0.0	0	0.0	11.17	4	0.025
29.	Muranga*	2	0.0	0	0.0	7	0.1	6	0.2	0	0.0	9.44	4	0.051
30.	Nairobi*	0	0.0	1	0.1	9	0.1	0	0.0	0	0.0	6.38	4	0.173
31.	Nakuru	37	0.8	19	1.3	93	0.9	50	1.9	2	7.7	34.66	4	0.001
32.	Nandi	0	0.0	1	0.1	14	0.1	0	0.0	0	0.0	10.18	4	0.038
33.	Narok	154	3.3	99	7.0	312	3.1	255	9.7	1	3.8	256.59	4	0.001
34.	Nyandarua	35	0.8	5	0.4	12	0.1	5	0.2	0	0.0	44.16	4	0.001
35.	Nyeri	316	6.8	11	0.8	12	0.1	88	3.4	0	0.0	674.13	4	0.001
36.	Samburu	454	9.8	39	2.7	216	2.1	670	25.6	5	19.2	1777.35	4	0.001
37.	Siaya	23	0.5	21	1.5	25	0.2	5	0.2	0	0.0	52.08	4	0.001
38.	Taita Taveta	789	17.0	67	4.7	534	5.3	265	10.1	2	7.7	584.62	4	0.001
39.	Tana River	266	5.7	112	7.9	529	5.2	214	8.2	0	0.0	44.04	4	0.001

No	County	Crop damage		Human death		Human injury		Predation		Property damage		Pearson test	Chi-square	
40.	Tharaka Nithi	12	0.3	11	0.8	295	2.9	4	0.2	0	0.0	190.76	4	0.001
41.	Trans Nzoia	7	0.2	3	0.2	9	0.1	8	0.3	0	0.0	7.43	4	0.115
42.	Turkana	0	0.0	21	1.5	101	1.0	0	0.0	0	0.0	81.66	4	0.001
43.	Uasin Gishu	0	0.0	0	0.0	0	0.0	3	0.1	0	0.0	18.60	4	0.001
44.	Vihiga*	0	0.0	1	0.1	2	0.0	0	0.0	0	0.0	3.88	4	0.423
45.	Wajir	0	0.0	107	7.5	998	9.9	95	3.7	0	0.0	558.50	4	0.001
46.	West Pokot	5	0.1	22	1.5	140	1.4	6	0.2	0	0.0	77.31	4	0.001

*Non significant cases

Table A. 3: Results of the negative binomial parameter for the 20 ranges counties in Kenya 2007-2016

Type of trend	**Outcome**	**Effect**	**County**	**Estimate**	**Standard Error**	**DF**	**t Value**	**Pr > |t|**
Inter-annual	Human Death	County	BARINGO	39.5516	12.5832	158	3.14	0.002
	Human Death	County	ELGEYO MARAKWET	2.9879	4.8332	158	0.62	0.5373
	Human Death	County	GARISSA	-6.5912	4.4011	158	-1.5	0.1362
	Human Death	County	ISIOLO	-12.7773	5.2317	158	-2.44	0.0157
	Human Death	County	KAJIADO	-18.3739	7.8188	158	-2.35	0.02
	Human Death	County	KILIFI	-13.1449	3.6628	158	-3.59	0.0004
	Human Death	County	KITUI	-4.6134	4.8011	158	-0.96	0.3381
	Human Death	County	KWALE	-8.9529	4.4316	158	-2.02	0.045
	Human Death	County	LAIKIPIA	-9.1686	10.3877	158	-0.88	0.3788
	Human Death	County	LAMU	-5.48	4.0307	158	-1.36	0.1759
	Human	County	MACHAKOS	-3.2194	9.8307	158	-0.33	0.7437

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Death							
	Human Death	County	MANDERA	-17.0061	3.0219	158	-5.63	<.0001
	Human Death	County	MARSABIT	-16.3031	4.3966	158	-3.71	0.0003
	Human Death	County	NAROK	34.8955	17.3975	158	2.01	0.0466
	Human Death	County	SAMBURU	22.7577	8.3875	158	2.71	0.0074
	Human Death	County	TAITA TAVETA	-5.3239	5.7676	158	-0.92	0.3574
	Human Death	County	TANA RIVER	-1.5953	3.2349	158	-0.49	0.6226
	Human Death	County	TURKANA	25.8671	11.0573	158	2.34	0.0206
	Human Death	County	WAJIR	-11.1203	2.6762	158	-4.16	<.0001
	Human Death	County	WEST POKOT	14.7206	5.4272	158	2.71	0.0074
	Human Death	Rainfall		-0.00653	0.003403	158	-1.92	0.0569
	Human Death	Rainfall*TMax		0.000238	0.000111	158	2.15	0.0333

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Death	TMax*County	BARINGO	-1.5699	0.4147	158	-3.79	0.0002
	Human Death	TMax*County	ELGEYO MARAKWET	-0.3645	0.1647	158	-2.21	0.0283
	Human Death	TMax*County	GARISSA	-0.08618	0.1296	158	-0.67	0.507
	Human Death	TMax*County	ISIOLO	0.08927	0.1522	158	0.59	0.5583
	Human Death	TMax*County	KAJIADO	0.3553	0.2732	158	1.3	0.1954
	Human Death	TMax*County	KILIFI	0.1285	0.1148	158	1.12	0.2648
	Human Death	TMax*County	KITUI	-0.1298	0.1491	158	-0.87	0.3854
	Human Death	TMax*County	KWALE	0.02117	0.1429	158	0.15	0.8824
	Human Death	TMax*County	LAIKIPIA	0.06406	0.3902	158	0.16	0.8698
	Human Death	TMax*County	LAMU	-0.08288	0.1261	158	-0.66	0.5118
	Human Death	TMax*County	MACHAKOS	-0.1539	0.3302	158	-0.47	0.6419
	Human	TMax*County	MANDERA	0.2483	0.08994	158	2.76	0.0064

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Death							
	Human Death	TMax*County	MARSABIT	0.1942	0.1335	158	1.45	0.1478
	Human Death	TMax*County	NAROK	-1.634	0.6757	158	-2.42	0.0167
	Human Death	TMax*County	SAMBURU	-1.0275	0.273	158	-3.76	0.0002
	Human Death	TMax*County	TAITA TAVETA	-0.0968	0.1865	158	-0.52	0.6045
	Human Death	TMax*County	TANA RIVER	-0.2116	0.09697	158	-2.18	0.0305
	Human Death	TMax*County	TURKANA	-1.0796	0.3276	158	-3.3	0.0012
	Human Death	TMax*County	WAJIR	0.056	0.07868	158	0.71	0.4777
	Human Death	TMax*County	WEST POKOT	-0.7789	0.1818	158	-4.28	<.0001
	Human Death	Scale		0.06674	0.02646	.	.	.
	Human Injury	County	BARINGO	42.3775	12.1107	158	3.5	0.0006
	Human Injury	County	ELGEYO MARAKWET	16.9818	5.0914	158	3.34	0.0011

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Injury	County	GARISSA	-13.4912	5.0557	158	-2.67	0.0084
	Human Injury	County	ISIOLO	-23.2781	4.7392	158	-4.91	<.0001
	Human Injury	County	KAJIADO	-18.7826	9.2503	158	-2.03	0.044
	Human Injury	County	KILIFI	-8.6663	3.8976	158	-2.22	0.0276
	Human Injury	County	KITUI	1.3594	6.2232	158	0.22	0.8274
	Human Injury	County	KWALE	-17.2233	4.9394	158	-3.49	0.0006
	Human Injury	County	LAIKIPIA	18.9085	11.5551	158	1.64	0.1038
	Human Injury	County	LAMU	7.6552	4.309	158	1.78	0.0776
	Human Injury	County	MACHAKOS	-16.9104	12.6845	158	-1.33	0.1844
	Human Injury	County	MANDERA	-18.8776	3.7367	158	-5.05	<.0001
	Human Injury	County	MARSABIT	-21.8412	5.0183	158	-4.35	<.0001
	Human	County	NAROK	26.0678	27.3678	158	0.95	0.3423

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Injury							
	Human Injury	County	SAMBURU	37.4861	8.4207	158	4.45	<.0001
	Human Injury	County	TAITA TAVETA	-19.9299	6.7182	158	-2.97	0.0035
	Human Injury	County	TANA RIVER	-10.2041	4.122	158	-2.48	0.0144
	Human Injury	County	TURKANA	28.6115	9.0585	158	3.16	0.0019
	Human Injury	County	WAJIR	-8.6634	3.5351	158	-2.45	0.0153
	Human Injury	County	WEST POKOT	12.7362	4.769	158	2.67	0.0084
	Human Injury	Rainfall		-0.00936	0.004069	158	-2.3	0.0227
	Human Injury	Rainfall*TMax		0.000353	0.000132	158	2.68	0.0081
	Human Injury	TMax*County	BARINGO	-1.6059	0.3968	158	-4.05	<.0001
	Human Injury	TMax*County	ELGEYO MARAKWET	-0.8224	0.1702	158	-4.83	<.0001
	Human Injury	TMax*County	GARISSA	0.141	0.1485	158	0.95	0.3439

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Injury	TMax*County	ISIOLO	0.4307	0.1385	158	3.11	0.0022
	Human Injury	TMax*County	KAJIADO	0.4244	0.3241	158	1.31	0.1922
	Human Injury	TMax*County	KILIFI	0.02762	0.1236	158	0.22	0.8235
	Human Injury	TMax*County	KITUI	-0.2529	0.1931	158	-1.31	0.1921
	Human Injury	TMax*County	KWALE	0.3165	0.1597	158	1.98	0.0492
	Human Injury	TMax*County	LAIKIPIA	-0.9675	0.4354	158	-2.22	0.0277
	Human Injury	TMax*County	LAMU	-0.4388	0.1341	158	-3.27	0.0013
	Human Injury	TMax*County	MACHAKOS	0.3512	0.426	158	0.82	0.411
	Human Injury	TMax*County	MANDERA	0.3526	0.1124	158	3.14	0.002
	Human Injury	TMax*County	MARSABIT	0.4276	0.1533	158	2.79	0.0059
	Human Injury	TMax*County	NAROK	-1.2492	1.0602	158	-1.18	0.2405
	Human	TMax*County	SAMBURU	-1.464	0.2724	158	-5.37	<.0001

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Injury							
	Human Injury	TMax*County	TAITA TAVETA	0.4241	0.2169	158	1.96	0.0523
	Human Injury	TMax*County	TANA RIVER	0.0689	0.1225	158	0.56	0.5747
	Human Injury	TMax*County	TURKANA	-1.1256	0.2667	158	-4.22	<.0001
	Human Injury	TMax*County	WAJIR	0.03783	0.1038	158	0.36	0.7159
	Human Injury	TMax*County	WEST POKOT	-0.6654	0.1555	158	-4.28	<.0001
	Human Injury	Scale		0.2651	0.03218	.	.	.
Seasonal	Human Death	County	BARINGO	-2.6874	5.3538	199	-0.5	0.6162
	Human Death	County	ELGEYO MARAKWET	6.8356	6.0395	199	1.13	0.2591
	Human Death	County	GARISSA	-12.9249	3.2332	199	-4	<.0001
	Human Death	County	ISIOLO	-12.4509	5.3473	199	-2.33	0.0209
	Human Death	County	KAJIADO	-5.3008	2.2481	199	-2.36	0.0193

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Death	County	KILIFI	-7.4434	2.9002	199	-2.57	0.011
	Human Death	County	KITUI	-10.6503	2.351	199	-4.53	<.0001
	Human Death	County	KWALE	-7.1539	2.7759	199	-2.58	0.0107
	Human Death	County	LAIKIPIA	-14.3807	3.8673	199	-3.72	0.0003
	Human Death	County	LAMU	-7.0804	3.1194	199	-2.27	0.0243
	Human Death	County	MACHAKOS	-14.2176	2.3932	199	-5.94	<.0001
	Human Death	County	MANDERA	-5.6974	2.4948	199	-2.28	0.0234
	Human Death	County	MARSABIT	-7.8764	3.3624	199	-2.34	0.0201
	Human Death	County	NAROK	-7.4691	2.0576	199	-3.63	0.0004
	Human Death	County	SAMBURU	3.0838	5.6561	199	0.55	0.5862
	Human Death	County	TAITA TAVETA	-5.7872	2.4216	199	-2.39	0.0178
	Human	County	TANA	-6.9735	2.3258	199	-3	0.0031

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Death		RIVER					
	Human Death	County	TURKANA	-26.2115	7.0996	199	-3.69	0.0003
	Human Death	County	WAJIR	-10.5129	2.2323	199	-4.71	<.0001
	Human Death	County	WEST POKOT	-8.5956	6.1846	199	-1.39	0.1661
	Human Death	Rainfall		0.001118	0.000835	199	1.34	0.1821
	Human Death	TMax*County	BARINGO	-0.1765	0.178	199	-0.99	0.3224
	Human Death	TMax*County	ELGEYO MARAKWET	-0.5033	0.2162	199	-2.33	0.0209
	Human Death	TMax*County	GARISSA	0.115	0.09573	199	1.2	0.2312
	Human Death	TMax*County	ISIOLO	0.09302	0.1608	199	0.58	0.5636
	Human Death	TMax*County	KAJIADO	-0.1116	0.0827	199	-1.35	0.1789
	Human Death	TMax*County	KILIFI	-0.02256	0.09389	199	-0.24	0.8104
	Human Death	TMax*County	KITUI	0.07518	0.07404	199	1.02	0.3112

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Death	TMax*County	KWALE	-0.01952	0.09158	199	-0.21	0.8315
	Human Death	TMax*County	LAIKIPIA	0.2489	0.1463	199	1.7	0.0905
	Human Death	TMax*County	LAMU	-0.01028	0.0987	199	-0.1	0.9171
	Human Death	TMax*County	MACHAKOS	0.2248	0.0815	199	2.76	0.0064
	Human Death	TMax*County	MANDERA	-0.0811	0.0778	199	-1.04	0.2985
	Human Death	TMax*County	MARSABIT	-0.05587	0.1062	199	-0.53	0.5995
	Human Death	TMax*County	NAROK	-0.01268	0.08262	199	-0.15	0.8782
	Human Death	TMax*County	SAMBURU	-0.3872	0.1847	199	-2.1	0.0373
	Human Death	TMax*County	TAITA TAVETA	-0.0766	0.08083	199	-0.95	0.3445
	Human Death	TMax*County	TANA RIVER	-0.04267	0.0704	199	-0.61	0.5451
	Human Death	TMax*County	TURKANA	0.4554	0.2046	199	2.23	0.0272
	Human	TMax*County	WAJIR	0.05149	0.0667	199	0.77	0.4411

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Death							
	Human Death	TMax*County	WEST POKOT	-0.0001	0.1988	199	0	0.9996
	Human Death	Scale		0.03314	0.01998	.	.	.
	Human Injury	County	BARINGO	-5.8445	0.1472	200	-39.71	<.0001
	Human Injury	County	ELGEYO MARAKWET	-5.3534	0.2107	200	-25.41	<.0001
	Human Injury	County	GARISSA	-7.6957	0.1052	200	-73.16	<.0001
	Human Injury	County	ISIOLO	-7.6635	0.1251	200	-61.28	<.0001
	Human Injury	County	KAJIADO	-6.9316	0.1099	200	-63.08	<.0001
	Human Injury	County	KILIFI	-6.6021	0.1537	200	-42.96	<.0001
	Human Injury	County	KITUI	-5.8846	0.06308	200	-93.29	<.0001
	Human Injury	County	KWALE	-5.8683	0.1396	200	-42.03	<.0001
	Human Injury	County	LAIKIPIA	-6.4966	0.2556	200	-25.42	<.0001

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Injury	County	LAMU	-5.2561	0.1021	200	-51.47	<.0001
	Human Injury	County	MACHAKOS	-6.0465	0.08908	200	-67.88	<.0001
	Human Injury	County	MANDERA	-6.3481	0.07211	200	-88.04	<.0001
	Human Injury	County	MARSABIT	-7.081	0.07988	200	-88.64	<.0001
	Human Injury	County	NAROK	-6.6018	0.1946	200	-33.93	<.0001
	Human Injury	County	SAMBURU	-7.1538	0.1431	200	-49.98	<.0001
	Human Injury	County	TAITA TAVETA	-6.0898	0.09301	200	-65.47	<.0001
	Human Injury	County	TANA RIVER	-6.9097	0.08669	200	-79.7	<.0001
	Human Injury	County	TURKANA	-9.1757	0.2812	200	-32.64	<.0001
	Human Injury	County	WAJIR	-6.563	0.06223	200	-105.46	<.0001
	Human Injury	County	WEST POKOT	-7.3298	0.2521	200	-29.08	<.0001
	Human	Rainfall*Coun	BARINGO	0.003282	0.001783	200	1.84	0.0671

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Injury							
	Human Injury	Rainfall*Coun	ELGEYO MARAKWET	0.000326	0.002041	200	0.16	0.8732
	Human Injury	Rainfall*Coun	GARISSA	0.005261	0.001805	200	2.91	0.004
	Human Injury	Rainfall*Coun	ISIOLO	0.005207	0.002545	200	2.05	0.0421
	Human Injury	Rainfall*Coun	KAJIADO	0.00782	0.001504	200	5.2	<.0001
	Human Injury	Rainfall*Coun	KILIFI	0.005154	0.001975	200	2.61	0.0097
	Human Injury	Rainfall*Coun	KITUI	0.003654	0.000678	200	5.39	<.0001
	Human Injury	Rainfall*Coun	KWALE	0.004426	0.001863	200	2.38	0.0185
	Human Injury	Rainfall*Coun	LAIKIPIA	-0.00766	0.004246	200	-1.8	0.0726
	Human Injury	Rainfall*Coun	LAMU	0.001396	0.00107	200	1.31	0.1934
	Human Injury	Rainfall*Coun	MACHAKOS	0.003339	0.000993	200	3.36	0.0009
	Human Injury	Rainfall*Coun	MANDERA	0.005592	0.001545	200	3.62	0.0004

Type of trend	Outcome	Effect	County	Estimate	Standard Error	DF	t Value	Pr > |t|
	Human Injury	Rainfall*Coun	MARSABIT	0.00205	0.002043	200	1	0.317
	Human Injury	Rainfall*Coun	NAROK	0.000749	0.001924	200	0.39	0.6974
	Human Injury	Rainfall*Coun	SAMBURU	0.002089	0.002873	200	0.73	0.468
	Human Injury	Rainfall*Coun	TAITA TAVETA	0.002486	0.001367	200	1.82	0.0704
	Human Injury	Rainfall*Coun	TANA RIVER	0.002924	0.001583	200	1.85	0.0662
	Human Injury	Rainfall*Coun	TURKANA	0.008245	0.008803	200	0.94	0.3501
	Human Injury	Rainfall*Coun	WAJIR	0.001205	0.001321	200	0.91	0.363
	Human Injury	Rainfall*Coun	WEST POKOT	0.01038	0.003618	200	2.87	0.0045
	Human Injury	Scale		0.01357	0.003557	.	.	.

TMax - Maximum temperature in ^{o}C. * between effects represents an interaction. SE - Standard error, Df - Degree of freedom

Catalogue

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species

2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation

2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal

			Photosynthesis and Physiology
2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment

2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2

2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.

2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological context to functional integration