Spatial and temporal dynamics of human–wildlife conflicts in the Kenya Greater Tsavo Ecosystem

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Abstract: Biodiversity conservation in developing countries is faced with many and mounting challenges, including increasing huWcs, particularly those adjacent to protected areas, can adversely affect local stakeholder perceptions and support for conservation. We analyzed HWC reports for multiple wildlife species compiled >23 years (1995–2017) from the Greater Tsavo Ecosystem (GTE) in Kenya to determine HWC trends. The GTE is the largest protected area in Kenya, covering 22,681 km². Overall, 39,022 HWC incidents were reported in 6 GTE regions (i.e., Taveta, Mutomo, Kibwezi, Rombo, Galana, Bachuma). The 5 wildlife species most often implicated in HWC incidents were the African elephant (*Loxodonta africana*, 61.6%, *n* = 24,032), nonhuman primates (11.5%, *n* = 4,480), buffalo (*Syncerus caffer*, 6.2%, *n* = 2,432), African lion (*Panthera leo*, 4.2%, *n* = 1,645), and the hippopotamus (*Hippopotamus amphibius*, 3.8%, *n* = 1,497). The HWC reports also revealed spatial distinctions across the 6 GTE regions. More human–elephant conflicts (HECs; 43.3%, *n* = 10,427) were reported in the Taveta Rombo, and Mutomo region was the epicenter of primate, snake, and python (*Python* spp.) conflicts. More large carnivore depredations on livestock were reported in the Taveta Rombo, and Mutomo regions. Lions, spotted hyenas (*Crocuta crocuta*), and leopards (*P. pardus*) were implicated in more livestock depredations than other carnivores. The number of HWCs reported varied by year and season and were related to similar variations in the availability, quality, and distribution of food and water governed by rainfall fluctuations. Reported HECs were positively and linearly related to human, elephant, and livestock population densities. The Kenya Wildlife Service responded to >90% of the reported HWCs. In general, the number of HWCs and trends reported were higher in the regions that also exhibited the highest human population growth rates and densities. Sustainable biodiversity conservation in human-dominated landscapes i

Key words: Africa, biodiversity, carnivores, climate change, conservation, human population growth, human–wildlife conflicts, land-use change, livestock, protected areas

HUMAN–WILDLIFE CONFLICTS (HWCs) pose emerging challenges to biodiversity conservation in many ecosystems worldwide (Messmer 2000). In Africa, HWCs are exacerbated because of the diverse species of wildlife that 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 >80% of lessindustrialized nations depend (Mooney et al. 1997, Solomon 2007). Because biodiversity loss is often irreversible (Reed 2012), it is paramount that HWCs be mitigated.

Human–wildlife conflicts occur when resources are limited, leading to competition between humans and wildlife (Messmer 2000, Graham et al. 2005). Thus, human population growth and climate change in Africa pose serious conservation challenges as increasing per capita demand for resources exacerbates degradation and fragmentation of wildlife ecosystems. For example, increased bush meat harvesting for human use can severely impact ungulate off take and therefore change predator–prey population dynamics (Rentsch and Packer 2015, Allendorf and Hard 2009), leading to increased livestock depredation. Climate change, particularly 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). Thus, climate change may have long-term implications for the frequency and intensity of HWCs.

The Greater Tsavo Ecosystem (GTE), located in southeastern Kenya, is the largest contiguous protected area system in Kenya. However, wildlife regularly roam 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 may develop negative attitudes toward wildlife because they derive no benefits from the various programs of wildlife utilization (Smith and Kasiki 2000). Thus, wildlife may be viewed as a liability to their livelihood and, therefore, affected community members may resort to retaliatory killing of wildlife 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 GTE date as far back as the late twentieth century when the Kenya-Uganda railway was being built. The GTE became infamous then for the "Tsavo man eaters" - lions (Panthera leo) that hunted and killed many railway workers during this period (Kerbis Peterhans and Gnoske 2001).

Herein we analyze HWCs reported for 20 wildlife species around the GTE 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, cheetah (Acinonyx jubatus), and leopard (P. pardus; Patterson et al. 2004). Research on HWCs involving multiple species are very rare, and few have been completed in Kenya (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 previous research in that we analyze temporal and spatial dynamics of HWCs and the associated conflict species for 23 years. To complete our analysis, we accessed HWC data collected by the Kenya Wildlife Service (KWS) at the Tsavo Research Center from 1995 to 2017 and on wildlife mortality due to HWCs collected by the KWS Security Division from 1995 to 2016. Such long-term datasets provide a unique opportunity to unravel HWC temporal patterns and responses (Smith and Kasiki 2000).

Our main objective was to analyze spatial, seasonal, and inter-annual variation in humanwildlife conflicts, conflict species, and management responses to the conflicts in the GTE from 1995 to 2017. We also sought to identify and quantify common human-wildlife conflict types, outcomes, and hotspots. We used these data to evaluate hypotheses based on our initial expectations about conflict types, their frequencies, and consequences.

We hypothesized that HWC trends would increase over time, and timely government and agency responses will be important for sustaining community support for wildlife conservation on communal lands outside protected areas. More specifically, we hypothesized that human-elephant conflicts (HEC), including human attacks, would occur more frequently in areas with high elephant, human, and livestock population densities and close to protected areas. We therefore expected the Taveta region to experience higher HECs than all the other 5 GTE regions because this region has a high human population density and is adjacent to 2 of the largest national parks (Tsavo East and West) in Kenya. Because HECs often result in elephant mortalities due to government control and community retaliatory killing, increasing human-elephant conflicts over time should lead to more elephant deaths. Furthermore, we expected that HWCs related to crop raiding elephants would be higher in the densely populated Taveta, Kibwezi, and Rombo regions bordering the protected areas than in any of the other 3 regions. Besides elephant and buffalo (Syncerus caffer), we expected the leading causes of HWCs in the GTE to also include large carnivores, specifically the lion, leopard, and spotted hyena (Crocuta crocuta), which



Figure 1. Map showing the Tsavo Protected Area (PA) and the 6 adjoining regions that jointly make up the Greater Tsavo Ecosystem, southeastern Kenya. Fences put up to reduce human–wildlife conflicts are adjacent to the Tsavo PA. Taita Hills lies to the west of Voi Town.

have been previously implicated in livestock depredations. Other notable HWC-causing species should include crop-raiding primates, snakes, and pythons (*Python sebae*) that attack humans or livestock, and the hippopotamus (*Hippopotamus amphibius*) that attacks humans and destroys crops.

Lastly, we expected to find seasonal differences in HWCs because some large herbivores (such as the elephant and buffalo) require large amounts of food and water, both of which vary seasonally. We therefore expected HWCs to peak in the dry season months when water and food availability are most limiting in African savannas.

Study area

Our study area lies in southeastern Kenya between latitudes 0°58'S and 4°22'S and between longitudes 37°7'E and 39°59'E. It comprises 4 functional protected areas, namely Tsavo East (TENP; 11,747 km²) and Tsavo West (TWNP; 9,065 km²), Chyulu National Park (736 km²), and South Kitui National Reserve (SKNR; 1,133 km²). The latter is situated to the north of TENP. This region has the largest contiguous protected area in Kenya, covering 22,681 km² (Figure 1). The PA and its surrounding 6 regions, collectively covering about 66,300 km², constitute the GTE. Rainfall (200–700 mm/year) is bimodal and erratic, with the short rains falling from November to December and the long rains from March to May (van Wijngaarden 1985). Rainfall increases with elevation to a maximum of about 1,185 mm at the highest elevation of 1,810 m in Chyulu Hills (Pócs and Luke 2007).

The common large herbivores found in the GTE include the African elephant, buffalo, hippopotamus, and the critically endangered black rhinoceros (*Diceros bicornis*; Emslie 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 2 tree communities, including Commiphora spp. and Acacia spp., forming 3 broad types of communities: (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 tree harvesting 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 GTE. 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 incidents, we subdivided the GTE into 6 regions: Taveta, Bachuma, Galana Ranch, Mutomo, Kibwezi, and Rombo. Taveta (5,900 km²), encompassing Taita Ranches and sandwiched between TENP and TWNP, is home to the Taita people and an important wildlife dispersal area. The Taita Hills found in Taveta have high human density owing to high local rainfall (van Wijngaarden 1985). Bachuma (2,900 km²) is a wildlife dispersal area and corridor that connects TENP and the Shimba Hills National Reserve near the Indian Ocean coast. The Galana Ranch (11,200 km²), forming the eastern part of the study region, is used for extensive cattle



Figure 2. Aftermath of a carnivore attack on sheep (*Ovis aries*) and goats (*Capra hircus*) inside a wooden enclosure that is not fortified to withstand predator incursion in the Kenya Greater Tsavo Ecosystem, southeastern Kenya (*photo courtesy of the Community Wildlife Division, Kenya Wildlife Service*).



Figure 3. A sheep (*Ovis aries*) strangled to death by a python (*Python sebae*) in the Kenya Greater Tsavo Ecosystem, southeastern Kenya (*photo courtesy of Community Wildlife Division, Kenya Wildlife Service*).



Figure 4. A ripe crop of watermelons (*Citrullus lanatus*) raided and destroyed by elephants (*Loxodonta africana*; notice elephant dung) in the Kenya Greater Tsavo Ecosystem, southeastern Kenya (*photo courtesy of Community Wildlife Division, Kenya Wildlife Service*).

ranching as well as a wildlife dispersal area. Mutomo (11,600 km²) is located to the north of Tsavo. Kibwezi (7,000 km²) is found to the east of Chyulu National Park running northward along the Mombasa-Nairobi road. The Athi River separates Kibwezi and Mutomo, located within Makueni and Kitui counties, respectively. To the west of Chyulu National Park and TWNP, extending southward up to Oloitokitok town along the Tanzania-Kenya border, is Rombo, covering 5,000 km². The 6 regions adjoining the protected areas are important wildlife dispersal areas and experience many HWC incidents.

Land use varies across the 6 regions. Within the Taveta region, wildlife conservation and cattle ranching in 28 ranches are the prime land uses. The ranches are owned by local communities (n = 9 ranches), the Kenya Government (n = 8), and private entities (n = 11; Taita Taveta CountyGovernment, unpublished report). Further, smallscale agriculture, sisal (*Agave sisalana*) plantations, and mining are also practiced, whereas intensive infrastructure development and settlements are found in towns such as Voi (Ngene et al. 2017).

Bachuma is located in Kwale County. The most common land uses here are small-scale agriculture, settlements, mining, and quarrying, as most of the region is very arid and held under trust land by the state on behalf of the local communities (Thompson et al. 2009). Galana Ranch encompasses Kulalu Ranch in Kilifi and Tana River counties and is used predominantly for wildlife conservation and commercial livestock farming. However, the Kenya Government has converted part of Galana into an irrigated farmland, incompatible with wildlife conservation (Ombaka 2014). In Rombo, intensive rain fed and irrigated agriculture, horticulture, and wildlife conservation (in Kuku Ranch) are practiced. The local Maasai community primarily practice livestock rearing (Okello 2005). Agriculture is practiced more intensely in the relatively wetter Kibwezi than Mutomo regions. Additionally, the Kamba community inhabiting Makueni and Mutomo keep fewer livestock than their Maasai counterparts in Rombo (Figure 1).

Human population is growing steadily in all 6 regions. Data from the Kenya National Bureau of Statistics (KNBS) show that the total human population in all 6 regions was 1,316,898 in 1989 and 1,825,299 in 2009. The KNBS also projected the total human population size in the 6 regions



Figure 5. A Kenya Wildlife Service ranger displays water containers destroyed by wild animals (almost certainly elephants [*Loxodonta africana*]) in the Kenya Greater Tsavo Ecosystem, southeastern Kenya (photo courtesy of Community Wildlife Division, Kenya Wildlife Service).



Figure 6. An elephant (*Loxodonta Africana*) knocked down by a vehicle while crossing a highway in the Kenya Greater Tsavo Ecosystem, southeastern Kenya (*photo courtesy of Community Wildlife Division, Kenya Wildlife Service*).

at about 2.1 million by 2017 (KNBS 2017). Specifically, between 1989 and 2017, the average percentage annual human population growth rates for the 6 regions were 2.97, 2.97, 2.94, 2.94, 1.66, and 1.11 for Bachuma, Galana, Taveta, Rombo, Kibwezi, and Mutomo, respectively. The human population density was highest in Kibwezi and lowest in Galana regions.

The GTE is connected to Mkomazi National Park in Tanzania. We did not include the Mkomazi National Park in our study because data on HWCs were not available. We obtained the data for temporal trend in rainfall and related it to HWC for the GTE region from the Tsavo Research Center. Rainfall in the GTE, hence the availability of food and water for wild herbivores, decreased steadily over time.

Methods Human–wildlife conflict data

The KWS has partitioned Kenya into 8 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 of 1995 to 2017. Data were recorded in daily occurrence books at stations within TCA, such as Mutomo, and the books were collected periodically for compilation and archiving. The HWC information collected included 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). We identified 5 HWC categories: (1) attack on humans, (2) livestock attacks (Figures 2 and 3), (3) crop raiding (Figure 4), (4) property damage (Figure 5), and (5) "other" less common types (Figure 6) involving multiple species (Mukeka et al. 2018). We also included a variable indicating how KWS responded to reported HWC incidents based on records in the occurrence books. These records indicated whether KWS responded to HWC incidents or if the status of the response to the HWC incident was not specified.

The KWS responded to reported HWC cases by visiting conflict sites to scare away conflict animals, assess property or crop damage, or rescue communities in distress. The KWS did not respond to all HWC reports due to logistical or other constraints. Finally, some HWC reports did not specify whether KWS acted. We identified 14 conflict animal species, 5 groups each comprising 2 or more species, and a sixth "other" group (Mukeka et al. 2018).

Sometimes the HWCs resulted in the killing of wildlife species involved either by KWS or the affected communities. The KWS occasionally killed animals that threatened people or their livelihoods through its problem animal control program. Communities can also kill animals that threaten people or damage property through retaliatory killings (Acha et al. 2018). We also obtained data from KWS on all HWC-related elephant fatalities for the GTE for the period of 1995 to 2016.

Using human population growth rates obtained from KNBS, we interpolated the number of people between 1995 and 2009 and extrapolated up to 2017 because the human census is carried out every 10 years in Kenya. We used the human population data to examine the effect of HECs on elephant mortality in the GTE. We further computed the total length (km) of the boundary each region shares with the PA to examine the effect of proximity to the PA on HWC. We obtained livestock data, including cattle (Bos taurus) and "shoats" (sheep [Ovis aries] and goats [Capra hircus]) from the Directorate of Resource Surveys and Remote Sensing of Kenya for 1995 to 2017. Finally, we stratified the data into the 6 regions constituting the GTE based on the locations of conflict occurrence (Figure 1). We used these regions to examine spatial variation in HWC incidents in the GTE.

Data analyses

Because most of the HWC data are non-normally distributed counts, we used both nonparametric and parametric statistical methods to analyze the data. We used chi-square goodness-of-fit tests to examine differences in the relative frequencies of conflicts across the 6 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 HWCs across years. We also used simple bivariate correlations (Spearman's rank) and parametric linear regression to quantify the strength of the relationship between the shared length of the boundary between the PA and the 6 regions. We related the probability that an HEC incident resulted in elephant mortality using a generalized linear model with a binomial error distribution and a logit link function.

We related HECs summed over the entire ecosystem for each year to the corresponding population size of people, elephants, cattle, and shoats and their interactions using a negative binomial error distribution and a log link function. We used a multinomial model to analyze variation in HWC in space and time and in rela-

tion to human population, elephant and livestock population size, and their interactions. We considered a multinomial model with random time effect, but it was too large to fit in a reasonable amount of time. Thus, we fitted a simpler model without residual random time effects, which are currently not supported for multinomial distributions in the SAS GLIMMIX procedure we used to fit the multinomial models. The multinomial model we fit used a generalized logit link function and crop raiding as the reference conflict outcome for all the data. The predictors were region (with 6 levels); month (with 12 levels) and their interactions; human, elephant, sheep and goat, and cattle population sizes; and the interactions of region with people, elephants, cattle, and shoats. We modelled time trend in the conflict outcome probability using a constructed penalized cubic basis spline effect with 7 knots. The interaction between the constructed spline effect and region was used to model region-specific trends in the probability of human-wildlife conflict outcomes. We used the logarithm of the area of each region as an offset to account for differences in area across regions. We used the Kenward-Roger approximation for the denominator degrees of freedom for the negative binomial and the multinomial models (Kenward and Roger 2009). The models were fit by residual penalized quasi-likelihood (pseudolikelihood; Wolfinger and O'Connell 1993) in the SAS GLIMMIX procedure (SAS Institute 2020).

Because areal size can influence the total number of conflicts in a region, we used a chisquare goodness-of-fit test to further examine if the observed distribution of the total HWCs across regions differed from expectation assuming a distribution proportional to the area of each region. We conducted chi-square goodness-of-fit and Kruskal Wallis H tests using SPSS (version 24) and linear regressions using R (R Core Team 2018). We created maps using ArcGIS® software (Environmental Systems Research Institute, Redlands, California, USA). We assessed statistical significance at $\alpha = 0.05$, unless otherwise stated.

Results

Human-wildlife conflict spatial variation

Reported HWCs varied across the 6 regions. Overall, 39,022 HWC incidents were recorded for all 6 regions adjoining the PA from 1995 to

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No.	Species	Scientific name	χ^2	п	P-value
1	Elephant	Loxodonta africana	5,850.1	24,032	< 0.001
2	Primates	Papio spp. Cercopithecus spp.	3,853.0	4,480	< 0.001
3	Buffalo	Syncerus caffer	145.4	2,432	< 0.001
4	Lion	Panthera leo	489.7	1,645	< 0.001
5	Hippopotamus	Hippopotamus amphibius	2,102.8	1,497	< 0.001
6	Spotted hyena	Crocuta crocuta	573.5	925	< 0.001
7	Snake	Serpentes	3,546.6	789	< 0.001
8	Python	Python sebae	4,321.9	709	< 0.001
9	Leopard	Panthera pardus	280.5	672	< 0.001
10	Eland	Taurotragus oryx	286.7	363	< 0.001
11	Waterbuck	Kobus ellipsiprymnus	432.7	322	< 0.001
12	Crocodile	Crocodylus niloticus	373.7	319	< 0.001
13	Cheetah	Acinonyx jubatus	71.6	167	< 0.001
14	Antelope ^a		62.1	155	< 0.001
15	Pigs ^b		92.6	153	< 0.001
16	Others ^c		67.7	124	< 0.001
17	Zebra	Equus quagga	27.3	122	< 0.001
18	Small carnivores ^d		38.4	55	< 0.001
19	Wild dog	Lycaon pictus	25.8	39	< 0.001
20	Giraffe	Giraffa tippelskirchi	23.9	22	< 0.001

Table 1. Chi-squared goodness-of-fit test of the null hypothesis that the percentage human-wildlife conflict incidents attributed to each species or species group does not differ across the 6 regions in the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017 (n =total number of reported cases for each species, df = 5 for all the tests).

^aKirk's dik-dik (Madoqua kirki), common duiker (Sylvicapra grimmia), hartebeest (Alcelaphus buselaphu), impala (Aepyceros melampus), bushbuck (Tragelaphus scriptus), lesser kudu (Tragelaphus imberbis), reed buck (Redunca fulvorufula), Thomson's gazelle (Gazella thomsonii), Grant's gazelle (Gazella granti). ^bBush pigs (*Potamochoerus larvatus*), warthogs (*Phacochoerus africanus*), wild pigs (*Sus scrofa*). ^cConflict caused by many species, assorted birds, and accidents. ^dServal cat (*Leptailurus serval*), caracal (*Caracal caracal*), jackal (*Canis* spp.), mongoose (Herpestidae),

honey badger (Mellivora capensis), civets (Viverridae). All P-values are statistically significant at P < 0.01.

2017 (Table 1). The total HWC incidents averaged 6,503.7 ± 5,568.1 for each region from 1995 to 2017. The lowest regional total HWC incidents was 411 for Galana, whereas the highest was 14,240 incidents for Taveta.

Wildlife species implicated in HWCs also varied by and within regions. African elephants were involved in more HWC incidents overall and in 5 of the 6 regions. Primates were the second leading group of species to cause conflicts, with most (90%) occurring in the Rombo region. The buffalo and hippopotamus contributed the highest HWC in the Rombo region, while the plains zebra (Equus quagga) and giraffe (*Giraffa camelopardalis*) were implicated more in the Taveta region. Large carnivores caused fewer HWCs than the large herbivores and mostly in Taveta. The overall contribution of large carnivore species to HWCs, in decreasing order, were by the lion, leopard, and hyena. The lion was the main source of conflict carnivore in Taveta, followed by Galana. The spotted hyena and leopard were the most common conflict carnivores in Mutomo. Pythons and snakes were the fourth most reported causes of conflicts after large carnivores, although in smaller proportion, but their impacts were important because they cause injury and death

siash () is used to separate observed and expected values for the pair of regions being compared.									
Pair of regions compared	Observed	Expected	Kruskall-Wallis H	P-value					
Bachuma-Taveta	2,944/14,240	2,609/5,301	5.18	0.001*					
Bachuma-Rombo	2,944/12,079	2,609/4,457	4.43	0.001*					
Bachuma-Kibwezi	2,944/6,623	2,609/6,227	2.45	0.22					
Bachuma-Mutomo	2,944/2,725	2,609/10,405	0.26	1.00					
Bachuma-Galana	2,944/411	2,609/10,019	2.76	0.09					
Taveta-Rombo	14,240/12,079	5,301/4,457	0.76	1.00					
Taveta-Kibwezi	14,240/6,623	5,301/6,227	2.73	0.09					
Taveta-Mutomo	14,240/2,725	5,301/10,405	5.44	0.001*					
Taveta-Galana	14,240/411	5,301/10,019	7.69	0.001*					
Rombo-Kibwezi	12,079/6,623	4,457/6,227	1.98	0.71					
Rombo-Mutomo	12,079/2,725	4,457/10,405	4.68	0.001*					
Rombo-Galana	12,079/411	4,457/10,019	6.97	0.001*					
Kibwezi-Mutomo	6,623/2725	6,227/10,405	2.70	0.10					
Kibwezi-Galana	6,623/411	6,227/10,019	5.09	0.001*					
Mutomo-Galana	2,725/411	10,405/10,019	2.51	0.18					

Table 2. Multiple pairwise comparisons of the relative frequency of human–wildlife conflicts among the 6 study regions adjoining the Tsavo Protected Area in the Kenya Greater Tsavo Ecosystem, south-eastern Kenya, 1995–2017. *P*-values have been adjusted for multiple tests. An asterisk (*) indicates statistically significant differences in relative frequencies of HWCs between pairs of regions. A forward slash (/) is used to separate observed and expected values for the pair of regions being compared.

Table 3. Chi-squared goodness-of-fit tests of the null hypothesis that the percentage contribution of each conflict type to the total conflicts did not differ across the 6 regions in the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017 (df = 5 for all chi-square tests; all *P*-values are statistically significant at P < 0.01).

Conflict type	Percentage contribution of conflict type to the regional total (100%)								Chi-square	
	Bachuma	Taveta	Rombo	Kibwezi	Mutomo	Galana	п	χ_{5}^{2}	P-value	
Crop raiding	37.2	35.9	65.8	51.0	25.1	43.6	18,404	3094.0	< 0.001	
Human attack	49.5	50.0	26.5	41.5	51.2	45.5	16,106	1726.1	< 0.001	
Livestock attack	7.5	11.3	6.8	6.2	22.6	6.8	3,707	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	

to humans. More python and snake conflicts occurred in Mutomo. The giraffe was the least conflict-causing species, attacking 1 person every 2 years, and they were responsible for few crop raiding incidents. Nine (elephants, primates, buffalo, lions, hippopotamuses, hyenas, snakes, pythons, and leopards) of the 14 common species accounted for 95.3% of all the reported HWCs in the GTE. Overall, the relative frequencies of conflicts across the 6 regions differed (Table 1). Similarly, the relative contribution to the overall HWC cases of the 20 species differed among the 6 regions.

We expected HWCs 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, HWC incidents differed among the 6 regions ($\chi_5^2 = 88.590$, P < 0.001). The highest numbers of conflict incidents were reported in Taveta (n = 14,240) and Rombo (n = 12,079; Table 2). We also expected spatial differences in HWC incidents to increase with the length of the boundary shared between a



Figure 7. Total frequency of human–wildlife conflicts per region in the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017.

region and the PA through its impact on the number and frequency of HWC incidents in the region. Although positive, this relationship was very weak (r^2 = 0.15, $F_{1,5}$ = 0.72, P = 0.445). Taveta shared >70% of its boundary with the PA.

Furthermore, the number of HWC incidents differed across the 6 regions ($\chi_5^2 = 43,055$, *P* < 0.001). Thus, the relative frequency of conflicts in the GTE did not simply reflect the size of a region. The larger regions like Galana and Mutomo had far fewer conflicts than smaller regions, such as Taveta and Rombo. Thus, HWCs in the GTE are more related to regionally varying underlying factors than region size.

HWC frequencies by types and region

There were 4 common conflict types, and their relative frequencies varied 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 3; Figure 7). 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 did, except that attacks on humans were more prevalent in Taveta. Livestock attacks were predominantly concentrated in Taveta and Rombo. Property damage incidents were extremely rare in Mutomo and Galana relative to the other 4 regions (Table 3; Figure 7). Similar patterns emerged after we weighted the total number of regional conflicts with the area of the region (χ_5^2 = 43,055, *P* < 0.001). Overall, chi-square goodness-of-fit tests confirmed the relative frequencies of conflict types differed across the 6 regions (χ_5^2 = 3,829.1, *P* = 0.001).

HWC outcomes by region

Human–wildlife conflicts can have various physical or psychological consequences. Although most of the people involved in HWCs were neither injured nor killed, many felt threatened (Table 4). People were more likely to be threatened, injured, or

killed during HWCs in Taveta, Bachuma, and Mutomo than in the other regions. Elephants caused more human threats, injuries, and deaths in Taveta and Bachuma. Buffalo, snakes, and pythons also caused a few threats, injuries, and deaths in Taveta. In contrast, snakes and pythons caused most, while crocodiles (*Crocodylus niloticus*) caused few, human injuries and deaths in Mutomo.

Human–elephant conflicts

The interaction between people and elephants may exacerbate HECs. Indeed, HECs increased with increasing elephant and human population size. But a unit increase in elephant population size (Slope β = 8.4465, 95% CI = 5.6388–11.2542, $F_{1,20}$ = 39.38, P < 0.0001) had a stronger effect on HECs than a unit increase in human population size (β = 2.0383, 95% CI = 0.02753–4.0492, $F_{1,20}$ = 4.47, P = 0.0472), though elephant and human population size had a negative interactive effect (β = –3.5508, 95% CI = –4.6289 to –2.4727, $F_{1,20}$ = 47.2, P < 0.0001).

Problem animal control or retaliatory killings of elephants may be a consequence of HECs (Woodroffe et al. 2005). We expected increased HECs to result in increased elephant fatalities. The number of elephants, people, cattle, sheep, and goats all influenced the probability that an HEC resulted in elephant mortality (Table 5).

We also expected HECs to increase with increasing livestock numbers because of intensifying competition for limiting resources. However, HECs decreased with increase in the number of

Table 4. 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 6 regions in the Kenya Greater Tsavo
Ecosystem, southeastern Kenya, 1995–2017 (df = 5 for all chi-square tests).

						*				
Human-related conflict outcome	Percentage of conflict outcome within region								Chi-square test	
	Bachuma	Taveta	Rombo	Kibwezi	Mutomo	Galana	Total	%ª	χ_5^2	P-value
Nothing happened	50.34	49.93	73.47	58.80	50.35	54.50	22,957	58.83	1707.0	<0.001
Human felt threatened	44.06	45.28	24.42	39.54	14.35	41.12	13,874	35.55	1920.4	<0.001
Human was injured	4.48	3.76	1.62	1.27	31.85	3.16	1,828	4.68	4961.3	< 0.001
Human was killed	1.12	1.03	0.48	0.39	3.45	1.22	363	0.93	238.1	<0.001

^aPercentage contribution to the overall conflict outcome. All the *P*-values are statistically significant at P < 0.01.

Table 5. The probability that a human–elephant (*Loxodonta africana*) conflict resulted in elephant mortality in the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017.

		5			5		
Effect	Estimate	SE	df	<i>t</i> -value	$\Pr > t $	95% Lower	95% Upper
Intercept	245.75	48.8478	13	5.03	0.0002	140.22	351.28
Elephant	15.9063	33.1467	13	0.48	0.6393	-55.7027	87.5154
Elephant × Elephant	84.1281	30.1714	13	2.79	0.0154	18.9467	149.31
People	-756.23	175.75	13	-4.3	0.0009	-1135.92	-376.55
People × People	489.09	96.5739	13	5.06	0.0002	280.45	697.72
Elephant × People	-185.72	52.9399	13	-3.51	0.0039	-300.09	-71.3514
Shoats	-95.8892	21.7396	13	-4.41	0.0007	-142.85	-48.9237
Cattle	194.93	56.4323	13	3.45	0.0043	73.0132	316.84

Table 6. The variation in expected probability of human–wildlife conflicts in the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017, based on the multinomial generalized logit model. The NDF and DDF values are the numerator and denominator degrees of freedom, respectively. Spline is the constructed penalized cubic basis spline effect with 7 degrees of freedom.

Effect	NDF	DDF	<i>F</i> -value	$\Pr > F$	
Region	20	38470	117.82	< 0.0001	
Month	44	38470	7.7	< 0.0001	
Region × Month	221	38470	0.87	0.9145	
People	4	38470	589.71	< 0.0001	
People × Region	20	38470	44.89	< 0.0001	
Cattle	4	38470	34.63	< 0.0001	
Cattle × Region	21	38470	20.15	< 0.0001	
Shoats	4	38470	22.24	< 0.0001	
Shoats × Region	22	38470	16.48	< 0.0001	
Elephant	4	38470	0.42	0.7968	
Elephant × Region	20	38470	15.43	< 0.0001	
Elephant × Elephant	4	38470	3.51	0.0072	
People × People	4	38470	15.84	< 0.0001	
Spline × Region	154	38470	3.33	< 0.0001	



Figure 8. Interannual trend and seasonal fluctuations in the expected probabilities for 5 humanwildlife conflict types in each of the 6 regions of the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017, based on the multinomial generalized logit model.

shoats (sheep and goats; $\beta = -4.9515$, 95% CI = -7.3618 to -2.5413, $F_{1,20} = 18.36$, P = 0.0004) but increased with increase in cattle $\beta = 13.8649$, 95% CI = 8.1333–19.5964, $F_{1,20} = 25.46$, P < 0.0001) in the GTE.

Temporal variation in HWCs

The GTE experienced high HWC incidents annually from 1995 to 2017. The annual conflict totals averaged 1,696.6 ± 553.8 (range 724–2,008). Reported conflicts were the fewest (n = 724) in 1998 and the highest (n = 2541) in 2008.

The expected probability of conflicts differed across regions and varied with human, elephant, and livestock densities and their interactions with region and similarly across months for all regions (Table 6). Crop raiding, the most prevalent HWC type, generally decreased over time whereas attack on humans, the second most frequent HWC type, increased in all regions. Notably, the expected probability of attack on humans first increased until it surpassed and then either dropped below or remained above that for crop raiding depending on region. The expected probabilities of the other HWC types were generally low and decreased over time but were notably high for livestock attack in Mutomo (Figure 8).

Seasonal variation in HWC incidents

We expected reported HWCs to mirror rainfall seasonality, the principal climatic component governing variation in food and water availability and habitat quality for herbivores in savannas (Deshmukh 1984; Boutton et al. 1988; Ogutu et al. 2010, 2014*a*). As expected, HWCs displayed strong monthly seasonality besides a strong positive average trend from 1995 to 2017. The expected probability of crop raiding incidents spiked during maturity of crops and end of the wet season from January to February and June to July, while human attacks increased during the wet season from March to April and October to December (Figure 9).



Figure 9. Monthly averages of the expected probabilities for 5 human–wildlife conflict types in each of the 6 regions of the Kenya Greater Tsavo Ecosystem, southeastern Kenya, 1995–2017, based on the multinomial generalized logit model.

HWC responses

Between 1995 and 2017, the KWS responded to 81.9% of the conflict cases (n = 31,976). They did not respond to 14.9% (n = 5,812) cases, whereas the status of the remaining cases (3.2%, n = 1,234) could not be determined. The frequency of cases KWS responded 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.

Discussion

The GTE experienced a myriad of HWCs caused by different species at varying intensities that were not proportional to the areal size of the regions. Our results suggest that factors other than the size of a region determined the cause and frequency of HWCs. Elephants were responsible for most conflicts in the GTE. Taveta (third smallest region at 5,900 km²) followed by Rombo (second smallest region at 5,000 km²) reported most of the human–elephant conflicts. Taveta is an HEC hotspot in Tsavo. The HWCs reported reflected the rich wildlife diversity and large number and activities of humans in the GTE.

Two important developments appear responsible for increased conflicts involving the elephant and other large herbivores such as buffalo, hippopotous, zebras, and giraffes 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 GTE grew by 62.3%, greatly increasing the pressure on natural resources, agricultural intensification, and land fragmentation. The changes degrade and reduce wildlife habitats (Messmer 2000, Ogutu et al. 2014*a*), accentuating the frequency and intensity of humanwildlife conflicts. In Nepal (Acharya et al. 2016) and India (Gubbi et al. 2014), conflicts were also higher in densely settled areas.

Second, increasing elephant population size in the GTE was partly responsible for the increase in HEC in Tsavo. Tsavo is water-deficient (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. In addition, the large sisal plantations and irrigated schemes bordering the Tsavo PA provide nutritive food that attracts wildlife (Røskaft et al. 2014, Kumar et al. 2017), accentuating conflicts. Reduced rains may also have led to reduced agriculture in Taveta, leading, in turn, to fewer crop raiding than human attack incidents. Thus, these 2 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 Taveta and Rombo (Figure 1) to be accompanied by a corresponding reduction in HECs, 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. 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 regular maintenance (Gubbi et al. 2014) of fences is important. Increased livestock numbers in the GTE have resulted in increased HWCs due to competition for water, forage, and space (Ogutu et al. 2016). The elephant corridors in Taveta 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 HWCs.

Human–wildlife conflicts cause immense socioeconomic (Kanga et al. 2012) and physical losses and psychological stress. In the GTE, the subsistence farmers suffer considerable losses to crop raiding by elephants. Further, it was not uncommon to lose a family member, entire livestock herd, or other property through HWCs. This may explain why more people felt threatened in 4 of the 6 GTE regions.

High species diversity in the GTE contributed to more conflicts caused by other species like primates, carnivores, and herbivores (buffalo and hippopotamus). Our results were consistent with other studies (Smith and Kasiki 2000, Patterson et al. 2004, Kanga et al. 2012). The local communities were more impacted by HWCs because they are generally too poor to afford expensive prevention methods such as fencing.

We found clear geographic distinctions in the distribution of wildlife species causing HWCs around the GTE, including large carnivores. Taveta and Rombo accounted for 70% (n = 26,319) of the conflicts in the GTE, and they can be attributed to the major land uses in both regions. Large mixed livestock-wildlife ranches are the major land use in Taveta. As a result, livestock depredation was more common in this region because wild prey species are more difficult to hunt than livestock (Patterson et al. 2004).

The proximity of Taveta to the PA may also be contributing to increased conflicts. Even so, the relationship between PA boundary length and region was weak, consistent with other studies (Gubbi et al. 2014). While pastoralism was largely compatible with conservation, large livestock numbers or reduction of the natural prey base can lead to more frequent HWC incidents, elevating retributive carnivore killings.

Nonhuman primates can also be a major source of HWCs (Hill 1997, Syombua 2013, Gross et al. 2018). In Rombo, horticulture provided succulent food for primates. Snake and python conflicts that threaten human life and livelihoods were higher in arid Mutomo where water sources were scarce. The Mutomo region 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.

HWC trends

Human–wildlife conflicts in the GTE were perennial problems and increased steadily from 1995 to 2017. Further, reported HWCs showed strong seasonality. Reliable knowledge of seasonality in HWCs 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).

Conflicts decreased from 1997 to 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). The number of HWCs reported peaked in Tsavo from 2008 to 2009 because of a severe drought in Kenya (Ogutu et al. 2014*b*). 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 contact with people and livestock, resulting in more frequent and intense conflicts.

HWC conflict resolution

The KWS responded to most HWC incidents. The responses include visiting the area to drive the wildlife back to the parks (e.g., by using vehicles and thunder flashes to scare animals), setting traps to catch elusive carnivores, or camping overnight to provide a deterrent and surveillance. In addition, other preventive measures included the construction of fences that separate wildlife from human-inhabited areas.

However, we detected considerable interannual variation in the frequency of responses to HWCs. This temporal variability was attributed to the availability of such resources as vehicles necessary for effectively responding to HWCs. Over time, KWS actively expanded its ranger force to respond to wildlife issues, including HWCs and poaching. Timely response to HWCs is essential to sustaining the goodwill and support of local communities for conservation but is becoming increasingly expensive as conflicts increase and intensify over space and time.

HWC mitigation and conservation

Increasing human and livestock numbers and infrastructure development are leading to wildlife habitat degradation and loss. Sustainable conflict resolution of HWCs in the GTE 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 developing sustainable wildlife conservation enterprises and more innovative models of consumptive utilization of wildlife, abolished in Kenya in 2002 (Kameri-Mbote 2005). Elsewhere, community-based conservancies are proving to be effective tools for biodiversity conservation in Maasai Mara and other parts of Kenya (Msoffe et al. 2019).

Multiple wildlife species were responsible for HWCs involving people, livestock, crops, and property in the GTE. This complicates mitigation of HWCs, but spatial stratification should be used when developing mitigation measures to accommodate regional distinctions in conflict intensity, types, and outcomes. This would enable the development of targeted mitigation measures focusing, for instance, on HWCs involving snakes and pythons in the remote Mutomo region, such as provision of adequate and affordable antivenom drugs in local dispensaries.

Multiple mitigation strategies are necessary to address the multiplicity of species, types, and outcomes of HWCs. Conventional HWC mitigation strategies, such as problem animal control, scaring, and keeping guard dogs, are reactive rather than preventive and cannot effectively address certain types of conflicts, such as those involving nonhuman primates, which need a combination of multiple methods at any given time.

Carefully planned and managed provision of artificial watering points for wildlife during dry periods and managing protected areas to sustain functional heterogeneity can help reduce the probability of wildlife wandering to areas outside the PA and therefore limit interactions between wildlife and people in the dry season. The artificial water points should be sufficiently widely separated spatially to minimize potential deleterious effects on vegetation of wildlife concentrations around them (Owen-Smith 1996, Owen-Smith et al. 2012). This can allow wildlife to use the PA habitat in a way that promotes functional heterogeneity and retains more wildlife inside the PA. Further, and as a complement, land use planning is important to minimize habitat fragmentation outside the protected areas and to allow continuing movement of wildlife between the PA and adjacent conservancies, while minimizing negative interactions with farming regions that contain attractive forage.

The Taveta region will almost certainly continue to experience more HECs than the other regions because of its proximity to the Tsavo PA, large and growing elephant population, and wildlife ranches (Graham et al. 2012). Increased human–elephant conflicts lead to more elephant mortalities through state-sanctioned 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. Therefore, wildlife management (e.g., by KWS and non-governmental conservation organizations) should consider channeling more resources to this and other similarly important regions.

Management implications

Increased HWCs pose serious threats to the survival and conservation of many wildlife species as well as the socioeconomics of the affected communities. Better information about the magnitude of the HWCs and the effectiveness of timely responses may help mitigate in their resolution. To achieve this, we recommend HWC monitoring databases be enhanced to capture more useful details, particularly the precise geo-location of conflict incidents and why an animal was killed during conflicts. Further, the databases should provide a breakdown of the nature and timeliness of responses undertaken by wildlife managers in response to HWC complaints.

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Literature cited

- Acha, A., M. Temesgen, and H. Bauer. 2018. Human–wildlife conflicts and their associated livelihood impacts in and around Chebera-Churchura National Park, Ethiopia. Society and Natural Resources 31:260–275.
- Acharya, K. P., P. K. Paudel, P. R. Neupane, and M. Köhl. 2016. Human–wildlife conflicts in Nepal: patterns of human fatalities and injuries caused by large mammals. PLOS ONE 11(9): e0161717.
- Allendorf, F. W., and J. J. Hard. 2009. Humaninduced evolution caused by unnatural selection through harvest of wild animals. Proceed-

ings of the National Academy of Sciences 106:9987–9994.

- Boutton, T. W., L. L. Tieszen, and S. K. Imbamba. 1988. Seasonal changes in the nutrient of East African grassland vegetation. African Journal of Ecology 26:103–115.
- Collier, P., G. Conway, and T. Venables. 2008. Climate change and Africa. Oxford Review of Economic Policy 24:337–353.
- Deshmukh, I. K. 1984. A common relationship between precipitation and grassland peak biomass for east and southern Africa. African Journal of Ecology 22:181–186.
- Emslie, R. 2012. Black rhino, *Diceros bicornis*. The IUCN Red List of Threatened Species 2012: e.T6557A16980917, International Union for Conservation of Nature and Natural Resources, Gland, Switzerland, https://www.iucnredlist.org/species/6557/16980917>. Accessed July 29, 2018.
- Graham, M. D., W. M. Adams, and G. N. Kahiro. 2012. Mobile phone communication in effective human–elephant conflict management in Laikipia County, Kenya. Oryx 46:137–144.
- Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human–predator–prey conflicts: ecological correlates, prey losses and patterns of management. Biological Conservation 122:159–171.
- Gross, E. M., B. P. Lahkar, N. Subedi, V. R. Nyirenda, L. L. Lichtenfeld, and O. Jakoby. 2018. Seasonality, crop type and crop phenology influence crop damage by wildlife herbivores in Africa and Asia. Biodiversity and Conservation 27:2029–2050.
- Gubbi, S., M. H. Swaminath, H. C. Poornesha, R. Bhat, and R. Raghunath. 2014. An elephantine challenge: human–elephant conflict distribution in the largest Asian elephant population, southern India. Biodiversity and Conservation 23:633–647.
- Hemson, G., S. Maclennan, G. Mills, P. Johnson, and D. Macdonald. 2009. Community, lions, livestock and money: a spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human–carnivore conflict in Botswana. Biological Conservation 142:2718–2725.
- Hill, C. M. 1997. Crop-raiding by wild vertebrates: the farmer's perspective in an agricultural community in western Uganda. International Journal of Pest Management 43:77–84.
- Hill, C. M. 2000. Conflict of interest between people and baboons: crop raiding in Uganda. International Journal of Primatology 21:299–315.

- Kameri-Mbote, P. 2005. Sustainable management of wildlife resources in East Africa. A critical analysis of the legal, policy and institutional frameworks. International Environmental Law Research Centre, Geneva, Switzerland.
- Kanga, E. M., J. O. Ogutu, H. P. Piepho, and H. Olff. 2012. Human–hippo conflicts in Kenya during 1997–2008: vulnerability of a megaherbivore to anthropogenic land use changes. Journal of Land Use Science 7: 395–406.
- Kenward, M. G., and J. H. Roger. 2009. An improved approximation to the precision of fixed effects from restricted maximum likelihood. Computational Statistics and Data Analysis 53:2583–2595.
- Kenya National Bureau of Statistics (KNBS). 2017. Statistical abstract 2017. Kenya National Bureau of Statistics, Nairobi, Kenya, https://www.knbs.or.ke/?wpdmpro=statistical-ab-stract-2017. Accessed March 8, 2018.
- Kerbis Peterhans, J. C., and T. P. Gnoske. 2001. The science of "man-eating" among lions *Panthera leo* with a reconstruction of the natural history of the "man-eaters of Tsavo." Journal of East African Natural History 90:1–40.
- Kumar, A., H. S. Bargali, A. David, and A. Edgaonkar. 2017. Patterns of crop rading by wild ungulates and elephants in Ramnagar Forest Division, Uttarakhand. Human–Wildlife Interactions 11:41–49.
- Messmer, T. A. 2000. The emergence of humanwildlife conflict management: turning challenges into opportunities. International Biodeterioration and Biodegradation 45:97–102.
- Mooney, H. A., P. R. Ehrlich, and G. E. Dail. 1997. Nature's services: societal dependence on natural ecosystems. Island Press, Washington, D.C., USA.
- Msoffe, F. U., J. O. Ogutu, M. Y. Said, S. C. Kifugo, J. de Leeuw, P. Van Gardingen, and R. Boone. 2019. Wildebeest migration in East Africa: status, threats and conservation measures. BioRxiv 546747.
- Mukeka, J. M., J. O. Ogutu, E. Kanga, and E. Røskaft. 2018. Characteristics of human–wildlife conflicts in Kenya: examples of Tsavo and Maasai Mara regions. Environment and Natural Resources Research 8:148–165.
- Ngene, S., F. Lala, M. Nzisa, K. Kimitei, J. Mukeka, S. Kiambi, Z. Davidson, S. Bakari, E. Lyimo, and C. Khayale. 2017. Aerial total count of elephants, buffaloes and giraffes in the Tsavo-Mkomazi ecosystem in February 2017. Kenya Wildlife Service, Nairobi, Kenya, http://www.

kws.go.ke/content/aerial-total-count-elephantsbuffaloes-and-giraffes-tsavo-mkomazi-ecosystem-february-2017-0>. January 1, 2018.

- Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola, and R. S. Reid. 2008. El Niño-Southern Oscillation, rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara-Serengeti ecosystem. African Journal of Ecology 46:132–143.
- Ogutu, J. O., H. P. Piepho, M. Y. Said, and S. C. Kifugo. 2014a. Herbivore dynamics and range contraction in Kajiado County Kenya: climate and land use changes, population pressures, governance, policy and human–wildlife conflicts. Open Ecology Journal 7:9–31.
- Ogutu, J. O., H. P. Piepho, R. S. Reid, M. E. Rainy, R. L. Kruska, J. S. Worden, and N. T. Hobbs. 2010. Large herbivore responses to water and settlements in savannas. Ecological Monographs 80:241–266.
- Ogutu, J. O., H. P. Piepho, M. Y. Said, G. O. Ojwang, L. W. Njino, S. C. Kifugo, and P. W. Wargute. 2016. Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: What are the causes? PLOS ONE 11(9): e0163249.
- Ogutu, J. O., R. S. Reid, H. P. Piepho, N. T. Hobbs, M. E. Rainy, R. L. Kruska, and M. Nyabenge. 2014b. Large herbivore responses to surface water and land use in an East African savanna: implications for conservation and human–wildlife conflicts. Biodiversity and Conservation 23:573–596.
- Okello, M. M. 2005. Land use changes and human–wildlife conflicts in the Amboseli Area, Kenya. Human Dimensions of Wildlife 10:19–28.
- Ombaka, D. M. 2014. Of Kenya's eaters and eatists: hunger as a development and social justice challenge. Journal of Social Welfare and Human Rights 2:107–129.
- Omondi, P. 1994. Wildlife–human conflict in Kenya: integrating wildlife conservation with human needs in the Masai Mara region. Dissertation, McGill University, Montreal, Quebec, Canada.
- Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. South African Journal of Wildlife Research 26:107–112.
- Owen-Smith, N., G. J. Chirima, V. Macandza, and E. Le Roux. 2012. Shrinking sable antelope numbers in Kruger National Park: what is suppressing population recovery? Animal Conservation 15:195–204.

- Packer, C., D. Ikanda, B. Kissui, and H. Kushnir. 2005. Conservation biology: lion attacks on humans in Tanzania. Nature 436:927–929.
- Patterson, B. D., S. M. Kasiki, E. Selempo, and R. W. Kays. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Park, Kenya. Biological Conservation 119:507–516.
- Pócs, T., and Q. Luke. 2007. East African bryophytes, XXV: bryological records from the Chyulu range, Kenya. Journal of East African Natural History 96:27–46.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, D. D. H. 2012. Impact of Climate Change on Biodiversity. Page 505–530 *in* W.-Y. Chen, J. Seiner, T. Suzuki, and M. Lackner, editors. Handbook of climate change mitigation. Springer, New York, New York, USA.
- Rentsch, D., and C. Packer. 2015. The effect of bushmeat consumption on migratory wildlife in the Serengeti ecosystem, Tanzania. Oryx 49:287–294.
- Røskaft, E., B. Händel, T. Bjerke, and B. P. Kaltenborn. 2007. Human attitudes towards large carnivores in Norway. Wildlife Biology 13:172–185.
- Røskaft, E., T. Larsen, R. Mojaphoko, A. H. M. Raihan Sarker, and C. Jackson. 2014. Human dimensions of elephant ecology. Pages 269–288 *in* C. Skarpe, J. T. du Toit, and S. R. Moe, editors. Elephants and savanna woodland ecosystems: a study from Chobe National Park, Botswana. Wiley Blackwell, London, United Kingdom.
- Saji, N. H., B. N. Goswami, P. N. Vinayachandran, and T. Yamagata. 1999. A dipole mode in the tropical Indian Ocean. Nature 401:360–363.
- SAS Institute Inc. 2020. SAS system for windows, version 9.4. SAS Institute Inc., Carey, North Carolina, USA.
- Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. 2007. Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom, and New York, New York, USA.
- Smith, R. J., and S. M. Kasiki. 2000. A spatial analysis of human–elephant conflict in the Tsavo ecosystem, Kenya. IUCN/Species Sur-

vival Commission African Elephant Specialist Group, Human–Elephant Conflict Task Force, Gland, Switzerland.

- Syombua, M. J. 2013. An analysis of human–wildlife conflicts in Tsavo West–Amboseli agro-ecosystem using an integrated geospatial approach: a case study of Taveta District. Dissertation, University of Nairobi, Nairobi, Kenya.
- Thirgood, S., R. Woodroffe, and A. Rabinowitz. 2005. The impact of human–wildlife conflict on human lives and livelihoods. Pages 13–26 *in* R. Woodroffe, S. Thirgood, and A. Rabinowitz, editors. People and wildlife, conflict or co-existence? Cambridge University Press, Cambridge, United Kingdom.
- Thompson, D. M., S. Serneels, D. O. Kaelo, and P. C. Trench. 2009. Maasai Mara–land privatization and wildlife decline: can conservation pay its way? Pages 77–114 *in* K. Homewood, P. Kristjanson, and P. C. Trench, editors. Staying Maasai? Studies in Human Ecology and Adaptation. Volume 5. Springer, New York, New York, USA.
- Thouless, C. R., and J. Sakwa. 1995. Shocking elephants: fences and crop raiders in Laikipia District, Kenya. Biological Conservation 72:99–107.
- van Wijngaarden, W. 1985. Elephants-treesgrass-grazers. Relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). Dissertation, Wageningen University, Wageningen, Netherlands.
- Wildlife Act. 2013. The Wildlife Conservation and Management Act, 2013. Kenya Gazette Supplement No. 18/ (Acts No. 47), Republic of Kenya, Nairobi, Kenya, http://kenyalaw.org/ kl/fileadmin/pdfdownloads/Acts/WildlifeConservationandManagement%20Act2013.pdf>. Accessed May 8, 2018.
- Wolfinger, R., and M. O'Connell. 1993. Generalized linear mixed models a pseudo-likelihood approach. Journal of Statistical Computation and Simulation 48:233–243.
- Woodroffe, R., S. Thirgood, and A. Rabinowitz, editors. 2005. People and wildlife, conflict or co-existence? Cambridge University Press, Cambridge, United Kingdom, and New York, New York, USA.

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