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Differentiated drivers in wildlife-induced damage necessitate species-specific mitigation strategies in the western Serengeti, Tanzania

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ABSTRACT

In agriculturally dependent regions interspersed with wildlands, crop damage and livestock depredation by wildlife threatens rural livelihoods and undermines conservation efforts. Determining the species, human activities and landscape features correlated with losses to wildlife is critical for developing effective mitigation approaches. To better understand drivers of wildlife damage, we surveyed 419 households in the western Serengeti of Tanzania about agricultural practices and wildlife-induced losses. Using a causal inference framework and hierarchical Bayesian models, we assessed the influence of environmental and household characteristics on damage by different wildlife species. Crop loss to elephant was the most widespread form of damage; crop loss to baboon and vervet monkey was less common. Livestock depredation by hyena was widespread and common, while depredation by lion was rare and localized. The majority of respondents perceived wildlife as the greatest threat to crop production, whereas reproductive efficiency and environmental factors were seen as greater threats than wildlife to livestock. The risk of crop and livestock damage was consistently and negatively associated with human disturbance, and positively associated with farm and herd size. The influence of other factors, including woody cover, slope, and proximity to settlements varied across forms of damage and species. Our findings suggest that land use planning may be a generalizable approach to reducing wildlife damage, but variability in the drivers, extent, conservation status, and tolerance for losses indicate that species-specific mitigation strategies are required. Multi-species assessments offer broad insights into human-wildlife interactions and can aid in the identification and prioritization of mitigation measures.

1. Introduction

The increasing ecological footprint of humans, demand for resources, human population growth, and climate change has amplified pressures on wildlife populations (Pimm et al., 1995; Galanti et al., 2006; Singh et al., 2010; Woodroffe, 2000). Expanding human presence, particularly along wildland edges, restricts animal populations and increases rates of negative human-wildlife interactions, commonly referred to as human-wildlife conflict (HWC) (Hoare and Du Toit, 1999; Chen et al., 2013; Veldhuis et al., 2019). HWC includes wildlife damage to crops, livestock, and property, human death and injury, and the killing of wildlife via legal lethal control programs and retaliatory killings (Nyhus, 2016).

Globally, HWC is a leading cause of biodiversity loss, wildlife range collapse, population declines, and local extirpations, and has severe economic impacts, particularly in rural environments (Ogutu et al., 2016; Long et al., 2020). HWC is particularly severe across Africa, where the majority of people depend on agriculture for their livelihoods (Braczkowski et al., 2023; FAO, 2021; Gemeda and Meles, 2018). Across Africa, conflict with people is recognized as a leading driver of declines in elephant populations (Chase et al., 2016), and links between loss of livestock to carnivores and support for lethal control and retaliatory killings are well-documented and considered an important driver of

recent declines in carnivore populations (Inskip and Zimmermann, 2009; Dickman, 2012; Masenga et al., 2013). Wildlife induced damage can have severe consequences for farmer livelihoods, food security, and support for conservation and losses disproportionately impact those in low-income areas and developing economies (Butler, 2000; Braczkowski et al., 2023; Hill, 2000; Karanth et al., 2013; Kaswamila et al., 2007; Mackenzie and Ahabyona, 2012; Naughton-Treves, 1997; Ogada et al., 2003; Salerno et al., 2020; Woodroffe and Frank, 2005).

Managing HWC has become an increasingly important component of wildlife and protected area management (König et al., 2021; Messmer, 2009). The economic, labor, and opportunity costs of conflict mitigation efforts are often high (Denninger Snyder and Rentsch, 2020). Identifying conflict hotspots and the drivers of wildlife-induced damage can aid in targeting loss-reduction strategies, thereby making interventions more effective and efficient.

Current literature on wildlife damage often focuses on a single species or guild (e.g. carnivores), or determining the species of greatest threat in an ecosystem (Dickman, 2012). More comprehensive assessments are particularly relevant in mixed farming communities where households may experience damage to crops and livestock by multiple species concurrently (Karanth et al., 2012; Mwakatobe et al., 2014). In such communities, a comprehensive approach could offer important and practical insights into whether generalized strategies can be efficiently applied (or if species-specific tools are required) and options for prioritizing interventions based on relative severity.

Similarly, few studies attempt to disentangle the environmental and human behavioral drivers of HWC across species or types of interactions simultaneously. A joint understanding of the influence of household and environmental variables on wildlife-induced damage is required to better determine the scale at which mitigation strategies should be implemented (household, community, or landscape). Determining the scale at which strategies will be most efficacious, in combination with consideration of local attitudes, sustainability, and scalability, can contribute to the design of an effective mitigation toolkit (Denninger Snyder and Rentsch, 2020).

Here we examine how an integrated multi-species assessment of agricultural damage can inform the prioritization, selection, and generalizability of HWC risk mitigation strategies in rural, agriculturally-dependent communities adjacent to the world-renowned Greater Serengeti-Mara Ecosystem (GSME) in Tanzania. Reducing HWC is a national priority of Tanzania, and is perceived as a critical pathway to improve household security, effectively protect environmental resources, and ultimately to safeguard the conservation and tourism sectors (MNRT, 2020).

Specifically, in this paper we evaluate the relative importance of landscape and household-level drivers of conflict for five of the most commonly reported species causing agricultural damage in sub-Saharan Africa and in northern Tanzania: African elephant (*Loxodonta africana*), spotted hyena (*Crocuta crocuta*), lion (*Panthera leo*), olive baboon (*Papio anubis*), and vervet monkey (*Chlorocebus pygerythrus*). We model the probability of crop damage and livestock depredation to identify the landscape and household characteristics driving risk. We map predictions of conflict probability across the landscape, assess how the spatial distribution of conflict drivers vary by species, and explore how such information can be used to identify opportunities for and challenges to human-wildlife co-existence in the western Serengeti and in rural areas of high conservation value.

2. Methods

2.1. Study area

The study area (Fig. 1) is comprised of communities adjacent to the Ikorongo and Grumeti Game Reserves and Ikona Wildlife Management Area (IGGR) in northern Tanzania (1°45′–2°10′ S, 33°50′–34° 50′ E). These protected areas form an important buffer zone between Serengeti National Park and settlements, and contain several threatened species including cheetah (*Acinonyx jubatus*), elephant, leopard (*Panthera pardus*), lion, and black rhino (*D. bicornis michaeli*). It maintains habitat critical to the seasonal migration of wildebeest (*C. taurinus mearnsi*), zebra (*Equus quagga*), and gazelle (*Eudorcas thomsoni*) through the transboundary GSME.
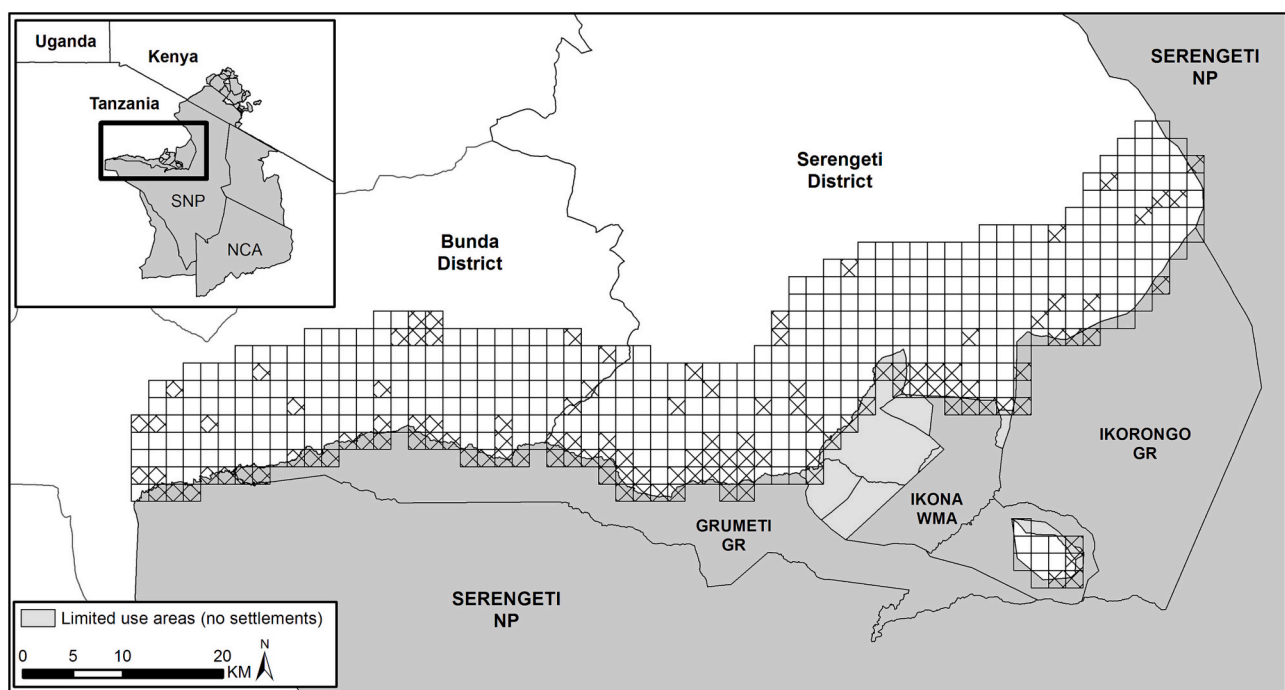

Fig. 1. Map of the western corridor of the Serengeti Ecosystem, which contains the Ikorongo and Grumeti Game Reserves, Ikona Wildlife Management Area, Serengeti National Park, and village-managed limited use areas, such as designated grazing land where permanent settlements are not allowed. The grid is the sampling frame used for the survey, uninhabited and inaccessible cells are illustrated with diagonal lines.

The elephant population in IGGR totals >1500 animals during the dry season and has increased by an average of 7.5 % per year since 2002 (Goodman and Mbise, 2018). The hyena population is stable, with annual estimates ranging between 400 and 500 individuals (Goodman and Mbise, 2018). While the lion population size is unknown, observations indicate the species was rare in 2003 and common as of 2018 (Goodman and Mbise, 2018). Olive baboons and vervet monkeys are locally abundant, though population estimates are unavailable.

The GSME is characterized by a bimodal rainfall regime and one distinct dry season. Crop damage peaks during periods of ripening and harvest, typically between May and July and November and December (Denninger Snyder et al., 2019). Livestock losses are most common during the rainy seasons, peaking between March and May (Fig. A1).

Elephant-induced crop damage is commonly reported and increasing in prevalence (Denninger Snyder et al., 2019). Community members reported that wildlife-induced damage, particularly due to elephants, has the greatest detrimental impact on household security (Grumeti Fund, 2016). In Tanzania, primates are excluded from the system of consolation payments, an important source of historical data on wildlife-induced damage (Dangerous Animals Consolation Regulations of 2011). Consequently, little is known locally about the influence of primates on crop loss.

Information on trends in livestock losses to carnivores is limited. Monitoring records of 284 self-reported and verified livestock losses (Table A1) indicate that predators killed 1137 livestock and injured an additional 182 in adjacent villages between January 2017 and June 2020 (Table A2). Retaliatory poisoning events have resulted in lion fatalities (Jacob, 2014; Tengo, 2018).

2.2. Data collection

We conducted a household survey to collect data on wildlife damage characteristics in communities within a 12 km buffer of the reserve. Based on our localized understanding of elephant movement behavior, we expected this distance to extend beyond typical elephant movements from the protected area. Systematic sampling was used to cover the entire study area. We created a sampling grid composed of 3 km^2 cells and sampled one household per grid cell. This cell size was used to balance sampling effort and to ensure that multiple households were contained within a single cell in rural areas to protect respondents' privacy. We excluded grid cells that were inaccessible or did not contain settlements. We used high-resolution satellite images to identify uninhabited cells before sampling; additional cells were considered uninhabited when no homes could be located while surveying. In total, 419 cells were sampled (Fig. 1).

Surveys were conducted between February and July 2017 by local trained enumerators speaking Kiswahili. Questions were asked to the male or female head of household at the respondent's home. When a head of household was absent, we surveyed another adult at least 18 years of age. We asked respondents questions about types of damage, species involved, agricultural practices, and household characteristics (A2). To maximize recall and self-reporting accuracy, we asked respondents to limit responses to the previous calendar year (2016). We did not ask respondents to report farmed area by crop type. We only evaluated losses due to mammals. Respondents were provided with photos and names of wildlife species to aid accurate identification.

We assessed crop damage from the previous year as a binary yes/no question. In studies of crop damage, mismatches between the perceived and actual risk of damage by wildlife have been reported, and perceptions tend to be biased towards extreme events (Gillingham and Lee, 2003; Naughton-Treves, 1997). We tried to minimize this mismatch by limiting responses to the presence-absence of crop damage, rather than quantifying frequency.

We considered livestock damage with reference to cattle, dogs, donkeys, goats, and sheep. While we did ask respondents to report the number of each livestock type owned, we only considered total number of livestock owned in our analysis. We asked respondents to indicate how often they reported damage to local authorities for species that are listed under the Dangerous Animals Consolations Regulations (United Republic of Tanzania, 2011) to evaluate reporting rates. We calculated the estimated overall reporting rate as the weighted average of the proportion of respondents reporting at a given rate.

2.3. Environmental data

Environmental variables were selected if they were deemed relevant to crop or livestock damage based on previous published research (Table 1). We considered variables related to human disturbance, habitat features, and respondents' household characteristics. These variables were derived at a 30 m resolution. Our data sources can be found in Table 1 For variables considering the density or proportion cover of features, the environment of household locations was characterized by computing values for a species-specific buffer. We used species-specific buffer distances derived from calculated metrics of mean daily net displacement (Table A3). To derive this metric we used published GPS collar data to calculate the net displacement within each defined period, averaged across all days and individuals. For carnivores, we considered overnight net displacement (17:00–07:00) (Kolowski and Holekamp, 2006; Kolowski et al., 2007; Oriol-Cotterill et al., 2015), for primates daytime net displacement (05:30–20:00) (Isbell et al., 2017), and for elephants 24-h net displacement (Gaynor et al., 2018). Additional details on how variables were derived are in the Appendix (A3).

2.4. Modeling wildlife damage

2.4.1. Causal inference and directed acyclic graphs

We constructed directed acyclic graphs (DAG)s representing our hypothesized causal relationships between variables of interest for wildlife-induced crop (Fig. 2) and livestock (Fig. 3) damage. DAGs are a common tool in causal inference (Pearl, 2009), a topic separate from, but related to statistical inference (McElreath, 2020). Generalized linear models do not imply the direction of causality as information in both directions between variables of interest. DAGs, however, force researchers to explicitly state the direction of causality. DAGs are common in fields like epidemiology (Textor et al., 2016), but are increasingly common in the social and biological sciences (Laubach et al., 2021). Using a researcher's domain specific knowledge about their study system, one may propose a DAG about the causal relationships between predictors of importance and outcomes. Assuming a DAG is true, we can identify what covariates to include in an analysis to account for confounds, which covariates will introduce confounds (i.e. collider bias), and whether or not reliable inferences are even possible given our study system and/or the data we have or will collect.

Using the adjustmentSets function from the dagitty package in R (Textor et al., 2016), we estimated the minimal number of covariates we needed to include in a model. This function traces the flow of information in the DAG, and informs us what variables to include to close all backdoor paths of information flow through the DAG so that we may reliably estimate (if possible) the effect of a predictor on our outcomes in the simplest statistical model. From these adjustment sets outputs, we constructed unique models for each direct causal pathway (Figs. 2 and 3). We give a primer on DAGs and discuss our logic for constructing them in the context of this question in the Appendix (A4) and the file 04_tza_dags_appendix.Rmd in the Zenodo repository for this paper (Denninger Snyder et al., 2023).

The direct effects of the number of protection strategies on crop damage (Fig. 2) and the number of guards on livestock depredation (Fig. 3) could not be reliably estimated due to the double sided arrow in our DAGs, which is a consequence of the sampling design of our survey. We could not determine if our measures of crop and livestock protection causally reduced the probability of conflict or were a consequence of having experienced conflict.

Table 1
Predictor variables used in the study with data source and evidence of variable importance for crop and livestock damage.

Category	Predictor variable (*variable name*)	Data source	Evidence of effect on conflict risk
Human presence	Building density (*BD*)	Open Street Map digitized buildings	Reduced (Graham et al., 2010; Songhurst & Coulson, 2014) or increased (Sitati et al., 2003; Holmern et al., 2007) risk with increasing density
	Distance into settlements (from leading edge closest to protected area) (*SD*)	Manually digitized	Increased risk closer to boundaries of protected areas (Denninger Snyder et al., 2019; Mwakatobe et al., 2014; Naughton-Treves, 1998)
	Road density (*RD*)	Grumeti Fund, OSM	Species specific utilization or avoidance of road features
Environmental features	Proportion of dense wooded cover (*C70*)	Landcover map (Landsat 8 Random forest)	Increased or decreased risk at higher densities (Abade et al., 2014)
	Proportion of moderate wooded cover (*C2070*)	Landcover map (Landsat 8 Random forest)	Suitable wildlife habitat providing shade, cover, browse
	Cropland density (*CR*)	Landcover map (Landsat 8 Random forest)	Increased risk with greater density and increased likelihood of encountering crops
	Density of rivers (*RIV*)	Serengeti GIS and Data Center	Increased risk in proximity to water sources (Abade et al., 2014; Beattie et al., 2020)
	Slope (*SL*)	USGS SRTM (Farr et al., 2007)	Decreased risk with increased slope (Wall et al. 2006)
Household characteristics	Farm (*FS*)/herd size (*LSH*)	Survey	Increased risk with increasing farm and herd size (Sitati et al., 2003; Naughton-Treves, 1998)
	Household size (*HH*)	Survey	Decreased risk with increasing household size
	Farm visibility (*SEE*)	Survey	Increased guarding effort and decreased risk if unable to see farm (Sitati et al., 2005)
	Number of months crops planted (*MP*)	Survey	Increased risk with increasing number of months planted (Karanth et al., 2012,2013)
	Guarding strategies (*GU*)	Survey	Reduced risk with increased proportional guarding effort (Denninger Snyder & Rentsch, 2020; Sitati et al., 2005)

2.4.2. Fitting models

We fit hierarchical generalized linear mixed effects models based on the minimum number of covariates needed to estimate the direct causal pathways of predictors on our outcomes. Using a Bernoulli outcome with a logit link, we asked if a household experienced crop or livestock loss to wildlife (1) or not (0) in 2016.

We had two families of models that examined drivers of loss to the most commonly reported species. The first family asked if crop loss to baboons, elephants, or vervets was experienced. The second family asked if livestock loss to hyenas or lions was experienced.

In each model we estimated varying intercepts for each village, and varying intercepts and slopes for each species for all predictors. Including species as a varying effect in our models allowed us to partially-pool the information across all species and utilize correlations between varying effects in our variance-covariance matrices. In other words, knowing whether a farm experienced crop damage by vervet monkey can improve our predictions of the probability the same farm will experience crop damage by another species.

Models were fit in R (v 4.1.1) using the map2stan function in the rethinking package (v 2.21) (McElreath, 2021) which fits probabilistic models using rStan (v 2.21.5), a Hamiltonian Markov Chain Monte Carlo Probability sampler (Stan Development Team, 2022). All code for model fitting, graphs, and raw data can be found here.

All non-binary predictor variables were standardized with a z-score transform before analysis; effect sizes of regression coefficients correspond to standardized data. The number of livestock head was log transformed. Model predictions on graphs are transformed from z-scores back to the real scale, or log scale for number of livestock, to ease interpretation. When visualizing effect sizes from regression coefficients, we plotted the 89 % highest posterior density interval (HPDI)– the default setting in the rethinking package (Figs. 4, 5).

Household size was not reported for 34 survey respondents. Thus, we used Bayesian imputation to estimate household size in models where it was a covariate. Means of imputed values can be seen in corresponding figures, and the code for semi-automated Bayesian imputation is included in the code repository.

2.4.3. Mapping model predictions

Causal inference and prediction are different goals which often require different models. Confounded models often yield better out-of-sample predictions as informed by information criteria, but are misleading about causality (McElreath, 2020; Arif and MacNeil, 2022). We mapped model-averaged predictions (Burnham, 1998) of conflict within the study area. To achieve this we calculated weights of landscape variable models using the widely applicable information criterion (WAIC). Household-level variables were excluded. For models with WAIC weights > 0.001, we used data on environmental variables (see Table 1) for each 30 m raster cell in the study area to generate posterior predictions of conflict probability from all weighted models for each raster. We then drew 2000 total predictions from the ensemble of models weighted by WAIC values for each raster cell and then estimated a mean prediction per raster cell for each species. Using these predictions, we mapped spatial predictions of crop damage by baboons, elephants, and vervets and livestock depredation by lions and hyenas across the study area. This mean value was then used to generate a color gradient of the probability of conflict.

3. Results

3.1. Survey respondent characteristics

The average age of respondents was 39 years old (range 18–88 years). Respondents were evenly split between men (49.4 %) and women (50.6 %). The majority of respondents (79.5 %) were born in Bunda or Serengeti Districts. The reported average household size was eight people (range 2–28) and nearly all households surveyed grew crops (99 %) and raised livestock (74 %).

The mean total farm size was 2.4 ha (range: 0.4–28). Respondents grew a mean of 3 different crops (range: 1–10). Fields were planted an average of 9 months per year (range: 2–12). Respondents typically employed multiple strategies to prevent or deter wildlife from damaging
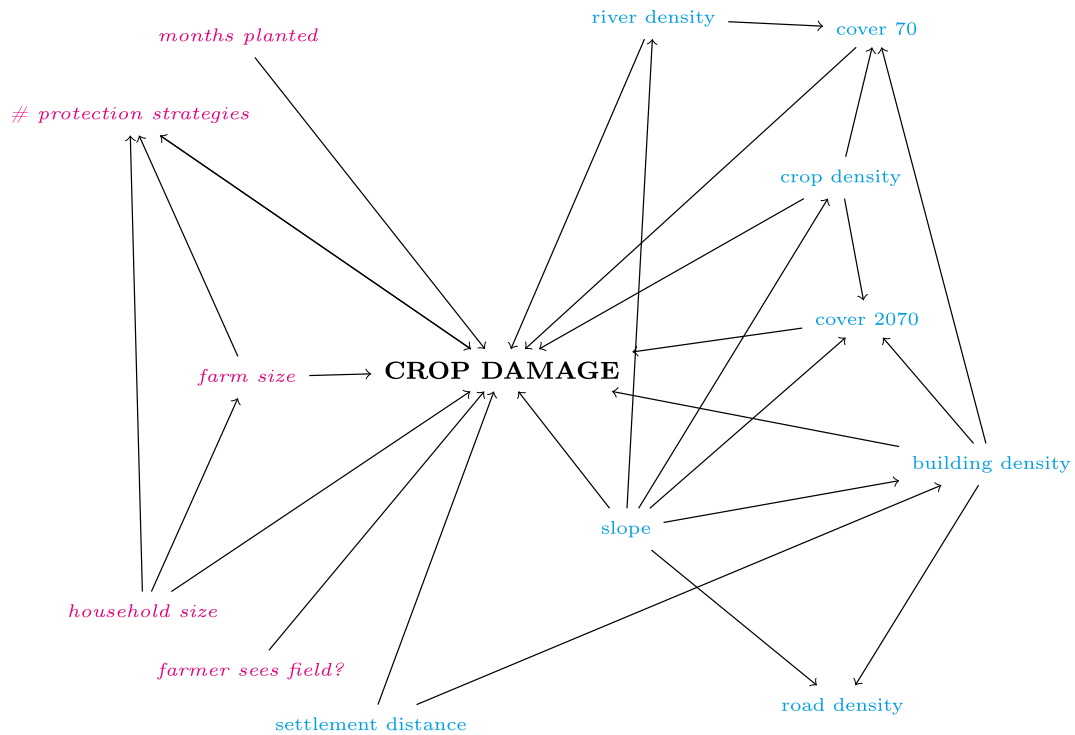
Fig. 2. DAG of proposed causal pathways and their influence on crop damage, the outcome variable of interest. Household-level nodes are italicized and in magenta, landscape-level nodes are in cyan. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
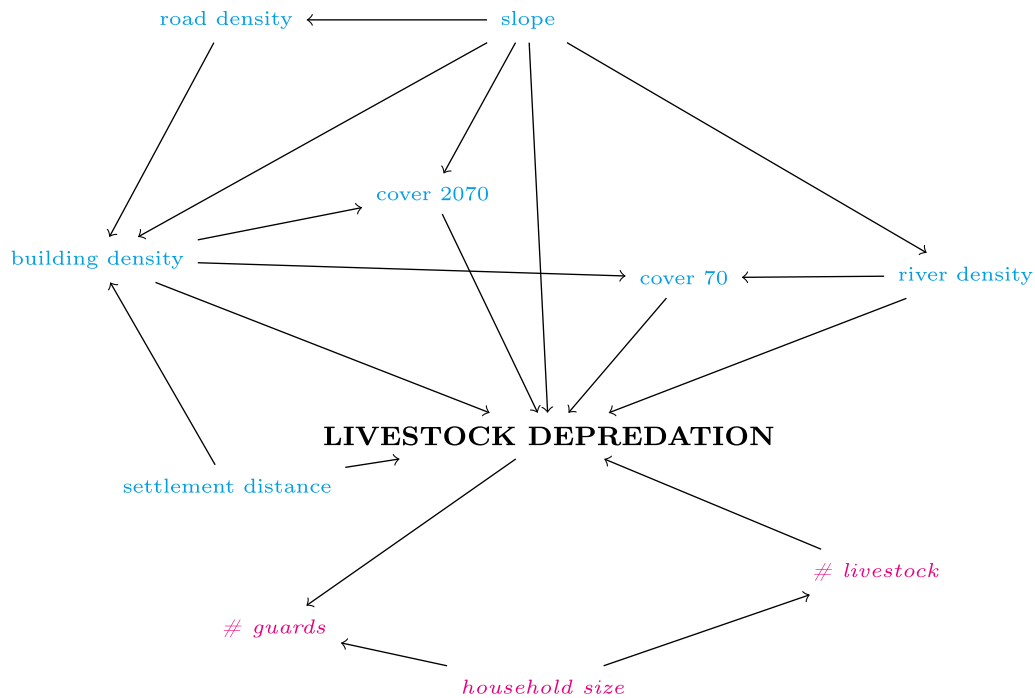

Fig. 3. DAG of proposed causal pathways and their influence on livestock depredation, the outcome variable of interest. Household-level nodes are italicized and in magenta, landscape-level nodes are in cyan. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

crops (mean = 2, range = 1–4), the most common being: shouting (72 %), guarding (67 %), chasing (23 %), and fire (22 %). The majority (60 %) of respondents indicated that damage due to wildlife, rather than disease, weather, depleted soils, or labor, was the greatest threat to crop production. The majority of farming households (81 %) suffered crop losses to wildlife in 2016, with elephants being the most commonly

identified species (Table 2). Nearly all (98 %) of those who experienced crop losses to wildlife indicated that among wildlife species, elephants posed the greatest threat.

On average, households owned 78 medium or large livestock (range: 1–764), consisting of 36 cattle (0–400), 23 sheep (0–300), 13 goats (0–100), three dogs (0–11), and less than one donkey (0–9). Almost all
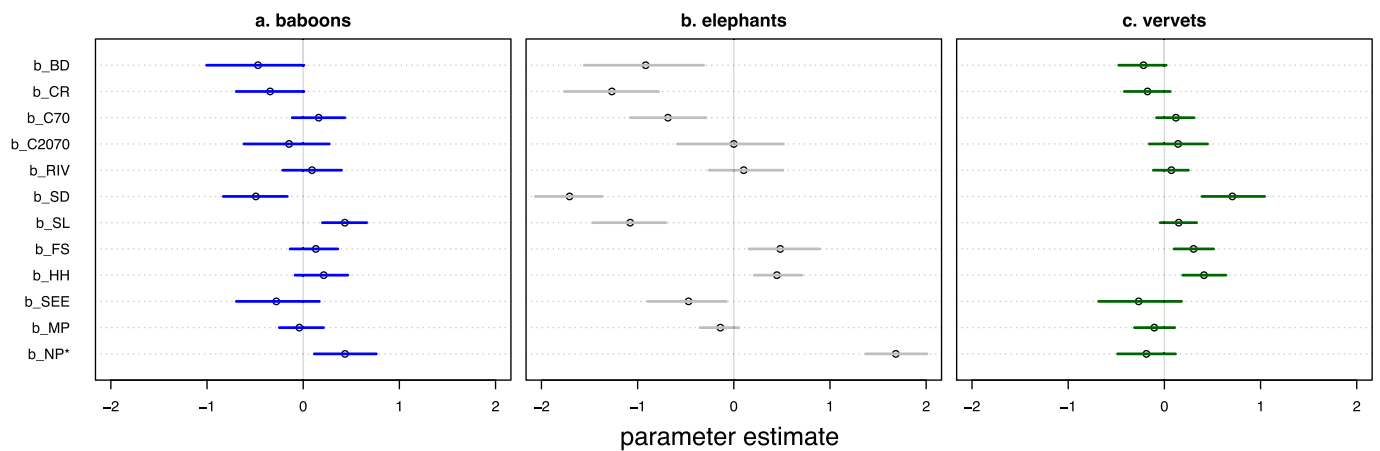
Fig. 4. Parameter estimates of the effect of covariates on crop damage. Point lies at the posterior median, lines indicate 89 % Highest Posterior Density Interval (HPDI) width. All data were standardized before being analyzed. BD is building density, CR is crop density, C70 is cover >70 % or densely wooded cover, C2070 is 20–70 % wooded cover, RD is road density, RIV is river density, SD is distance into settlements, SL is slope, FS is farm size, HH is household size, SEE is ability to see farm from house, MP is months planted, and NP is number of protection strategies. An asterisk (*) indicates likely confounded parameter estimates. Species-level effects plotted here are the sum of the population mean effect and species-level varying effects.
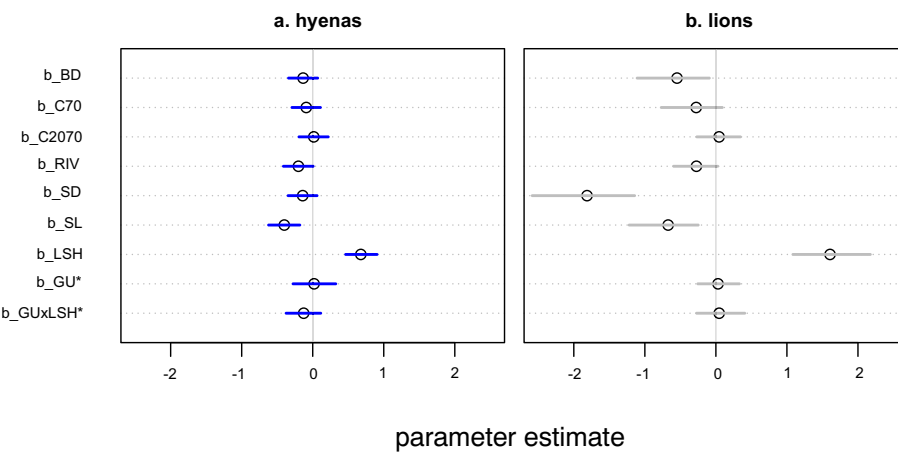
Fig. 5. Parameter estimates of the effect of covariates on livestock depredation. Point lies at posterior median, lines indicate 89 % HPDI width. All data were standardized before being analyzed. BD is building density, C70 is wooded cover >70 % or densely wooded cover, C2070 is 20–70 % wooded cover, RD is road density, RIV is river density, SD is distance to settlement leading edge, SL is average slope, GU is number of guards, LSH is log of livestock head, HH is household size. An asterisk (*) indicates likely confounded parameter estimates. Species-level effects plotted here are the sum of the population mean effect and species-level varying effects.

respondents reported guarding livestock (95 %) during the day and confining livestock (96 %) and using dogs for guarding (66 %) at night. Only 4 % of respondents identified losses to wildlife as the greatest threat to livestock; instead, low reproductive performance (57 %) was the most common response, followed by the availability of grazing land (18 %), weather (14 %), and disease (5 %). Roughly half of households owning livestock experienced losses due to wildlife in 2016, with most of these being due to hyenas, while losses to elephants, lions, and leopards were rare (Table 3). Among households experiencing livestock losses to wildlife, 90 % identified that hyenas posed the greatest threat among wildlife species.

Respondents indicated that their likelihood to report losses to local authorities varied by wildlife species. People who experienced losses were most likely to report crop damage by elephants to local authorities. Despite respondents indicating the livestock losses to hyena were the greatest concern, respondents were least likely to report livestock losses to hyenas to authorities.

3.2. Crop damage risk

Marginal model predictions of the probability of elephant-induced crop damage per household (0.907) were much greater than baboon (0.047) or vervet damage (0.060). Models containing landscape-level

predictors appeared to best predict the data compared to models containing household-level predictors (mc_bd, mc_landscape, and mc_sd in Tables A4/A5). Per species dotplots of parameter predictions from relevant models are visualized in Fig. 4. Plots of model parameter predictions for each species and variable are included in the supplemental materials (A5).

3.2.1. Landscape-level predictors for crop damage

Distance into settlements appears to be one of the most important predictors of the probability of crop damage in terms of effect size (Fig. 4; Table A4) and WAIC values across all models (Table A5). With increasing distance into settlements, the probability of crop damage by baboon ($b_{SD_{baboon}}$: Posterior Mean = −0.49, 89 % HPDI = [−0.83, −0.16]) and elephant ($b_{SD_{elephant}}$ = −1.71[−2.06 − 1.37]) strongly and reliably decreased (Fig. 4). In contrast, the probability of crop damage by vervet ($b_{SD_{vervet}}$ = 0.71[0.39, 1.04]) strongly and reliably increased with increasing distance into settlements (Fig. 4).

Building density had a negative relationship with the probability of crop damage across all species. This was most pronounced in elephants ($b_{BD_{elephant}}$ = −0.92[−1.56 − 0.31]) and to a lesser extent, baboons ($b_{BD_{baboon}}$ = −0.34[−0.70, 0.01]). Vervets ($b_{BD_{vervet}}$ = −0.22[−0.47, 0.02]) showed a near-zero preference for low building density areas, suggesting they are more tolerant of human presence

Table 2

Crop damage characteristics resulting from a systematic survey of households within 12 km of Ikorongo and Grumeti Game Reserves and Serengeti National Park. Reporting rates of buffalo damage not included because of the low number of occurrences. The elephant crop damage reporting rate was estimated based on the interval responses of how likely a household was to report damage to local authorities for consolation payments.

Characteristics	Details	Responses
Farming households	Total	413 (99 %)
Crop damage households (%)	Of farming households	81 %
Households impacted by species	Elephant	79 %
	Vervet	10 %
	Baboon	9 %
	Bushpig	2 %
	Hippopotamus	1 %
	Buffalo	<1 %
	Porcupine	<1 %
	Wildebeest	<1 %
	Mongoose	<1 %
Reporting elephant damage to Village Agricultural Officers (VAOs)	Always (100 %)	19 %
	Often (75 %)	43 %
	Sometimes (50 %)	19 %
	Rarely (25 %)	13 %
	Never (0 %)	6 %
Elephant-crop damage estimated reporting rate		64 %

Table 3

Livestock damage characteristics resulting from a systematic survey of households within 12 km of the reserve boundary. Reporting rates of elephants and leopards were not included because of the low number of occurrences. Hyena and lion livestock damage reporting rates were estimated based on the interval responses of how likely a household was to report damage to local authorities for consolation payments.

Characteristics	Details	Responses
Herding households	Total	312 (74 %)
Livestock damage households (%)	Of herding households	53 %
Households impacted by species	Hyena	52 %
	Lion	8 %
	Elephant	3 %
	Leopard	3 %
Reporting hyena damage to Village Agricultural Officers (VAOs)	Always (100 %)	3 %
	Often (75 %)	12 %
	Sometimes (50 %)	6 %
	Rarely (25 %)	29 %
	Never (0 %)	50 %
Hyena-livestock damage estimated reporting rate		22 %
Reporting lion damage to Village Agricultural Officers (VAOs)	Always (100 %)	21 %
	Often (75 %)	33 %
	Sometimes (50 %)	4 %
	Rarely (25 %)	21 %
	Never (0 %)	21 %
Lion-livestock damage estimated reporting rate		53 %

(Fig. 4).

Elephant crop damage is less likely to occur on high slopes ($b_{SL_{elephant}} = -1.08[-1.47 - 0.71]$) and is almost non-existent at extreme slopes. Vervets seem less affected by slope ($b_{SL_{vervet}} = 0.15[-0.04, 0.33]$), with a slight tendency to damage crops on high slopes, while baboons show a reliable tendency to damage crops on high slopes ($b_{SL_{baboon}} = 0.43[0.20, 0.66]$, Fig. 4).

The risk of crop damage is reduced in areas of high crop density for all species ($b_{CR_{elephant}} = -1.27[-1.76 - 0.78]$, $b_{CR_{baboon}} = -0.34[-0.70, 0.01]$, $b_{CR_{vervet}} = -0.18[-0.42, 0.06]$). This effect is most pronounced in elephants (Fig. 4).

The probability of elephant induced crop damage is greatly reduced in areas of dense wooded cover ($b_{C70_{elephant}} = -0.68[-1.08, -0.29]$). In contrast, vervets ($b_{C70_{vervet}} = 0.12[-0.08, 0.31]$) and baboons ($b_{C70_{baboon}} =$

$0.16[-0.11, 0.43]$) show uncertain, positive tendencies to damage crops in forested areas (Fig. 4). Areas of moderate wooded cover did not appear to be a strong or important predictor for crop damage by any species ($b_{C2070_{baboon}} = -0.15[-0.62, 0.27]$, $b_{C2070_{elephant}} = 0.00[-0.59, 0.52]$, $b_{C2070_{vervet}} = 0.14[-0.16, 0.45]$, Fig. 4).

There is no strong evidence that river density influences crop damage. All species show a slightly positive, but highly uncertain, relationship ($b_{RIV_{baboon}} = 0.09[-0.21, 0.40]$, $b_{RIV_{elephant}} = 0.10[-0.26, 0.51]$, $b_{RIV_{vervet}} = 0.07[-0.11, 0.25]$, Fig. 4).

3.2.2. Household-level predictors for crop damage

Household-level effects were consistent across species. The probability of crop damage by all species is positively predicted by farm size ($b_{FS_{baboon}} = 0.13[-0.14, 0.36]$, $b_{FS_{elephant}} = 0.48[0.16, 0.89]$, $b_{FS_{vervet}} = 0.30[0.10, 0.51]$), and this effect is most pronounced in elephants. We see a similar positive relationship with household size ($b_{HH_{baboon}} = 0.21[-0.08, 0.46]$, $b_{HH_{elephant}} = 0.45[0.21, 0.71]$, $b_{HH_{vervet}} = 0.41[0.19, 0.64]$, Fig. 4).

The number of months a field was planted during the year was weakly negatively associated with crop damage for all species ($b_{MP_{baboon}} = -0.04[-0.25, 0.21]$, $b_{MP_{elephant}} = -0.14[-0.35, 0.05]$, $b_{MP_{vervet}} = -0.11[-0.31, 0.11]$), but these effects were near zero and uncertain. A farmer's ability to see their field, (b_{SEE}), reduced the probability of crop damage across all species ($b_{SEE_{baboon}} = -0.28[-0.70, 0.17]$, $b_{SEE_{elephant}} = -0.47[-0.90 - 0.08]$, $b_{SEE_{vervet}} = -0.27[-0.68, 0.18]$), although this effect was small (Fig. 4).

The number of protection strategies used was positively correlated with the risk of crop damage by elephants and baboons; the relationship with risk of damage by vervets was near-zero and uncertain (Fig. 4). Our one-off survey was unable to resolve the confounding relationship between the number of protection strategies a household employs and the risk of crop damage (Fig. 2).

3.2.3. Spatial predictions of crop damage risk

Fig. 6a–c shows the model-averaged predicted crop damage risk surfaces based on WAIC weights (wWAIC in Table A5). The risk of losses to elephants was the most widespread, whereas the risk of damage by baboons was clustered and damage probability by vervets was concentrated away from the protected area. While the risk of elephant-induced crop damage appears largely driven by distance into settlements, risk only begins to lessen 3 km into settlements, and at 8 km the marginal model prediction of household risk still exceeds 0.5 (Fig. A4b). The highest probability of crop damage by elephants occurs on the border of the reserve and in Robanda village, which is situated within the Ikona Wildlife Management Area. The risk of losses to vervets, while low, extends far into settlements (Fig. A4c).

3.3. Livestock depredation risk

The estimated probability that a household experienced livestock depredation, as estimated from the coefficients in model ml_lsh, was much higher for hyena induced losses (0.537) than those by lion (0.035). The number of livestock owned by a household was the most reliable and important variable that informed the risk of livestock depredation by hyena and lion. Per species dotplots of parameter predictions for relevant models are visualized in Fig. 5. Plots of model parameter predictions for each species and variable are included in the supplemental materials (A6).

3.3.1. Landscape level predictors of livestock depredation

Livestock depredation by lions is more probable in areas of lower building density ($b_{BD_{lion}} = -0.55[-1.11 - 0.09]$). Hyenas appear to be more tolerant of high density areas, with depredation risk being slightly more probable in areas of lower building density, but this effect is small and uncertain ($b_{BD_{hyena}} = -0.14[-0.34, 0.07]$, Fig. 5).
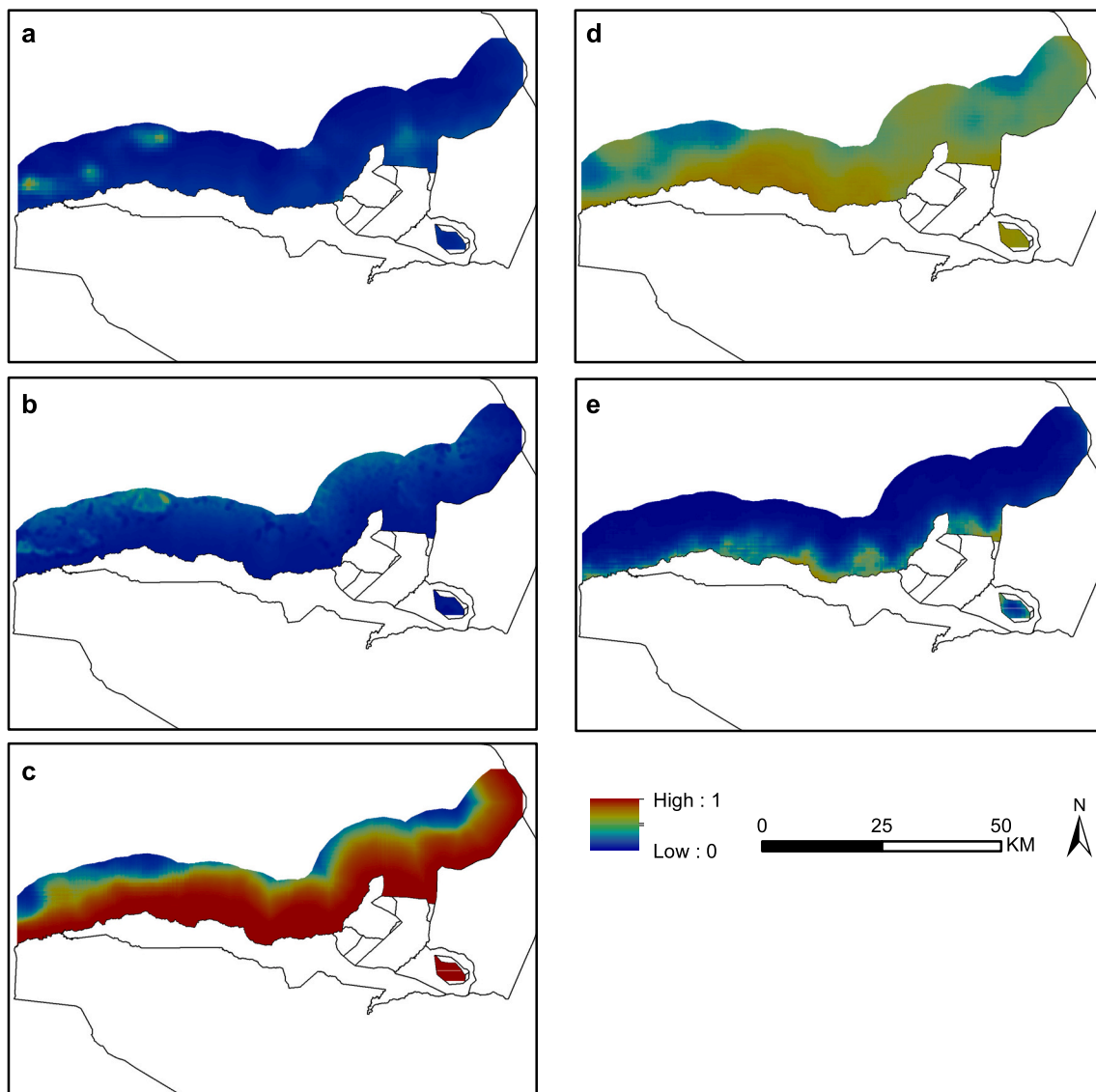
Fig. 6. Map of model averaged predictions of the probability of crop damage or livestock depredation for a 12 km buffer around the reserve for (a) baboons, (b) vervets, (c) elephants, (d) hyenas, and (e) lions (30 m resolution).

Distance into settlements had a large negative effect on the risk of depredation by lions ($b_{SD_{lion}} = -1.81[-2.59, -1.14]$), whereas it had a negative but near-zero effect on the risk of losses to hyenas ($b_{SD_{hyena}} = -0.14[-0.35, 0.06]$, Fig. 5).

Slope was a reliably negative predictor of livestock depredation by both species, with a more pronounced effect in lions ($b_{SL_{lion}} = 0.67[-1.22 - 0.25]$) than hyenas ($b_{SL_{hyena}} = -0.40[-0.62 - 0.18]$). River density was also a reliably negative predictor across species, although these effects were small ($b_{RIV_{hyena}} = -0.20[-0.41, 0.01]$, $b_{RIV_{lion}} = -0.27[-0.59, 0.03]$, Fig. 5).

Dense wooded cover showed a small, uncertain negative relationship with livestock depredation by lions ($b_{C70_{lion}} = -0.28[-0.77, 0.09]$), with a negative but near zero influence on losses to hyenas ($b_{C70_{hyena}} = -0.09[-0.29, 0.11]$). Moderate wooded cover had a reliably near zero effect on the risk of depredation by both species ($b_{C2070_{hyena}} = 0.01[-0.19, 0.22]$, $b_{C2070_{lion}} = 0.05[-0.27, 0.35]$, Fig. 5).

3.3.2. Household level predictors of livestock conflict

Livestock herd size had a large and reliable positive effect on depredation risk by both hyena and lion ($b_{LSH_{hyena}} = 0.68[0.46, 0.91]$,

$b_{LSH_{lion}} = 1.61[1.08, 2.17]$). The risk of lion depredation was close to zero for small herds but increased sharply as herd size surpassed 75 animals (Fig. A23b). Hyenas were more likely than lions to predate upon livestock in smaller herds (Fig. A23a).

The average number of guards per day did not have an influence on the probability of livestock depredation by either lion or hyena and the interaction between number of livestock head and number of guards and the associated influence on livestock depredation is unclear (Fig. 5). Adding guards may reduce the risk of depredation by hyena on larger herds, but for confounds described in the methods and further discussed in A4, causality of the influence of guarding effort on depredation risk cannot be resolved here. While the two highest ranked models were those including measures of guard effort (Table A7), this is likely due to the fact that they are confounded.

3.3.3. Spatial predictions of livestock predation risk

Fig. 6 shows the model-averaged predicted risk surfaces of livestock depredation by hyena and lion based on wWAIC values (Table A7). The risk of losses to lions were restricted along the reserve edge, while the risk of livestock depredation by hyena is seemingly not influenced by metrics of human disturbance, including building density and distance

into settlements.

4. Discussion

With increasing human populations and land use changes along protected area boundaries, interactions between humans and wildlife are increasing. Human-wildlife interactions vary along axes of frequency, intensity, and impact (Nyhus, 2016). Multi-species assessments are useful tools for conceptualizing how species-specific forms of damage are positioned along these axes and how communities, government agencies, and protected area managers may best prioritize mitigation measures. In addition, holistic assessments can assist in identifying similarities and differences in drivers across forms of HWC, creating opportunities for generalized mitigation solutions, highlighting where species-specific solutions are needed, and identifying challenges to and opportunities for human-wildlife co-existence.

In the western Serengeti, most households engage in both crop and livestock production and are susceptible to wildlife-induced losses from an array of species. We found some consistencies across forms of damage and species, most importantly that the risk of wildlife-induced damage was reduced in heavily disturbed areas. Clustered development and land use planning offer some promise as a generalized strategy to reduce conflict exposure.

However, important differences in drivers, spatial extent, conservation status, and tolerance for losses highlight the value of species-specific approaches and the need for prioritization. Crop damage by wildlife was perceived as a comparatively more severe threat to livelihoods than livestock depredation. Our study confirms previous findings that effective mitigation strategies are needed most urgently to address crop damage by elephants, which was the most widespread and impactful form of damage in the western Serengeti (Mfunda and Røskaft, 2011). The widespread nature of elephant-induced crop damage requires high-level coordination across the landscape (Shaffer et al., 2019). The mitigation of livestock losses to lions is also a high priority, due to the particularly low tolerance for losses to lions and the high conservation value of this species (Muriuki et al., 2017). The spatially restricted nature of livestock depredation by lions suggests that more targeted interventions are appropriate; a combination of land use guidelines and household-level prevention may effectively prevent losses to lions.

4.1. Drivers of crop damage

In our study, the most influential driver of crop damage by elephant and baboon was a negative association with distance into settlements - damage was most likely to occur within communities closest to the protected area and adjacent natural habitat. This finding is consistent with previous studies on crop damage by elephants and primates (Denninger Snyder et al., 2019; Graham et al., 2010; Guerbois et al., 2012; Kagoro-Rugunda, 2004; Karanth et al., 2012; Mwakatobe et al., 2014; Naughton-Treves, 1998; Mackenzie and Ahabyona, 2012). In contrast, crop damage by vervets was positively associated with distance into settlements. In South Africa, rates of crop damage by vervets were primarily shaped by avoidance of baboon presence (Findlay and Hill, 2020; Willems and Hill, 2009). In the western Serengeti, vervets may damage crops more frequently in areas farther from protected areas where baboons are less likely to be present and predation risk is reduced.

Elsewhere, findings on the influence of human disturbance are mixed– elephant crop damage has been found to be most likely in isolated areas (Graham et al., 2010; Songhurst and Coulson, 2014), at moderate levels of disturbance (Denninger Snyder et al., 2019), and in areas of higher human density and closer proximity to towns (Sitati et al., 2003). We found that all species generally avoided areas of high human disturbance, as measured by multiple indicators of human disturbance (building and cropland density), providing strong support that elephant, baboon, and vervet generally avoid high areas of

disturbance.

Crop damage by elephants and primates is often associated with proximity to wooded cover and water sources (Fehlmann et al., 2017; Graham et al., 2010; Hill, 2000; Naughton-Treves, 1998; Nyhus and Sumianto, 2000; Pozo et al., 2018; Saj et al., 2001; Wallace and Hill, 2012). We found that damage by baboon and vervet were positively associated with dense wooded cover and river density, which is likely due to the species' high dependence on trees for sleeping sites and to avoid predators (Bidner et al., 2018), and the close association between forest and rivers in the study area. In contrast to other studies, we found that crop damage by elephant was negatively associated with dense wooded cover, and that the positive relationship with river density was weak and highly uncertain. This discrepancy may be a function of the overall spatially restricted presence of dense cover in the study area, particularly outside the protected area, or differences between studies in how variables are measured (i.e. proximity vs density, scale differences).

Previous research has shown that agricultural practices influence the risk of damage by wildlife. We found that larger farms were at increased risk of damage, as has been reported elsewhere in East Africa and may be related to encounter probability or decreased guarding effort relative to farm size (Sitati et al., 2005; Naughton-Treves, 1998). We found that farms which were not visible from the home were at increased risk of damage by elephants and primates, which contradicts findings in Kenya, where farms located farther from homes where more likely to be actively guarded and experienced lower levels of crop damage (Sitati et al., 2005). We did not find a clear relationship between number of months a farm is planted and crop damage risk, as has been reported in India (Karanth et al., 2012, 2013). This disparity could be due to differences in types of crops planted and associated palatability and time to maturation.

The use of deterrents and preventative measures, particularly those that provide advanced warning such as guarding, have been demonstrated to reduce the risk of crop damage (Denninger Snyder and Rentsch, 2020; Sitati et al., 2005). We were unable to examine the influence of individual household deterrents, or infer a causal relationship with the number of deterrents used, but we observed that elephant-induced crop damage remained a widespread and significant issue despite nearly all respondents reporting that they employed household-level protection strategies.

4.2. Drivers of livestock depredation

Our results indicate that while livestock depredation by both hyena and lion was less likely further from protected areas and in areas of high human disturbance, this effect was much stronger for lions. Livestock depredation by hyena was reported far from protected areas and in areas of relatively high building density, which aligns with other studies (Holmern et al., 2007). In the Maasai Mara, studies of hyena movement found that hyenas modified their behavior in human impacted areas and that their flexibility may allow the species to persist in human-dominated landscapes (Green and Holekamp, 2019). Depredation by lion is more commonly associated with proximity to protected areas and low human density (Holmern et al., 2007; Loveridge et al., 2010; Mbise et al., 2018; Weise et al., 2019).

Previous studies have found that livestock depredation is more common near water sources, where prey is more likely to be abundant and carnivores, particularly lions, are most likely to hunt (Abade et al., 2014; Beattie et al., 2020; Davidson et al., 2013; Weise et al., 2019). However, this relationship seems to be restricted to depredation incidents when livestock are grazing, rather than when livestock are corralled (Abade et al., 2014). In the western Serengeti, livestock losses were less common in areas of high river density. Two factors are likely to drive this pattern – first, most livestock depredation events in the study area occur overnight at bomas (Holmern et al., 2007; Kissui, 2008). Second, peaks in livestock depredation tend to correspond with low densities of natural prey (Patterson et al., 2004; Kolowski and

Holekamp, 2006). In the western Serengeti, livestock losses are highly seasonal and predominantly occur during the wet season when prey is widely dispersed and not restricted by water availability (Fig. A1).

We found that the risk of livestock depredation was lower in areas of dense wooded cover. This corresponds with what has been reported elsewhere in Tanzania in the context of livestock depredation, and may be related to the increased visibility of livestock and improved hunting success in open areas, and that most depredation events in bomas tend to occur at night, when vegetation is not needed to provide cover (Abade et al., 2014).

5. Management applications

Concentrated development, the implementation of suitable buffer zones where human activities are not attractive to wildlife, increased engagement in wildlife-compatible activities, and designating wildlife corridors are potential strategies to reduce negative interactions between people and wildlife (Pozo et al., 2018; Nelson et al., 2003; Fernando et al., 2005). Our results suggest that applying land use planning principles to inform the spatial arrangement of farms, homes, and livestock bomas may reduce the risk of crop damage and livestock depredation by wildlife. Maximizing the density of converted areas, minimizing the distance between farms and homes, and implementing minimum distances between protected areas (and nearby refuge habitat) and livestock bomas may reduce the risk of losses to wildlife. Guidelines dictating building density and farm arrangement may be most effective within 10 km of protected area boundaries where elephant induced crop damage, the most widespread and impactful form of damage, is at greatest risk of occurrence.

The western Serengeti has already been largely converted for agriculture (Veldhuis et al., 2019). Locally, the most relevant applications of land use planning may be to increase effective buffer zones by preserving and strictly managing remaining grazing and village open areas along reserve edges, and to implement statutes guiding the spatial arrangement of future development. Given the widespread nature of crop damage by elephants, landscape-level interventions that prevent elephant access to farms are necessary. Options include organized community guarding, electric fencing, and the application of other deterrents, such as beehive fences, along agricultural boundaries (Denninger Snyder and Rentsch, 2020; King et al., 2017; Kioko et al., 2008; O'Connell-Rodwell et al., 2000; Pekor et al., 2019; Scheijen et al., 2018). The implementation of large-scale strategies will require community organization, support, and investment.

Nearly all households that experienced losses to carnivores indicated that among wildlife species, hyena posed the biggest threat to livestock. However, households were more likely to report losses due to lions to local officials, and while retaliatory killings in response to lion depredation have occurred on multiple occasions in the area since 2014, no retaliatory killings of hyena have been recorded. These findings support previous research which has found that losses to lions have greater economic impact and are less tolerated by pastoral households, despite hyena posing a greater risk to households in terms of total predation events and number of livestock lost (Muriuki et al., 2017). The reduced tolerance for losses to lions may be linked to observations that lions are often disproportionately responsible for the depredation of cattle, which are of high monetary value and cultural significance A2 (Mkonyi et al., 2017; Mbise et al., 2018; Kissui et al., 2019; Kissui, 2008; Kolowski and Holekamp, 2006). The low tolerance for losses and high conservation value of lions necessitates the development of strategies to reduce human-lion conflict.

The spatially restricted nature of livestock losses to lions indicates that developing strategies for human-lion coexistence is seemingly feasible by reducing spatiotemporal overlap between livestock and lions (Beattie et al., 2020; Petracca et al., 2019). Losses to lions were rare and risk was spatially restricted to protected area edges. In the western Serengeti, grazing areas and natural water points are concentrated along protected area edges in locations with high lion depredation risk. As livestock losses are most prevalent during the wet season, daytime losses while grazing could be avoided by delineating wet season grazing areas further from protected areas, and dry season grazing in areas closer to protected areas with increased vigilance around surface water, where dry season depredation risk is expected to be highest (Beattie et al., 2020). Overnight losses at bomas may be reduced by implementing high-quality husbandry practices, particularly among households with large herds of livestock (>75 animals). Positioning overnight corrals farther from protected areas may greatly reduce the risk of losses to lions - at 2 km, risk declined by half (Fig. A17b). The accessibility of grazing areas may limit opportunities for boma placement, other options include reinforcing bomas, using guard dogs, and maintaining high levels of human activity in and around bomas (Lichtenfeld et al., 2015; Ogada et al., 2003).

While our study focuses on the dynamics of HWC in the western Serengeti, conflict between people and wildlife is a global issue and the approach utilized here is widely applicable to addressing the challenges to co-existence faced by rural communities living alongside wildlife. Multi-species examinations of HWC are a valuable approach to identify opportunities for and limitation to generalized mitigation strategies, and to better understand whether species specific solutions are necessary, feasible, and optimally aligned with conservation objectives.

CRediT authorship contribution statement

Kristen Denninger Snyder: Conceptualization, Methodology, Data Curation, Supervision, Funding acquisition, Writing - original draft, reviewing, editing
Kate Tiedeman: Methodology, Formal Analysis, Data Curation, Writing - original draft, reviewing, editing
Brendan Barrett: Methodology, Formal Analysis, Writing - original draft, reviewing, editing
Mackiana Kibwe: Investigation
Robert J Hijmans: Writing - Reviewing and Editing, Supervision
George Wittemyer: Writing - Reviewing and Editing, Supervision

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential; a link to the code repository is shared in-text.

Data statement

The household survey data that has been used is confidential. Survey respondents were assured raw data would remain confidential and would not be shared outside the scope of the original research objective.

Code used to clean data, fit the GLMMs, generate graphs and tables, and generate predictions for maps can be found here: https://doi.org/10.5281/zenodo.7764138

Institutional review

Survey protocols and verbal consent documents were reviewed and approved by Ethical and Independent Review Services (protocol 17013-01).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110202.

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