

Evidence for increasing human-wildlife conflict despite a financial compensation scheme on the edge of a Ugandan National Park

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Abstract

The conflict of large carnivores and agro-pastoral communities is a key driver of carnivore decline globally. The East African state of Uganda relies heavily on tourism as a GDP contributor and large carnivores are important for generating visitor revenue in its national parks. African leopards, spotted hyenas and African lions are three species that draw significant tourist attention but also cause damage to the livestock of human communities living on Ugandan national park edges. A private safari lodge in the Lake Mburo National Park has been using a financial compensation scheme in an attempt to stem conflict between these species and human communities living in the region since 2009. Financial compensations have produced mixed results with some studies reporting successes in reducing carnivore deaths, while others warn against their use, citing moral hazard, financial unsustainability and weakened protection of livestock by farmers. We sought to assess the characteristics of this compensation scheme and the patterns of conflict between Bahima pastoralist communities and carnivores that the scheme aims to mitigate. Using a dataset of 1,102 leopard and hyena depredation events (January 2009–December 2018) we found that spotted hyenas were responsible for the overwhelming majority of livestock depredation (69%) around Lake Mburo. Depredations occurred mostly at night (97% and 89% of all depredation for spotted hyenas and leopards respectively) and inside livestock protective pens (bomas). Depredation was more likely to occur in rugged areas, closer to human settlements, and the national park border, and further away from water. We could find no evidence of seasonality in depredation events. Our most important, albeit worrying result was that conflict had increased dramatically over time and the number of depredation claims had tripled in the period from 2014–2018 when compared to 2009–2013, risking financial unsustainability of the scheme. Our results are important for future conservation stakeholders attempting to implement financial compensation in the broader Ugandan landscape. They suggest

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that careful thought needs to be placed into fund sustainability, increasing claims over time and the development of clear rules that underpin compensation claims.

KEYWORDS

depredation risk, financial compensation, human-carnivore conflict, human-wildlife conflict

1 | INTRODUCTION

In Uganda, East Africa, conflicts between large carnivores and human communities are common (Mudumba, 2011; Sheppard, 2014; Uganda Wildlife Authority, 2010). Extremely high livestock densities and small, isolated protected areas with porous borders contribute to this high prevalence (Plumptre et al., 2019; Venter et al., 2016). Many Ugandans have a very strong cultural and economic connection to cattle production, and with an average of 50 cows/km² (Cook, 2015) the country has the highest density of cattle anywhere on the continent, and the eighth highest in the world (Robinson et al., 2014). Large carnivores regularly raid cattle and other livestock (Ochieng, Ahebwa, & Visseren-Hamakers, 2015) and are killed in retaliation through poisoning, trapping or shooting (Braczkowski et al., 2020; Tweheyo, Tumusiime, Turyahabwe, Asiimwe, & Orikiriza, 2012). Examples of this conflict include at least 19 African leopards (hereafter leopards) being killed on the boundary of the Lake Mburo National Park in a 4-year period from 2003 to 2006 (CITES 2014), and at least 47 adult and sub-adult lions being killed between 2006–2012 in the Queen Elizabeth Conservation Area (Braczkowski et al., 2020). These conflicts are classic examples of human–carnivore conflicts, which are a global conservation challenge (Treves & Karanth, 2003).

One common tool for reducing this type of human-wildlife conflict in sub-Saharan Africa, and globally, is to compensate financially for depredation of livestock. Financial compensation is used by both governments (e.g., South African National Parks; Anthony & Swemmer, 2015), and conservation NGOs alike (e.g., Landmark Foundation Leopard and Predator Project; McManus, Dickman, Gaynor, Smuts, & Macdonald, 2015). The evidence for their efficacy in stemming rates of carnivore killings is mixed. Several studies report positive results (e.g., Bauer, Müller, Van Der Goes, & Sillero-Zubiri, 2017; Hazzah et al., 2014; MacLennan, Groom, Macdonald, & Frank, 2009; McManus et al., 2015), while others criticize compensation, citing that it creates inter alia an environment for moral hazard, weakened care of livestock by farmers and is not a financially viable model for long term conservation impact (Nyhus, Fischer,

Madden, & Osofsky, 2003; Nyhus, Osofsky, Ferraro, Madden, & Fischer, 2005).

We sought to study the characteristics of one such financial compensation scheme (privately funded by the Mihingo Safari Lodge) and the human-carnivore conflict it sought to mitigate on the edge of a small but regionally important Ugandan National Park; the Lake Mburo National Park (hereafter LMNP). Local Bahima pastoralists belonging to the Banyankole tribe around LMNP generally view large carnivores like spotted hyenas *Crocuta crocuta* and leopards *Panthera pardus* as a threat to their livelihoods. The predation of livestock by these species causes financial burden to these pastoralists (Infield & Namara, 2001; Tweheyo et al., 2012) and there have been retaliatory killings of these carnivores. This in turn has ramifications for local safari lodges, tourism operators and the Ugandan Wildlife Authority (UWA), which rely on tourism revenue. For example, in 2018 alone, 1,585 people purchased a night game drive permit for leopard viewing in the park, which generated US\$47,550 in park fees alone for the Ugandan Wildlife Authority (A. Kule pers. comm.).

To better understand the nature of this conflict and the potential of financial compensation as a human-carnivore conflict mitigation tool we investigated four lines of inquiry in this paper; (1) the sustainability of the Mihingo financial compensation scheme (hereafter Mihingo Conservation Fund, MCF) based on historic data, (2) which carnivore species are responsible for the majority of conflict in the LMNP region, (3) what are the spatial drivers of depredation, and (4) how knowledge of landscape drivers could better inform compensation payments and other conflict mitigation interventions in the future.

We hypothesized (1) that livestock depredation by spotted hyenas and African leopards (hereafter leopards) would follow a clear seasonal pattern, as there is a higher density of wild herbivores outside the borders of LMNP in the wet season (Rannestad, Danielsen, Moe, & Stokke, 2006). This would reduce reliance on domestic species (Khorozyan, Ghoddousi, Soofi, & Waltert, 2015), leading to more depredation in drier months. LMNP and the surrounding livestock farming areas also have many granite inselbergs. We therefore hypothesized that

degradation would be more likely in areas of rugged terrain due to the cover they provide for spotted hyenas and leopards. We also hypothesized that areas of thick bush, and in close proximity to water would be similarly prone to high probabilities of depredation in the landscape. These have been found to be important predictors of depredation probability (Abade, Macdonald, & Dickman, 2014; Rostro-García et al., 2016; Wang & Macdonald, 2006).

Our assessment of Mihingo's financial compensation scheme and the landscape-level drivers of human–carnivore conflict in the region represent the first investigation of this kind in Uganda. With tourism steadily growing in the country our results have some important ramifications for potential problems associated with future compensation schemes and the landscape variables, which contribute to livestock depredation probability.

2 | METHODS

2.1 | Study area and history of the financial compensation scheme

We implemented our study in the Lake Mbuo National Park (LMNP; 370 km²; 30° 47' – 31° 04'E and 00° 30' – 0° 30' S), Kiruhura district, south-western Uganda (Figure 1). The park falls within the Akagera savannah ecosystem, which extends from Rwanda and north-

western Tanzania down into south-western Uganda (Van De Weghe, 1990). Most of the region is dominated by Pleistocene—recent deposits which give rise to fine sandy loams along ridges and slopes, as well as peat and alluvial clays at the bottom of the valleys (Rwaguma et al., 1997). The park experiences a bimodal annual rainfall pattern (October–December, and February–June) averaging 800 mm, and daily temperature averages 28°C (Moe, Loe, Jessen, & Okullo, 2016). The park's woody vegetation is characterized by dry *Acacia* savannah dominated by *Acacia hockii*, woodlands, thickets and swamps, which occur on the edges of the lakes Kachera, and Mbuo (Rannestad et al., 2006). The most common grasses include *Loudetia kagerensis*, *Chloris gayana*, and *Sporobolus pyramidalis*.

LMNP is bordered by a matrix of small human settlements, small-scale subsistence crops, dairy ranches, and communal grazing lands (Ochieng et al., 2015). The pastures around LMNP are mainly degazetted national park land, an artifact of the fall of the Milton Obote political regime that initially evicted 300,000 Banyankole pastoralists (mostly of the Bahima tribe) when originally gazetted (Infield & Namara, 2001; Kingdon, 1985). The Bahima are a Bantu-speaking ethnic group, which rely heavily on livestock production, mainly the Ankole long horn cows (Kyagaba, 2004). The pastures around LMNP have significant numbers of wild herbivores, particularly in the rainy season (Rannestad et al., 2006). This makes livestock pastureland suitable for large carnivores (leopards and spotted hyenas are the only species remaining, with

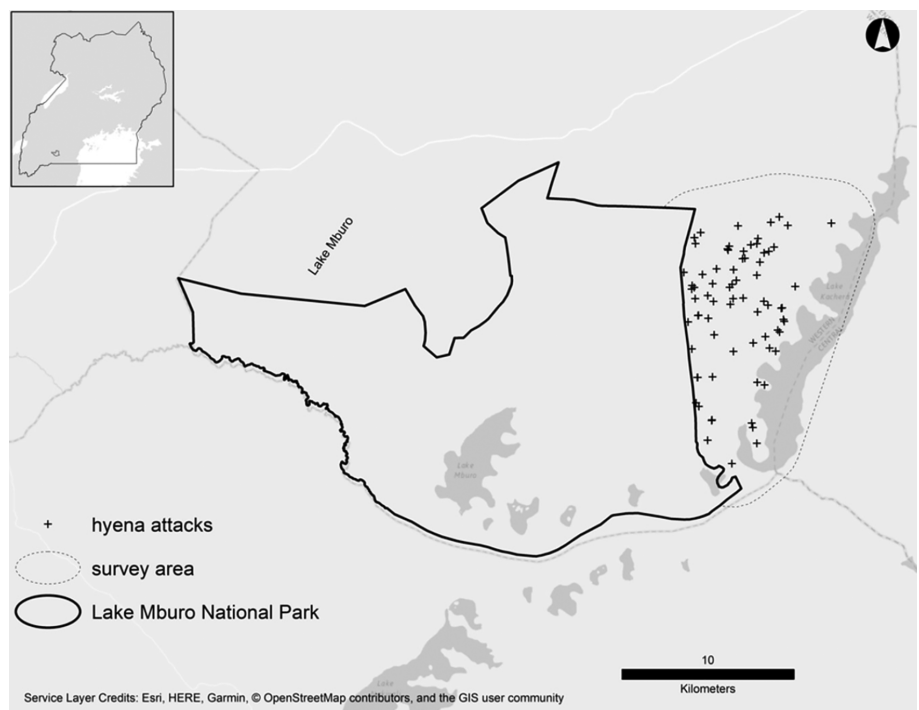


FIGURE 1 The 370 km² Lake Mbuo National Park in south-western Uganda, with spotted hyena, and African leopard depredations on livestock

lions going functionally extinct circa. 2008, UWA, 2010), and regular predation of livestock occurs. Specifically, the surrounding pastoralist areas support one of the last two remaining populations of impala *Aepyceros melampus* in Uganda, the most common and preferred prey of the African leopard (Hayward et al., 2006). The park also has populations of Burchell's zebra *Equus burchelli*, Cape buffalo *Syncerus caffer*, Defassa waterbuck *Kobus ellipsyprymnus defassa*, bushbuck *Tragelaphus scriptus* and warthog *Phacochoerus africanus* (Rannestad et al., 2006). Preferred prey of both these predators is available beyond the borders of the LMNP, and Rannestad et al. (2006) noted higher densities of bushbuck, impala, reedbuck *Redunca redunca*, waterbuck and zebra outside of LMNP during the wet season.

2.2 | The Mihingo Conservation Fund and depredation data

The Mihingo Conservation Fund (MCF) was established in late 2007 due to the longstanding conflict between Bahima pastoralists, and large carnivores on the borders of LMNP. For example, at least 19 leopards were killed on the boundary of LMNP between 2003 and 2006, and two hyena clans that were regularly viewed by tourists were poisoned in 2007 (each >14 members in size; Ralph Schenk pers. obs). The MCF's aim is to "encourage co-existence of wildlife and humans beyond the boundaries of LMNP." The MCF is privately funded by the Mihingo Safari Lodge and all compensation funding is accrued through guest spa visits, community nature walks, donations and an annual marathon fundraiser (The Mihingo Marathon). The rules of the compensation scheme are as follows: (1) any depredations must be reported within a 24 hr period to the Mihingo Lodge, (2) evidence of a livestock carcass must be made upon arrival of the monitors, (3) if there is evidence of negligence of livestock protection (through herding or penning) a penalty will be applied to the compensation payment (~20 to 50% of the market value of the animal). Importantly, compensation is only paid for livestock for which carcasses were recovered.

We used data for the 10-year period on human-carnivore conflict extending from January 2009 to December 2018. Livestock depredation events were defined as any incident in which a predator killed or injured one or more livestock, meaning that several livestock could be depredated in a single event (Kissui, 2008). Depredation events were reported by livestock farmers on the edge of LMNP and collected by Mihingo Lodge managers and two scouts trained in the identification of animal tracks and predator depredation

characteristics (i.e., bite marks and drag marks) whenever they were reported on the lodge's telephone line. The scouts would visit farms reporting depredation (typically within a 24-hr period). At each conflict location, we noted the identity of the animal killed or injured, and the identity of the predator responsible for the depredation. This was determined through a combination of visual examination of animal tracks, feeding sign, or injury marks left on livestock, and through the eye-witness reports of the livestock herder or owner (Kissui, 2008; Ogada, Woodroffe, Oguge, & Frank, 2003). The livestock herders in this region generally have extensive experience in identifying the main predators responsible for depredations due to regular contact with their livestock. For each event additional information on the time of the depredation, we noted the location of the depredation (i.e., inside boma or outside), site characteristics, and the type and age of the livestock killed. We recorded GPS locations of the depredation site for 329/1102 depredation events attributed to spotted hyenas and leopards.

3 | DATA ANALYSES

3.1 | Patterns of depredation around LMNP

We assessed the observed frequencies of predation on different livestock types, and the spatial context of depredations (i.e., inside boma, outside boma or chased/dragged outside by a predator that was outside the boma), by spotted hyenas and leopards, which were the most common predators (1,102 of 1,125 livestock depredation reports; 98%). We tested whether the number of depredation events on each livestock type by spotted hyenas and leopards differed from 50:50 using a Chi-squared test. To assess the temporal distribution of depredations across seasons, and more specifically across wet and dry months, we used a negative binomial regression. We grouped depredations by month and year (e.g., January 2009, March 2011, and so forth) and used these monthly depredation occurrences as our response variable. We then used long term, monthly rainfall data from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory (version 2018–1891–2016; see: <https://www.esrl.noaa.gov/psd/data/gridded/data.gpcc.html>) for the region around LMNP at 0.5° latitude × 0.5° longitude resolution. We calculated the monthly mean of the 4 cells, which encompassed the LMNP between January – December for the years 2009–2016. We assessed the influence of rainfall on the number of depredations for spotted hyena and leopard depredations per month separately, and in

combination. We also used the logarithm of month days as a response variable due to some months being longer than others.

3.2 | Financial sustainability of the MCF

We calculated the total yearly budget spent on financial compensation and compared the difference to funds accrued from tourist activities from fundraising for the 2012–2018 financial years. We compared yearly and mean monthly compensation payments between total income, and compensation costs, and between species (i.e., compensation costs of spotted hyenas vs. leopards) using a two-sample *t* test. We also tested for differences in the total number of attacks in the first 5 years (2009–2013) of the compensation scheme and compared these to the last 5 years (2014–2018) through a one-way ANOVA.

3.3 | Landscape predictors of livestock depredation by African leopard and spotted hyena

We were also interested in the effects of landscape variables on the probability of depredations by leopard and hyena. Accordingly, we built multivariable logistic regressions analogous to a resource selection function in a used vs. available design (Manly, McDonald, Thomas, McDonald, & Erickson, 2007) at the first order of selection (Johnson, 1980; Meyer & Thuiller, 2006). We used spatially explicit locations of leopard and hyena depredations as presence data. To define the domain of availability to sample environmental conditions, we built a convex polygon encompassing all the depredation points (Fattebert, Robinson, Balme, Slotow, & Hunter, 2015; Miller, 2015). We generated random pseudo-absences at a 1:5 ratio to used locations (Fattebert, Morelle, Jurkiewicz, Ukalska, & Borkowski, 2019). We extracted landscape variables at each used, and available point using the package raster (Hijmans et al., 2013) in the R environment (Pinheiro, Bates, DebRoy, & Sarkar, 2018; R Core Team, 2018). We chose a suite of candidate explanatory variables based on previous large carnivore occurrence or conflict studies (Abade et al., 2014; Balme, Hunter, & Slotow, 2007; Dhanwatey et al., 2013; Fattebert et al., 2015; Rostro-García et al., 2016), which have highlighted their importance as potential drivers of both occupancy and depredation probability (see Miller, 2015 for a comprehensive review). These included a measure of tree cover, terrain ruggedness, and distance to rivers, and water bodies, to roads and vehicle tracks, to human settlements, and to the national park boundary (Table 1).

We built two models, one for each species, and applied a manual backward-stepwise model selection procedure, removing all nonsignificant variables from the multivariate model, until the effects of all remaining variable were significant ($p \leq .05$; Hosmer Jr, Lemeshow, & Sturdivant, 2013). We then projected the predicted values spatially, as:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)$$

where β_i is the coefficient for the variable x_i . Because pseudo-absences could sample areas where depredation did occur but were not recorded, this RSF is proportional to a resource selection probability function (RSPF) in a used-unused design and is not bounded between 0 and 1 (DeCesare et al., 2012). Therefore, we reclassified the projected values into 10 equal-area bins using percentile breaks at 10% intervals for mapping (Fattebert et al., 2018). Because so many attacks occurred inside livestock bomas, it is plausible that boma placement location in the landscape alone could explain attack probability. Therefore, we wanted to examine if our models were reflecting boma location instead of the variable of interest. To this end, we created a separate model of boma distribution, and generated pseudoabsences in the broader landscape. If model coefficients were similar between each carnivore depredation and the boma models, we would not be able to tease apart broader landscape effects on attack probability.

4 | RESULTS

4.1 | Impacts and temporal trends of predation by spotted hyena and African leopard

We recorded 1,125 livestock depredation events between January 2009, and December 2018. Spotted hyenas, and leopards were deemed responsible for the overwhelming majority of events ($n = 1,102$; 98%), and spotted hyenas caused more than twice the total depredation losses compared to leopards (69 vs. 31% of all events; Figure 2). This difference was significant across the livestock species depredated ($X = 110.38$, $p < .05$). Depredation events by other species comprised male lion (1), olive baboons *Papio anubis*, African rock pythons *Python sebae*, and unidentified species ($n = 23$ or 2% of all depredation events). The majority of spotted hyena depredation reports were of cattle (64%). In contrast, leopard depredation reports comprised 30% cattle, and 70% goats and sheep (Table 2). Multiple killings (i.e., where ≥ 2 animals were killed in the same depredation event), were

recorded in 52 events for leopards (15% of all leopard depredation reports), and 99 events for spotted hyenas (13% of all hyena depredation reports). Adult livestock were preyed upon most often by both spotted hyenas and leopards (Table 3), followed by juveniles, and sub-adults.

African leopard depredation reports were primarily (82%) inside bomas or involved chasing livestock outside of them. Similarly, 64% of hyena depredation events were reported from inside bomas (or involved chasing livestock out of them; Table 3). Our GLMs indicated no

TABLE 1 Spatial covariates used in our multivariate logistic regression examining spotted hyena and leopard depredation probability in the LMNP, south-western Uganda

Covariate	Layer year	Layer spatial resolution	Metric calculated	Source	URL
Road density	2019	250 m	Euclidean distance to roads	OpenStreetMap	https://tinyurl.com/y2px4hck
Waterholes and rivers	2019	250 m	Euclidean distance to rivers and waterbodies	Uganda Bureau of Statistics	https://tinyurl.com/y4tdpp88
	2014	250 m		OpenStreetMap	https://tinyurl.com/y2px4hck
Human settlement density	2015	30 m resampled at 250 m	Euclidean distance to human settlements	Columbia University	https://tinyurl.com/y3qwx5d5
Vegetation continuous field (VCF)	2018	250 m	Focal mean	United States Geological Survey	https://tinyurl.com/y2eabech
Terrain Ruggedness Index (TRI)	2018	30 m resampled at 250 m	Focal mean	Regional Centre for Mapping Resource for Development	https://tinyurl.com/y5tk9h6q
Protected area (LMNP)	2019	250 m	Euclidean distance to protected area	World Database on Protected Areas	https://tinyurl.com/y2cw4hdx

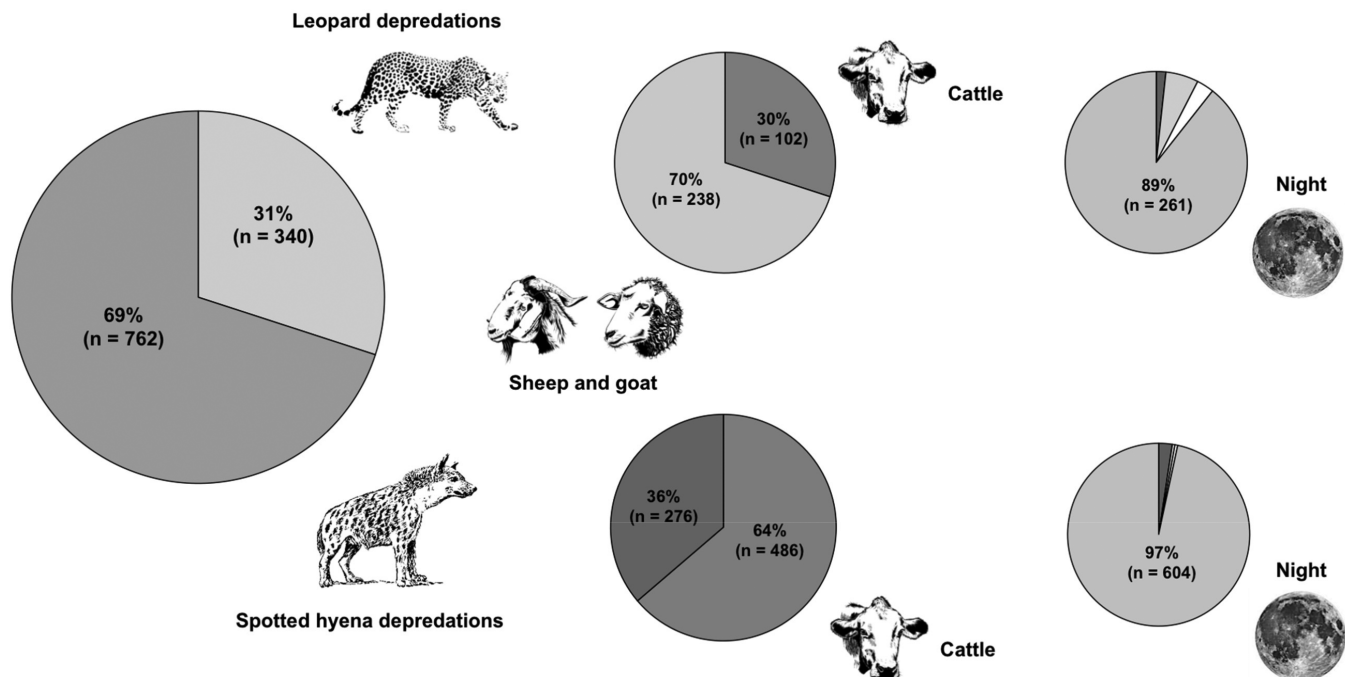


FIGURE 2 Sample sizes and proportions of spotted hyena and African leopard livestock depredation events at the edge of LMNP (collected between January 2009 and December 2018), and the proportion of depredation events that took place at night (vs. dawn, day, and dusk). The contribution of cattle, and sheep and goats in the diet of leopards and spotted hyenas was almost perfectly inversely proportional

TABLE 2 Distribution of cattle, sheep and goats injured and killed by spotted hyenas, and leopards (collectively termed depredation) between 2009 and 2018. Other depredation events are provided as footnotes a-d underneath this table.

Year	Number of livestock killed by leopards		Number of livestock killed by hyenas		Number of livestock injured by leopards		Number of livestock injured by hyenas		Total
	Cattle	Sheep and goats	Cattle	Sheep and goats	Cattle	Sheep and goats	Cattle	Sheep and goats	
2009	1	6	12	9	0	0	2	0	30
2010	3	12	13	15	1	1	2	3	50
2011	5	8	19	19	1	1	2	1	56
2012	7	13	11	15	2	1	2	0	51
2013	13	10	33	8	0	2	5	0	71
2014	8	58	44	25	2	2	7	2	148
2015	9	20	91	11	10	2	9	0	152
2016	10	27	71	60	6	1	3	2	180
2017	10	27	86	50	3	8	3	2	189
2018	7	38	64	53	4	1	7	1	175
Total	73	219	444	265	29	19	42	11	1,102

Note: Total number of records for entire dataset is 1,125 depredations. Total number of leopard and hyena records is 1,102 depredations.

^aLion kills across all years amounted to 1 (1 goat).

^bBaboon kills across all years amounted to 1 (1 goat).

^cPython across all years amounted to 1 (1 goat).

^dUnidentified kills/injuries across all years amounted to 20 (6 cow kills, 10 goat kills, 2 injured cows and 2 injured goats).

TABLE 3 Distribution of age-classes of livestock preyed upon by spotted hyenas, and leopards (collectively termed depredation), and the depredation locations of livestock for spotted hyenas and leopards (with missing data values).

Species	Age class				Depredation location			
	Adult	Sub-adult	Juvenile	No data	Inside boma	Outside boma	Chased/dragged	No data
Spotted hyena	514	43	73	132	136	148	129	349
African leopard	170	37	73	60	90	33	58	159
Total	684	80	146	192	226	181	187	508

significant effect of monthly rainfall (adjusted for time) on depredation of livestock by spotted hyenas, leopards (Table 4) or the combined attacks of the two species (Table 4). However attacks increased linearly and there was a significant increase in depredations between the 2009–2013 and 2014–2018 periods for both leopards ($F[1,93] = 21.82, p \leq .0001$, Figure 3), spotted hyenas ($F[1,93] = 54.52, p \leq .0001$, Figure 4) and total attacks ($F[1,93] = 54.52, p \leq .0001$).

4.2 | Landscape predictors of spotted hyena and African leopard depredations

Depredation probability by spotted hyenas (Figure 5) increased with distance away from water sources, and

also in areas closer to the National Park boundary, and human settlements (Table 5). Hyena depredations also happened in areas that are more rugged. The highest probability of depredation by leopards (Figure 6) was also closest to human settlements, in areas with rugged terrain, close to the national park boundary, and away from water. Distance to roads, and proximity to dense vegetation had no significant association with depredation probability for either species of predator. The boma occurrence model contrasted with the results of our predator attack risk models. Only ruggedness and proximity to settlements were similar in predicting both depredations and the presence of bomas (Table 6). This suggested that the other landscape-level variables were important in shaping attack probability of leopards and spotted hyenas on livestock.

TABLE 4 Results of negative-binomial regressions testing the effect of monthly rainfall adjusted for month length on spotted hyena, leopard and total depredation occurrences on the edge of LMNP, Uganda, 2009–2016.

Model	Coefficient	β	SE	z-value	p-value
Spotted hyena depredation	Intercept	1.620384	0.172932	9.37	<.00001
	Rainfall (adjusted for month)	0.007308	0.047591	0.154	.878
Leopard depredation	Intercept	-0.86358	0.199	4.33	<.00001
	Rainfall (adjusted for month)	0.2024	0.05451	0.371	.71
Total depredation	Intercept	2.00485	0.15209	13.182	<.00001
	Rainfall (adjusted for month)	0.01159	0.04183	0.277	.782

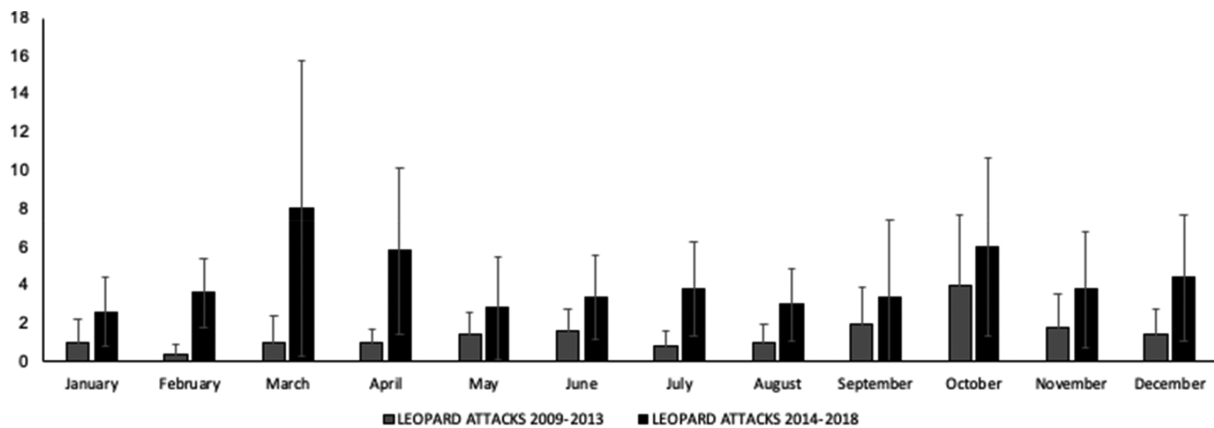


FIGURE 3 Mean leopard attacks per month for the 2009–2013 and 2014–2018 periods. The number of attacks increased significantly between these two periods

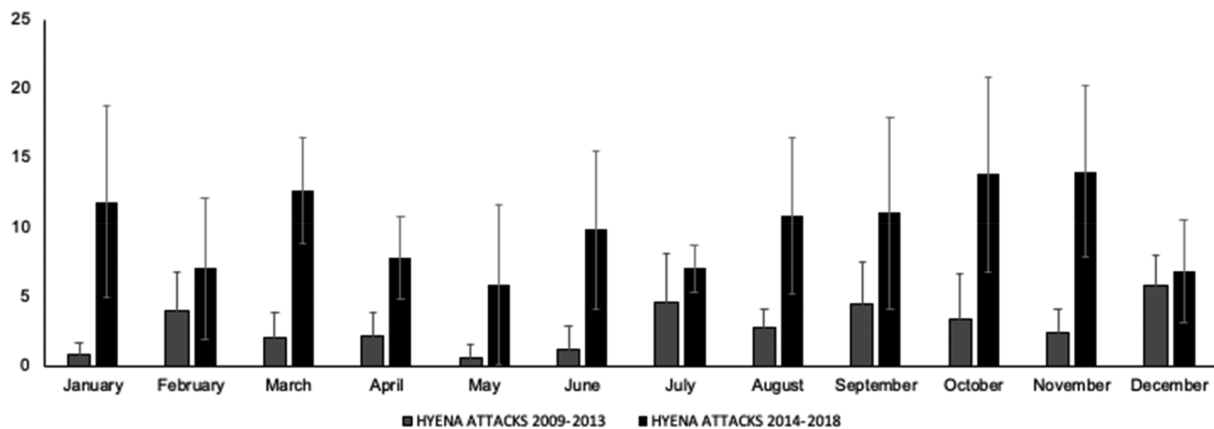


FIGURE 4 Mean spotted hyena attacks per month for the 2009–2013 and 2014–2018 periods. The number of attacks increased significantly between these two periods

4.3 | Financial compensation fund sustainability

The MCF compensation scheme paid mean total annual compensation of \$6,188 USD, and, raised mean \$7,439 USD in total revenue from tourism activities (Figure 7). Mean total monthly compensation paid for spotted

hyena, and leopard depredation events combined was \$335 USD. Mean monthly compensation payments were significantly higher for spotted hyenas than for leopards ($t = 6.33$; $df = 111$; $p < .05$), with spotted hyena compensation averaging \$266 USD per month, opposed to leopard compensation payments, which averaged \$69 USD per month. Annual compensation costs were not

FIGURE 5 Spatial risk map for livestock depredation probability due to spotted hyenas, at the edge of the LMNP, south-western Uganda

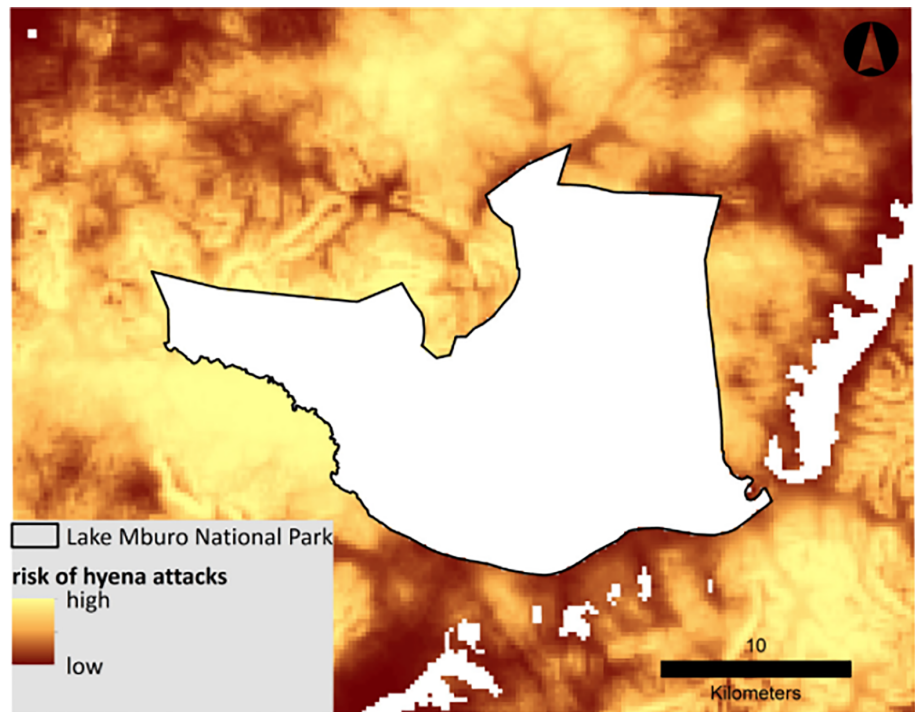


TABLE 5 Results of logistic regressions testing the effect of spatial covariates on leopard and spotted hyena livestock depredation probability in LMNP, Uganda, 2009–2018.

Model	Coefficient	β	SE	z-value	p-value
Spotted hyena depredation	Intercept	-131	0.36	-3.62	<.01
	Distance to water	-0.0007	0.0001	5.60	<.01
	Distance to settlements	-0.0007	0.0001	-5.70	<.01
	Distance to national park	-0.0002	0.00004	-4.17	<.01
	Terrain ruggedness	-0.02	0.01	2.59	<.01
Leopard depredation	Intercept	-1.75	0.60	-2.91	<.01
	Distance to water	0.0007	0.0002	3.84	<.01
	Distance to settlements	-0.0009	0.0002	-3.86	<.01
	Distance to roads	0.0005	0.0002	2.13	<.05
	Distance to national park	-0.0002	0.00007	-2.40	.02
	Terrain ruggedness	0.03	0.01	2.31	.02

significantly different from the annual total MCF income ($t = 0.64$; $df = 12$; $p = .53$), and only the 2014 and 2017 years recorded higher compensation costs than MCF income. However, excepting for the 2015 year, the MCF fund spent more funds than it collected (mean annual expenditure was \$14,531 USD), mainly on other community development projects. We found no relationship between the monthly costs of financial compensation, and monthly rainfall (Table 7). The MCF compensation claims increased linearly over time increasing from \$1,290 annually in 2009 to \$7,291 in 2018. Notably, the total compensation payments had

more than tripled between two 5-year periods (2009–2013, compensation total = \$1,122 USD vs. 2014–2018, compensation total = \$37,822 USD).

5 | DISCUSSION

We provide the first scientific assessment of livestock depredation and financial compensation characteristics in Uganda. We found spotted hyenas were the most significant source of cattle depredation which aligns with the overwhelming majority of human-carnivore conflict

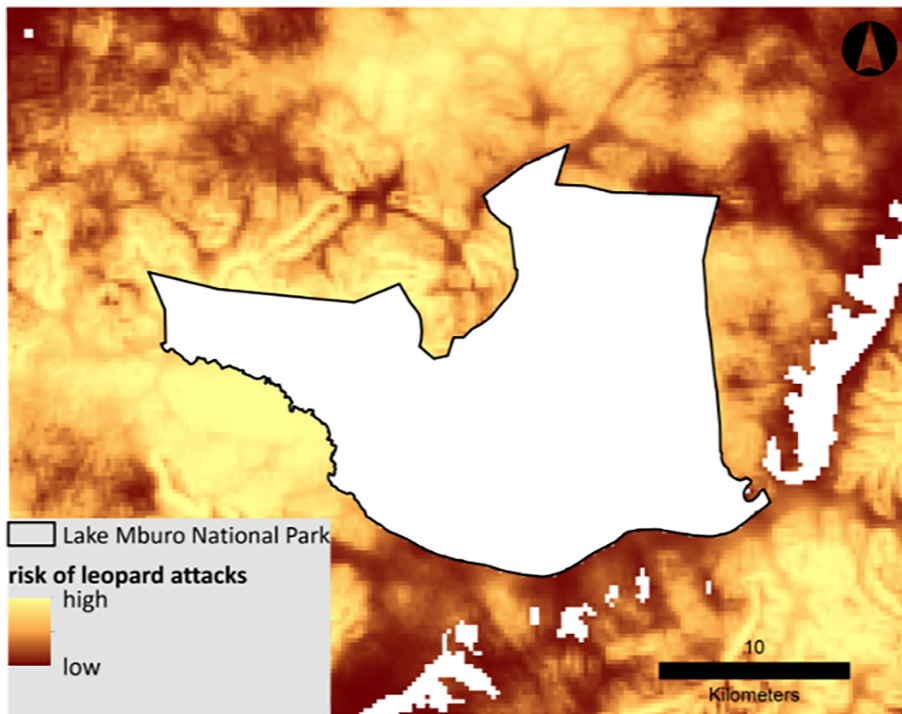


FIGURE 6 Spatial risk map for livestock depredation probability due to leopards at the edge of the LMNP, south-western Uganda

TABLE 6 Results of logistic regression testing the effect of spatial covariates on boma occurrence probability in LMNP, Uganda.

Model	Coefficient	β	SE	z-value	p-value
Boma occurrence model	Intercept	-0.38	0.32	-1.19	.23
	VCF	-0.07	0.02	-3.45	<.01
	Distance to water	-0.0002	0.0001	-2.05	<.05
	Distance to settlement	-0.00006	0.0001	-5.19	<.01
	Terrain ruggedness	0.03	0.01	3.40	<.01

studies in East and southern Africa (e.g., Hazzah et al., 2014; Hemson, MacLennan, Mills, Johnson, & Macdonald, 2009; Koziarski, Kissui, & Kiffner, 2016). In contrast, leopards mainly preyed upon goats and sheep. The risk of depredation was highest close to human settlements, the national park boundary, in areas that are more rugged, and away from water and roads for both predators. Most livestock depredation occurred either inside livestock bomas, or livestock were dragged or chased outside of them. Despite this, our boma model contrasted with our predator depredation models (bomas were more likely to be located close to water, areas of thick vegetation, and away from the national park). While the MCF compensation fund raised enough funds from tourism activities to cover livestock compensation costs in 5 of 7 years, compensation payments increased over time and outstripped the community fund on the latter years of its implementation. This is because these funds were also used for other fund activities (e.g., building schools, and paying school fees), and

revenue from bed nights was used to sustain the compensation payments. Worryingly, compensation payments were more than triple in the most recent 5 years of the compensation scheme when compared to the first five.

5.1 | Livestock depredation characteristics and spatial drivers of depredation locations

The proportions of different livestock species depredated by leopards and spotted hyenas reflected their prey size preference. Leopards typically prefer species weighing 15–40 kg (Hayward et al., 2006), while spotted hyenas prefer prey weighing 56–182 kg (mode = 102 kg; Hayward, 2006). However, the predominance of cattle in the hyena depredation records was considerably higher than previous studies implemented in both Kenya, and Tanzania (e.g., Kissui, 2008; Mitchell, Bruyere, Otieno, Bhalla, & Teel, 2019). These studies found stronger

FIGURE 7 Total MCF compensation scheme income, compensation costs, and other costs (defined as school fees, building of schools, and the administration of the annual Mihingo Marathon) recorded by Mihingo Lodge management between the 2012 and 2018 financial years

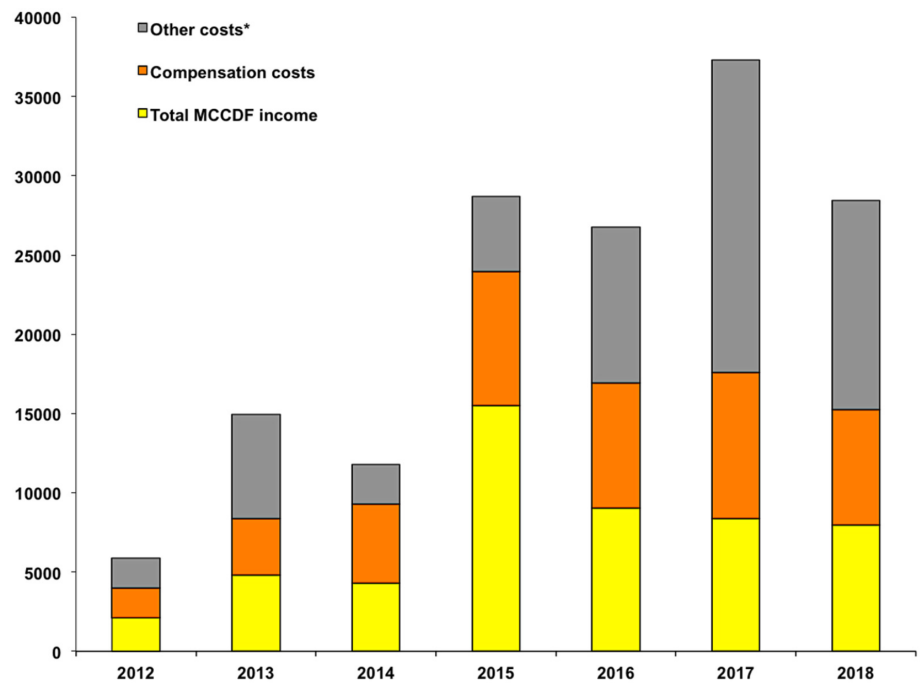


TABLE 7 Results of linear regressions testing the effects of monthly rainfall on financial compensation for spotted hyena, leopard and total depredation events in LMNP, Uganda, 2009–2016.

Model	Coefficient	β	SE	z-value	p-value
Hyena compensation	Intercept	230.25	54.49	4.39	<.0001
	Rainfall	0.4	0.48	0.833	.407
Leopard compensation	Intercept	64.38	15.41	4.18	<.0001
	Rainfall	0.05	0.14	0.35	.72
Total compensation	Intercept	294.63	60.24	4.89	<.00001
	Rainfall	0.45	0.55	0.82	.42

overlap between leopard and hyena diets. A possible explanation for this is the higher cattle to goat and sheep ratio in the Bahima pastoralist lands on the edge of the LMNP (Ocaido, Muwazi, & Opuda-Asibo, 2009).

We expected to see more depredation events during dry months. Wet season migrations of large carnivore prey from protected areas to communal lands have been noted widely in Tanzania and Kenya (e.g., Kissui, 2008, TMCP 2000; Kahurananga & Silkiluwasha, 1997; Kahurananga, 1981; Lamprey, 1964), and evidence for this was found in our study area during 1993–1995 by Baranga, Siefert, and Ocaido (1996), and in 2003 by Rannestad et al. (2006). However, we found no evidence of an effect of seasonality on depredation frequency. This contrasted with studies in other East African sites. For example, Karani (1994) and Rudnai (1979) found more livestock depredation during periods of drought in the farming systems of Kenya. In contrast, Kissui (2008) and Patterson, Kasiki, Selempo, and Kays (2004) found more livestock depredation by these species during the wet season. These authors postulated that the explanation for the wet season peak in these

sites was due to carnivores following the migratory prey onto pastoral land, and increasing their contact rates with livestock. This is an example of resource supplementation and apparent competition hypotheses (Ng'weno et al., 2019) that predict that an abundant prey species attracts a large carnivore, leading to the less abundant prey species facing a higher than normal predation pressure (Vanak & Gompper, 2009).

Our results supported our second hypothesis that granite inselbergs would explain depredations, and we found that rugged terrain coupled with proximity to human settlements, the national park edge and distance away from water were the most important variables that increased the likelihood of both leopard and hyena livestock depredations. These spatial characteristics make ecological sense as explanatory variables for livestock depredations, as (1) human settlements are typically associated with livestock bomas, and higher livestock densities (Abade et al., 2014; Rostro-García et al., 2016; Wang & Macdonald, 2006), and (2) high predation risk close to LMNP's edge also suggests resident hyena and

leopards may be temporarily using pastoralist lands to make their kills, before returning to the national park (Kissui, 2008). Our pattern of increased depredations close to the LMNP edge follows several other studies which have shown reserve edges are often the site of some of the most intense human-carnivore conflicts (Goodrich & Miquelle, 2005; Nyhus & Tilson, 2004).

5.2 | Characteristics of the MCF compensation scheme

The MCF financial compensation scheme is unique amongst a suite of East African, and Southern African compensation schemes in that it attempts to only use money raised by tourism activities to support itself. We found that revenue from tourism activities outpaced compensation costs; however, the MCF compensation scheme struggled to meet its annual operational costs as it contributed to activities beyond livestock compensation. Another reason that the scheme struggled to cover its annual expenses was due to the fairly flexible rules around compensation of livestock depredations. Typically compensation payments by the MCF were still made in part, even if reports of livestock loss were made late, or livestock were left to wander. This was sometimes due to threats of poisoning by livestock owners. This is evidenced by the fact that 18 and 36% of leopard and hyena depredations happened outside of bomas. Many other compensation schemes penalize claimants of compensation for any losses that occur outside protection bomas (e.g., Okello, Bonham, & Hill, 2014). If rules around depredations made outside of bomas were tightened, compensation costs could be reduced. For example, in the Amboseli-Tsavo region of Kenya, compensation schemes withheld a portion of the compensation where husbandry practices were inadequate (i.e., animals left outside of protective bomas), and this withholding was shown to decrease the percentage of claims over time (although the authors contend they remained high; Bauer et al., 2017). However, withholding compensation can result in more killings of carnivores (Hazzah et al., 2014), suggesting a need for balancing penalties with other forms of interventions, such as carnivore protection programs in areas where views towards conservation are negative (e.g., Lion Guardians in Kenya; Hazzah et al., 2014).

Our findings show a pattern of near linear increases in overall compensation over time, with recent compensations three times higher than 2009–2013 levels. This increase in compensation could be due to the presence of more livestock in the area, more attacks being made by spotted hyenas and leopards, or due to an increase in moral hazard (i.e., weakened care of livestock by farmers).

5.3 | Data limitations

We acknowledge uncertainty around the relative importance of landscape variables on depredation probability in the Lake Mburo landscape. First, we randomly sampled the background in a used-available design. Doing so enabled us only to predict a risk proportional to a true probability of risk that a use-unused design (DeCesare et al., 2012; Yackulic et al., 2013), or an occupancy-modeling framework would generate (Goswami, Medhi, Nichols, & Oli, 2015). This is however typical of resource selection function studies reporting habitat selection probabilities (e.g., from tracking data), as GPS collars only record use locations (DeCesare et al., 2012; Fattebert et al., 2015; Fattebert et al., 2018; Fattebert et al., 2019).

While it is unlikely that we missed conflict events in the area as reporting depredations was motivated by the perspective of being compensated, we do acknowledge that our spatially-explicit dataset is a subset of c. a third the 1,102 conflict events we recorded in total. In future we recommend that authors implementing similar studies make use of either an occupancy approach (Goswami et al., 2015), or the case-control/random approaches recommended in Keating and Cherry (2004) where conflict monitors are primed in monitoring the landscape (or cells thereof) in nondepredation locations, on a monthly or even weekly basis. The spatial variation in depredation events observed in our models may also be reflective of the observational process (i.e., lower reporting in some locations vs. others due to some factor). The assessors of the causes of killed livestock used a combination of carcass characteristics, the presence of predator tracks, and verbal confirmation from claimants. These are widely accepted forms of livestock depredation assessment (Abade et al., 2014; Kissui, 2008; Ogada et al., 2003). The overwhelming majority of livestock depredation events in our 10-year sample were only paid compensation when physical evidence of a carcass was produced. However, this does not rule out the chance that some of the animals that were reported as killed died from poor body condition, disease, and were left to be eaten by the predators. This may have been particularly the case when assessments were made late (i.e., two or more days after the day of the depredation).

5.4 | Management recommendations

Human-carnivore conflict is an important process that affects both large carnivores, and human livelihoods in the LMNP region. This is evidenced by the functional extinction of African lions in the region (UWA, 2010). The single most important result from our assessment of

conflict at the edge of the LMNP is that most depredation events occurred while livestock were inside livestock holding facilities (bomas; 82% for leopards, and 64% for spotted hyenas). Spotted hyenas are known to break through poorly fortified boma walls, while leopards simply jump or dig underneath them (Kissui, 2008). Our results mirror those of Kissui (2008), who found that a high percentage of bomas in northern Tanzania were poorly built and contributed to increased depredations.

We make two important management recommendations for the MCF scheme based upon our results. First, because our results illustrate that the majority of livestock depredations took place inside bomas, it may be prudent to apply a temporary treatment period where there is a transfer of funds from direct compensation of livestock losses, to the strengthening of livestock protection bomas, and/or the provision of human or non-human herders. Ogada et al. (2003) found that a higher herder to livestock ratio reduced rates of depredation in Kenya. Similarly, Lichtenfeld, Trout, and Kisimir (2015), and Abade et al. (2014) found the fortification of livestock protection bomas in Tanzania led to significant decline in predation rates. This is also supported by the fact that compensation claims and attacks have increased linearly over time. This means that in the best case scenario, compensation could be assisting or maintaining some tolerance of farmers to depredation (this is unproven), it does not solve the problem of reducing attacks. At this stage, it may be possible that compensation does not provide an incentive to strengthen livestock bomas. The original aim of the MCF was to encourage coexistence between farmers and carnivores and act as a buffer against the killing of carnivores. The "living walls" sustainable bomas initiative in Tanzania by Lichtenfeld et al. (2015) cost US\$125 each. These bomas are made using a combination of native tree species, and wire. The average total compensation paid annually through the MCF compensation fund was USD\$6,187, which translates to at least 49 of these bomas. The number of bomas built could increase even further if the MCF channeled most of the net income from their program to the erection of bomas (even for 1 or 2 years). Relating to this, we suggest that any grazing areas close to granite inselbergs and other rugged terrain have bomas built near them as these areas feature elevated level of depredation risk. Our second recommendation is to tighten the rules of the compensation scheme. If claimants did not place livestock in protective bomas at night, or if there is evidence of gross negligence on the part of livestock owners/herders, either withhold or drastically reduce payments. Nyhus et al. (2005) and Nyhus et al. (2003) warned of the dangers of moral hazard in compensation programs, and these have been echoed in several other studies (Mmopolwa & Mpolokeng, 2008). Although we cannot explicitly say that

this moral hazard is being observed in this system, it is one potential explanation for the increased attacks (along with increase in carnivore attacks due to environmental reasons or an increase in livestock in the region).

Although it is not yet proven whether the compensation scheme has reduced the killings of large carnivores on nonprotected land surrounding LMNP, our study makes important recommendations on how to better manage the MCF to ensure financial sustainability for the fund and similar proposed schemes in the future. More importantly it re-emphasizes some of the concerns highlighted by Bauer et al. (2017) and Nyhus et al. (2003) in that financial sustainability (in terms of the source of compensation funds and the size of the fund itself) of any compensation fund requires careful thought. In a Ugandan human-carnivore conflict context further investigations are required into how the communities affected by carnivore depredation could be more involved in the mitigation process. Models such as those in Kenya (e.g., Okello et al., 2014) and Nepal (e.g., Lamichhane et al., 2019) where community members are directly involved in the management and enforcement of financial compensation and intervention scheme rules should be investigated.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Alexander Braczkowski, Julien Fattebert, Martine Maron, and Ralph Schenk conceived the manuscript. Alexander Braczkowski, Julien Fattebert, and Christopher O'Bryan analyzed the data. Alexander Braczkowski, Julien Fattebert, Christopher O'Bryan, Duan Biggs, and Martine Maron wrote the manuscript.

DATA AVAILABILITY STATEMENT

All data are available at the request of the lead author, A. B. who can be contacted directly via email.

ETHICS STATEMENT

This research did not use animals or human subjects and only reported on livestock loss, price, and location data. We therefore did not require an animal ethics approval certificate from the Office of Research Ethics at the University of Queensland.

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