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Spatial Pattern Analysis Reveals Randomness Among Carnivore Depredation of Livestock

Claire F. Hoffmann[1*†], *Bernard M. Kissui*[2] *and Robert A. Montgomery*[1]

[1] *Research on the Ecology of Carnivores and Their Prey (RECaP) Laboratory, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, United States,* [2] *Center for Wildlife Management Studies, The School for Field Studies, Karatu, Tanzania*

Carnivore depredation of livestock is a global problem which negatively impacts both agropastoral livelihoods and carnivore population viability. Given the gravity of this issue, research has increasingly focused on applied techniques capable of quantifying the factors that increase the risk of livestock depredation. One such technique is risk modeling. This multivariate approach is designed to produce predictions of the spatial configuration of depredation so as to prioritize interventionist activities. Thus, the efficacy of subsequent interventions is, in part, dependent upon the accuracy of the predictions deriving from the risk models. The predictability of spatial patterns in carnivore depredation of livestock is influenced by the degree of spatial autocorrelation evident in the data distributions. We conducted a multi-year assessment to quantify the degree of spatial autocorrelation within livestock depredation data. We centered our study in the Maasai steppe of Tanzania, which experiences some of the highest rates of human-carnivore conflict in the world. We applied three geostatistical measures to assess spatial clustering in data describing livestock depredation by lions (*Panthera leo*), leopards (*Panthera pardus*), spotted hyenas (*Crocuta crocuta*), black-backed jackals (*Canis mesomelas*), and cheetahs (*Acinonyx jubatus*) at the household (i.e., livestock enclosure) scale. Using an ordinal spatial scan statistic, a Bernoulli spatial scan statistic, and the Getis-Ord local spatial statistic, we found that the spatial patterns in carnivore depredation of livestock tended not to significantly differ from random. As the predictive ability of spatial risk models may be limited where spatial patterns of carnivore depredation of livestock do not statistically differ from random, explicitly assessing such patterns is an important component of conflict mitigation efforts. We discuss the inferences of this analysis for the optimization of interventionist activities intending to develop sustainable solutions for human-carnivore conflict.

Keywords: human-carnivore conflict, livestock depredation, spatial autocorrelation, risk modeling, conflict intervention

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***Correspondence:**
Claire F. Hoffmann
hoffm523@msu.edu

†ORCID:
Claire F. Hoffmann
orcid.org/0000-0001-7312-4459

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INTRODUCTION

Large carnivore hunting and killing of domesticated livestock represents one of the most common triggers of human-carnivore conflict globally (Mizutani, 1999; Frank et al., 2005; Maggi et al., 2014). Within this context, people who have experienced livestock losses will often retaliate against those carnivores perceived to be responsible or in an effort to prevent future livestock losses

(Kissui, 2008; Hazzah et al., 2009; Goldman et al., 2013; Dickman et al., 2014; Lichtenfeld et al., 2014; Kahler and Gore, 2015). Termed "livestock depredation," this driver of conflict has been exacerbated by increasing population growth, range expansion, and meat dependency among the global human population (Naughton-Treves et al., 2003; Treves and Karanth, 2003; Ripple et al., 2014). Today, >75% of the world's large carnivore species are experiencing population declines, and retaliatory killing in response to depredation is one of the primary threats to the conservation of these species (Treves and Karanth, 2003; Linnell et al., 2012; Inskip et al., 2013; Chapron et al., 2014; Ripple et al., 2014). Given the importance of this issue, much research has been devoted to documenting the biotic and abiotic conditions that correlate with carnivore depredation of livestock (Miller, 2015; Montgomery et al., 2018a,b).

Typically, this research seeks to develop predictions capable of optimizing the implementation of interventionist activities meant to decrease carnivore attacks on livestock (Treves et al., 2011; Meena et al., 2014; Miller, 2015). There are a number of models used to predict spatial patterns in carnivore depredation of livestock, which are often referred to as risk models. These models generally fall into one of three categories including correlation modeling, spatial interpolation, and spatial associations (Miller, 2015). Correlation modeling and spatial interpolation inherently test for associations between depredation incidents and the landscapes in which they occur (Hebblewhite et al., 2005; Northrup et al., 2013). Spatial association analyses, in contrast, test for spatial autocorrelation among depredation locations independent of the landscape (Baruch-Mordo et al., 2008; Dale and Fortin, 2014; Peeters et al., 2015). Across the three categories, the models developed to predict carnivore depredation of livestock are all informed by the principles of spatial autocorrelation (Miller, 2015). Thus, if spatial patterns in depredation are spatially autocorrelated then the number of carnivore-killed livestock should exhibit clustering at close distances and dispersion with increasing distance. The calculations of clustering or dispersion are carried out via a comparison of the data to a completely spatial random pattern (Aldstadt, 2010; Chakraborty, 2011; Diggle, 2014).

As such, prior to predictive model fitting, diagnostic tests, including the calculation of spatial autocorrelation, should be assessed (Baruch-Mordo et al., 2008; Chakraborty, 2011; Miller, 2015). If tests of this type are not assessed or described in risk mapping of carnivore depredation of livestock, it is unclear whether measured spatial patterns in these data conform to the principles of spatial autocorrelation. It might be more challenging to derive applied management actions from the outputs of spatial risk models if patterns in carnivore depredation of livestock are not statistically different from random. Correspondingly, this would hamper the implementation of interventions built from those models.

Here we conducted a series of diagnostic tests, typically carried out prior to predictive spatial modeling, to determine the degree of spatial autocorrelation evident in carnivore depredation of livestock data. Our objective was to explicitly assess the assumption of spatial autocorrelation. In doing so, we hope to draw conclusions about important considerations in future depredation risk modeling studies, to increase the efficacy of the management and intervention efforts that are based on such models. As there are multiple possible approaches to testing for spatial autocorrelation within a data set, and given that these tests are rarely described in the risk mapping literature, we used a triangulation approach to further verify our results. We applied three diagnostic tests (the ordinal spatial scan statistic, the Bernoulli spatial scan statistic, and the Getis-Ord local spatial statistic) of spatial autocorrelation to our depredation data. We discuss the results of our analysis for spatial modeling of carnivore depredation data and the interventionist activities that are typically associated with this research. Spatially autocorrelated patterns of livestock depredation are used to inform predictions of future predation risk, and management efforts to reduce this risk. Therefore, the ecological inferences that derive from such analyses have important implications for the optimization of activities that are meant to alleviate conflict between humans and carnivores.

METHODS

Study Area

We positioned our study in the Maasai steppe of Northern Tanzania, a 22,000 km^2 landscape consisting of a complex matrix of protected areas and village lands (**Figure 1**). Twenty-three villages with an estimated 350,000 people largely maintaining agro-pastoral lifestyles are interspersed among Tarangire National Park (2,800 km^2), Lake Manyara National Park (330 km^2), and Manyara Ranch Conservancy (140 km^2; Nelson, 2005; Kissui, 2008). These villages are dispersed across a mosaic of wards, a Tanzanian administrative unit consisting of multiple villages. Villages are organized within wards which are organized within districts (see **Figure 2**). The villages are also flanked to the northwest by the 8,290 km^2 Ngorongoro Conservation Area (**Figure 1**). Livestock-owners keep sheep and goats (collectively referred to as shoats), cattle, and donkeys. All of these livestock are vulnerable to depredation, especially at night when they are herded into enclosures (hereafter referred to as bomas; Ogada et al., 2003, Kissui, 2008). The landscape also supports large numbers of wildlife, including a globally important population stronghold for lions (*Panthera leo*; see Riggio et al., 2013), as well as robust populations of leopards (*Panthera pardus*) and spotted hyenas (Crocuta crocuta; Bauer et al., 2004, 2015; Kissui, 2008). Within this system, and in East Africa more broadly, these three species are commonly responsible for the majority of depredation of livestock (Kolowski and Holekamp, 2006; Kissui, 2008; Linnell et al., 2012), though to a lesser extent black-backed jackals (*Canis mesomelas*) and cheetahs (*Acionyx jubatus*) also contribute (Maingi et al., under review). Due to the high spatial overlap between human communities and this sympatric suite of carnivores, the Maasai steppe experiences some of the highest rates of human-carnivore conflict triggered by livestock depredation in the world (Graham et al., 2005; Kissui, 2008; Ripple et al., 2014; Mkonyi et al., 2017a,b; Kissui et al., 2019).

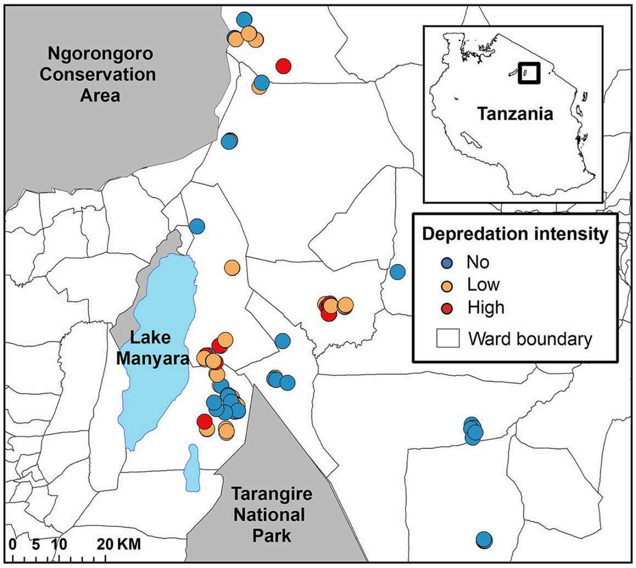

FIGURE 1 | The spatial configuration of bomas in the Maasai steppe of Northern Tanzania. The depredation intensity of each of the 113 bomas between June 2009 and October 2013 is represented by the symbol color. Bomas that experienced no depredation are in blue, those that experienced low depredation intensity are in orange, and those that experienced high depredation intensity are in red.

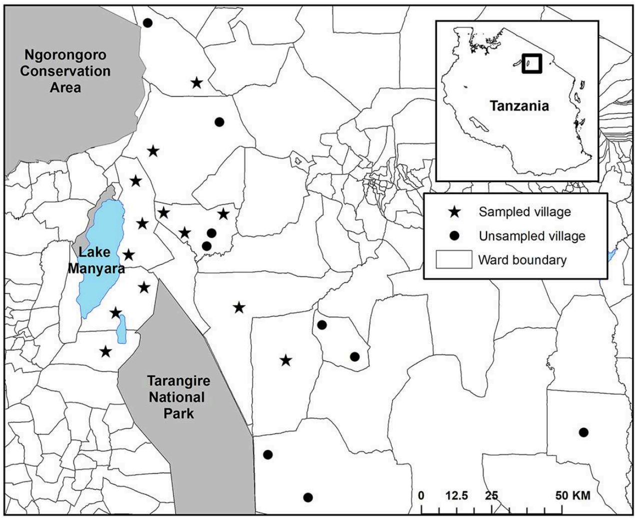

FIGURE 2 | The spatial configuration of villages in the Maasai steppe of Northern Tanzania, categorized by study inclusion. Villages that were sampled for livestock depredation intensity are indicated with a star, those that were not sampled are indicated by a circle.

Data Collection

Between 2009 and 2013, we collected detailed records of livestock depredation events across our study area as part of the Tarangire Lion Project's long-term human-carnivore conflict monitoring program (Kissui, 2008; Kissui et al., 2019; **Figure 1**). We collected this data among 13 focal villages in the Maasai steppe (Emboreet, Engaruka, Esilalei, Kakoi, Lokisale, Losirwa, Makuyuni, Minjingu, Mswakini, Naiti, Olasiti, Oltukai, and Selela). These villages were distributed among nine distinct wards (**Figure 2**). We selected bomas for monitoring according to a stratified random sample designed to incorporate the breadth of boma structures present in our study region. We defined a depredation event as a discrete occasion where a carnivore killed or injured ≥1 head of livestock (e.g., cattle, shoats, or donkeys). We collected data on livestock depredation evens through a combined approach, wherein the entire suite of study bomas were monitored through regular revisits on a 30-days cycle and bomas were visited within 24 h of a reported depredation event. In the occasional case when extenuating circumstances made it unfeasible to conduct the standard monthly visits, we applied an additional approach to collect depredation records. In these instances, an additional interview was conducted with the boma owner as soon as possible to collect information on depredation attempts within the previous 30 days. For reported depredation events, initial reports were collected by local residents who were trained to collect detailed records of livestock depredation events. These local assistants then alerted our research team so we were able to conduct a visit to the boma to verify the depredation event via semi-structured interviews with herders or livestock owners. Notably, there is no active compensation scheme for livestock depredation in Tanzania. Thus, there is minimal incentive to report loss of livestock, and it is likely that fewer livestock depredation events were reported than occurred leading to an underestimate in the extent of depredation (Kissui, 2008). At all reported events, we collected the following information: (*i*) type and number of livestock attacked, *(ii)* GPS location of the boma, *(iii)* outcome of the attack (whether the livestock was injured or killed), and (*iv*) species of the responsible carnivore whenever possible. Identification of the carnivore species responsible for each attack was determined via direct sightings of carnivores by respondents or distinctive tracks, signs, and behavioral characteristics that are commonly known and easily differentiated among the raiding carnivores in the region. Thus, the final database for analysis consisted of multiple depredation events at the household scale (sensu Montgomery et al., 2018a). Each entry included a categorical response variable, with bomas reporting either livestock depredation event = 1 or no event = 0. In the case of the former, the entry included additional details regarding the depredation event. We combined all records by boma, resulting in a total count of depredation events for each boma during the study period. We then categorized these values into three bins, representing the intensity of livestock depredation events at each boma (No, Low, and High). We determined the break values for each category using the Jenks natural breaks method. This method, also known as the goodness of fit variance, reduces within class variance while maximizing variance between classes (Jenks, 1977).

Data Analysis

We evaluated the degree of spatial autocorrelation inherent to these data using the ordinal spatial scan statistic, the Bernoulli spatial scan statistic, and the Getis-Ord local spatial statistic. We chose these three statistical approaches given two key considerations. First, the spatial association analyses conducted had to be capable of accurately testing for spatial autocorrelation among categorical data (i.e., modeling discrete events; see Aldstadt, 2010). As there are multiple ways to do so, we chose to use three different statistical tests as a triangulation approach to verify our results. Second, there is a clear research-implementation gap that separates risk modeling for human-carnivore conflict and the development of policies designed to conserve these species (Miller, 2015; Gray et al., 2019). Thus, our secondary consideration involved the scale of inference of the statistic. We chose statistics with analytical and inferential power at fine scales, as those are the scales most relevant to the implementation of human-carnivore conflict mitigation efforts (Jarvis et al., 2015; Montgomery et al., 2018a).

Ordinal Spatial Scan Statistic

Using SaTScan ver. 9.5 (http://www.satscan.org), we applied the spatial scan statistic to evaluate spatial clustering in the intensity of carnivore depredation of livestock, modeled as an ordinal distribution (Jung et al., 2007). Spatial scan statistics detect spatial or temporal clusters with significantly high or low event occurrence. The resulting clusters are ranked according to the statistical likelihood that the observed event occurrence differs from that in the background population (Kulldorff, 1997, 1999, Fukuda et al., 2005, Riitters and Coulston, 2005). While it has been used in epidemiological studies for decades, the spatial scan statistic has only recently been applied to ecological research. Nevertheless, the statistic has been identified as having great promise for assessments of ecological data (Dale and Fortin, 2014).

Under the ordinal distribution, the probability of depredation of any given intensity (k) occurring within the scanning window (p_k) is equal to the probability of depredation of the same intensity outside of the scanning window (q_k).

$$H_0: p_1 = q_1, \ldots\ p_k = q_k$$

Within this hypothesis testing framework the alternative hypothesis articulates that the detected clusters represent a set of bomas in which the probability of high intensity depredation is significantly (at the $\alpha < 0.05$ level) different than that outside the scanning window. At least one inequality must be strict, and the inequalities can be reversed when assessing for cold spots (Jung et al., 2007).

$$H_a: \frac{p_1}{q_1} \leq \frac{p_2}{q_2} \leq \ldots \leq \frac{p_k}{q_k}$$

The test compares all categories individually, as well as in ordered groups. For example, the likelihood of bomas with no depredation can be compared to the likelihood of bomas with low depredation intensity and bomas with high depredation intensity combined. The order of the categories is maintained, and at least one category must be isolated to produce a likelihood ratio ordering (Jung et al., 2007).

Bernoulli Spatial Scan Statistic

Next, we modeled these data using the spatial scan statistic as a Bernoulli distribution (Kulldorff and Nagarwalla, 1995). The Bernoulli distribution allows for an examination of spatial patterns among two states. We first compared bomas with no depredation, to those with high depredation intensity. We then tested bomas with no depredation against those with low or high intensity. Our interest here was to compare bomas with no livestock depredation to those with livestock depredation. Under the null hypothesis in the Bernoulli model, the probability of having a boma with livestock depredation of the specified intensity is the same inside and outside the scanning window (Kulldorff and Nagarwalla, 1995; Kulldorff, 1997). As in the ordinal model, the corresponding alternative hypothesis is that the probability differs within and outside the scanning window. Such a result indicates non-random patterns in the spatial distribution of livestock depredation by carnivores (Chen et al., 2008).

For each of the spatial scan statistics (i.e., the ordinal and Bernouli models), we tested for both low and high clusters. We set the maximum cluster size to 50% of the total population (Jung et al., 2007), and the scanning windows centered on the boma locations. We evaluated the distribution of maximum likelihood under the null hypothesis using the Monte Carlo hypothesis testing set with 999 simulations (Fukuda et al., 2005; Riitters and Coulston, 2005; Jung et al., 2007). In both cases, we mapped the resulting clusters in ArcMap 10.5 (ESRI, Redlands, CA).

Getis-Ord Local Spatial Statistic

Finally, we used the Getis-Ord G_i^* statistic to evaluate the presence and significance of spatial hot- and cold-spots of depredation intensity in the study area (Getis and Ord, 1992). This statistic measures the degree of association in a given variable by evaluating the level to which each point is surrounded by points with similar values of that variable (Getis and Ord, 1992; Haining, 2003; Ord and Getis, 2010; Peeters et al., 2015). More specifically, G_i^* compares the concentration of values within a set distance of the point of interest (i.e., the "neighborhood") to the concentration of values of that variable across the entire study area. Each point is spatially weighted, and the concentration is given by the sum of the values for these points (Getis and Ord, 1992; Baruch-Mordo et al., 2008; Ord and Getis, 2010; Peeters et al., 2015). Thus, this technique allows for the identification of hot spots (i.e., statistically significant clustering) or cold spots (i.e., statistically significant dispersion) in the spatial data. We defined this neighborhood as the ward (see **Figure 5**). Here;

G_i^* is defined as:

$$G_i^* = \frac{\sum_{j=1}^{n} w_{ij}\left(d\right) x_j}{\sum_{j=1}^{n} x_j} \quad j \text{ may equal } i, \tag{1}$$

where the expected value (assuming complete randomness) depends on the number of local neighbors:

$$E\left(G_i^*\right) = \frac{1}{n} \sum_{j=1}^{n} w_{ij} \tag{2}$$

G_i^* measures the degree of association in depredation count for j points within distance d of point i within each ward (Ord and Getis, 1996; Dale and Fortin, 2014). Locations of high spatial

TABLE 1 | The number of bomas that experienced livestock depredation.

Depredation intensity	Category	# of depredation attempts	*n*	%
1	No	0	50	44.25
2	Low	1–2	47	41.59
3	High	≥3	16	14.16

Each boma is categorized by a depredation intensity determined by the total number of depredation incidents recorded at that location. Both the number (n) and corresponding percentage (%) of all bomas studied are reported.

TABLE 2 | The number and percentage of bomas experiencing no, low, and high livestock depredation intensity (see **Table 1**) in the Maasai steppe, Tanzania collected from 2009 to 2013.

Species	No		Low		High	
	n	%	*n*	%	*n*	&
Hyena	52	46.02	48	42.48	13	11.50
Lion	111	98.23	2	1.77	0	0.00
Leopard	108	95.58	5	4.42	0	0.00
Jackal	111	98.23	2	1.77	0	0.00
Cheetah	112	99.12	1	0.88	0	0.00

The data is shown for each responsible carnivore.

association (hot spots) will be indicated with positive z-scores near the maximum ends of the data distribution, while locations of low spatial association (cold spots) will be indicated with low z-scores near the minimum ends of the data distribution. Z-scores >1.96 or < −1.96 indicate significant (at the $\alpha < 0.05$ level) hot spots and cold spots, respectively (Baruch-Mordo et al., 2008; Dale and Fortin, 2014; Meena et al., 2014). We calculated the G_i^* statistic to identify clusters of bomas based on the intensity of livestock depredation. We used the "zone of indifference" spatial relationship, which is most appropriate for point data without sharp boundaries in neighborhood relationships (Getis and Aldstadt, 2010; Peeters et al., 2015).

RESULTS

Between 2009 and 2013 we collected a total of 170 records from 113 bomas, including 119 confirmed livestock depredation events. Just under half of the bomas surveyed (44.2%, n = 50 of 113) experienced no livestock depredation activity ("no depredation"), 41.6% (n = 47) experienced 1–2 depredation events ("low intensity"), and the remaining 14.2% (n = 16) experienced three or more events ("high intensity"; **Table 1**). Close to 90% (n = 107) of depredation events were by spotted hyenas, with only 4.2% (n = 5) by leopards, 2.5% (n = 3) each by lions and black-backed jackals, and 0.8% (n = 1) by cheetahs. Hyenas killed livestock at low and high intensity, whereas the other species were only responsible for low intensity depredation at any given boma (**Table 2**).

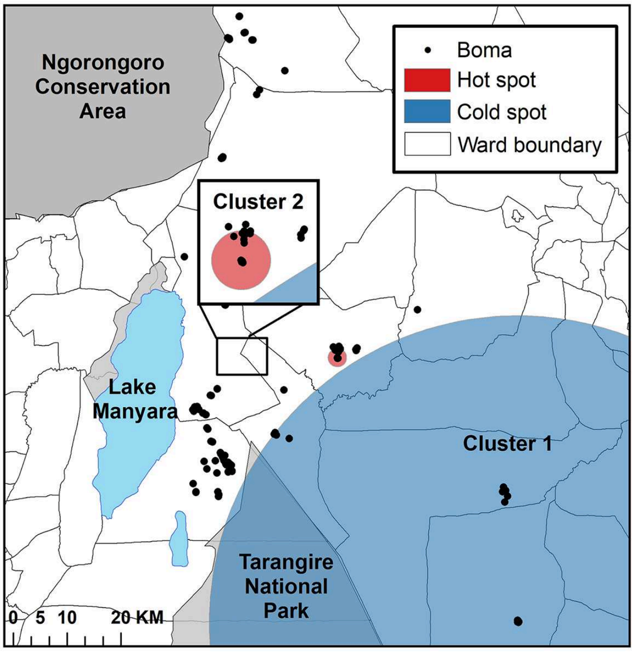

FIGURE 3 | The results of the cluster analysis mapping the intensity of livestock depredation by carnivores in the Maasai steppe, TZ from 2009 to 2013, conducted using the spatial scan statistic under the ordinal model.

Ordinal Spatial Scan Statistic

Via the ordinal spatial scan statistic we detected two significant clusters (**Figure 3**). Cluster one was the most likely cluster identified (LLR = 12.68, $p < 0.001$), while Cluster two (LLR = 9.56, $p < 0.05$) was a lower-likelihood secondary cluster, with the clusters ordered by their statistical significance (**Table 3**; **Figure 3**). Cluster one was a cold spot, in which the number of high intensity depredation bomas was lower than expected, as compared to that in the area outside the scanning window. More specifically, this cluster identified an area with a low number of bomas with low and high depredation intensity combined. Cluster two was a hot spot, identifying an area with a higher than expected number of bomas with high depredation intensity (**Figure 3**).

Bernoulli Spatial Scan Statistic

The Bernoulli spatial scan statistic identified one significant cluster when comparing high depredation intensity bomas to control bomas (**Figure 4A**; **Table 3**). This cluster (LLR = 9.52, $p < 0.01$) was a hot spot, indicating a higher proportion of high intensity bomas inside the scanning window than outside. The second component of the statistic, which compared bomas with low and high depredation intensity combined to bomas with no depredation, revealed two significant clusters (**Figure 4B**; **Table 3**). Cluster one (LLR = 10.69, $p < 0.01$) was a cold spot, and Cluster two (LLR = 7.91, $p < 0.05$) was a hot spot.

Getis-Ord Local Spatial Statistic

Application of the Getis-Ord G_i^* statistic detected 19 bomas (16.8%) that were significantly clustered (i.e., Z-scores of ≥

TABLE 3 | The results of the cluster analysis for intensity of livestock depredation by carnivores in the Maasai steppe, Tanzania from 2009 to 2013, conducted using the spatial scan statistic with the ordinal and Bernoulli models.

		Radius (km)	Categories	#O/#E	RR	LLR	*p*-value	Implication
Ordinal model	Cluster 1	57.07	(1, [2,3])	2.26, 0	2.75, 0	12.68	0.0009	Cold spot
	Cluster 2	1.71	(1, 2, 3)	0, 1.09, 3.85	0, 1.10, 5.56	9.56	0.0150	Hot spot
Bernoulli model	Cluster 1	1.71	1, 3	4.13	6.00	9.52	0.0028	Hot spot
	Cluster 1	36.68	1, [2, 3]	0.00	0.00	10.69	0.0014	Cold spot
	Cluster 2	3.10	1, [2, 3]	1.69	1.95	7.91	0.0240	Hot spot

Results are shown for all responsible carnivore species combined. The heading Categories is the intensity of depredation (see ***Table 1****) compared for each cluster, #O/#E is the ratio of number of events observed to number of events expected, RR is the relative risk of each category, and LLR is the log-likelihood ratio.*

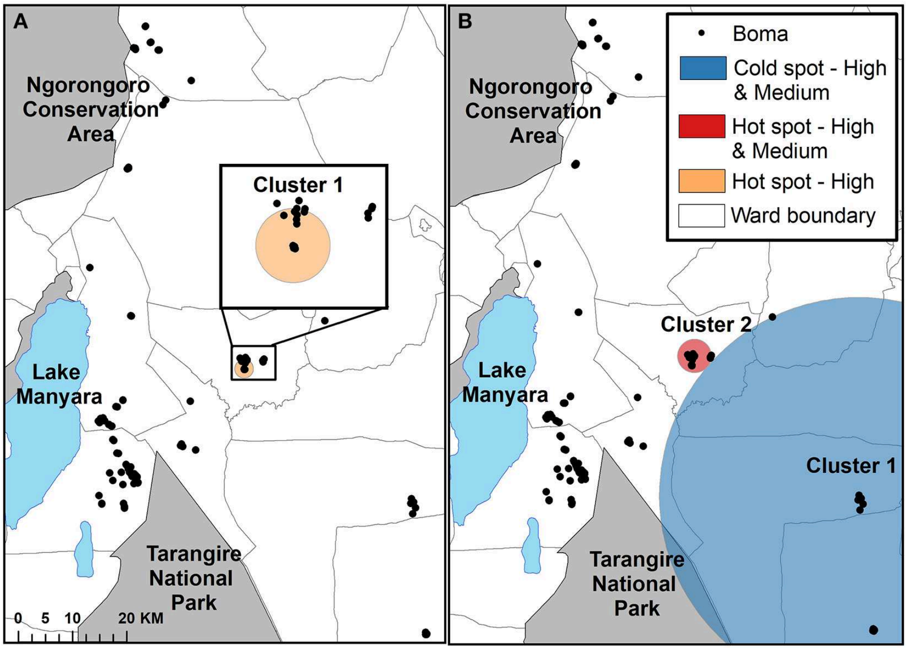

FIGURE 4 | The results of the cluster analysis mapping the intensity of livestock depredation by carnivores in the Maasai steppe, TZ from 2009 to 2013, conducting using the spatial scan statistic under the Bernoulli model. **(A)** Shows the results for the comparison of high depredation intensity and no depredation. **(B)** Shows the results for the comparison of low and high depredation intensity combined vs. no depredation.

1.96). Of these bomas, 18 were tightly clustered within one ward (**Figure 5**). There were eight bomas with Z-scores of $\leq$-1.96, indicating a significant cold spot. These bomas were dispersed in clusters of two to three bomas each, within two neighboring wards (**Figure 5**).

DISCUSSION

Via the application of three different model diagnostic approaches, we detected little evidence of spatial patterning in the intensity of carnivore depredation of livestock data. All three statistical methods identified just one primary hot spot consisting of only 18 bomas (15.9% of those studied) located in a cluster north of Tarangire National Park (**Figures 3–5**). Thus, in terms of the intensity of livestock depredation events, the majority of our study site did not differ from a completely spatial random pattern. This result suggests that there may be some other processes, potentially ecological or methodological in form, influencing or obscuring the spatial patterns of livestock depredation in this region. Without an understanding of such processes, and incorporation of that knowledge into spatial pattern analyses of this nature, the ability to develop accurate predictive models for human-carnivore conflict will be limited. Here, we discuss the potential processes that could inform this observed spatial randomness.

We had anticipated that patterns in livestock depredation would be non-random, indicating the presence of behaviorally-grounded carnivore hunting strategies similar to those observed in wild prey predation by the same species. This assumption was supported by previous research showing that the risk of livestock depredation by hyenas increased with vegetative cover (Kolowski and Holekamp, 2006) and depredation risk from lions was significantly higher near riverine habitats (Abade et al., 2014). Nevertheless, the majority of the spatial patterns

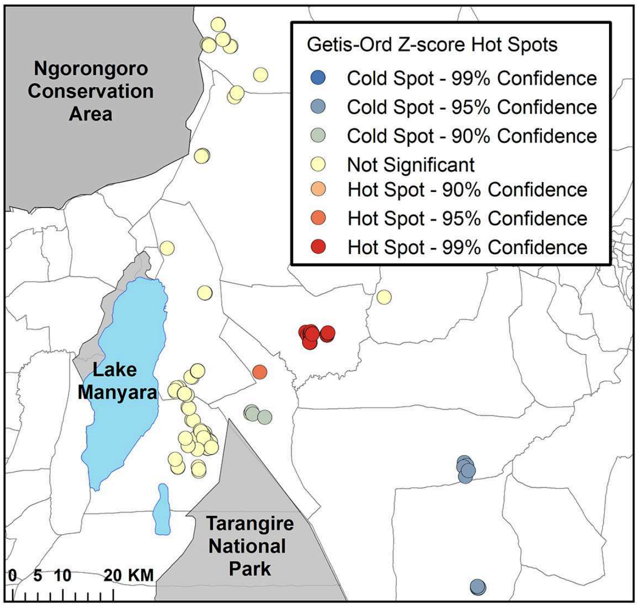

FIGURE 5 | The results of the Getis-Ord G_i^* hot spot analysis for intensity of livestock depredation in the Maasai steppe, TZ from 2009 to 2013. The bright red circles depict significant clustering of livestock depredation event hot spots ($Z \geq 1.96$), and the dark blue circles depict significant cold spots ($Z \leq -1.96$).

of livestock depredation events examined here exhibited spatial randomness even though extensive research has documented that large carnivores do not pursue wild prey randomly (Hopcraft et al., 2005; Hayward, 2006; Hayward et al., 2006; MacNulty et al., 2007). As an example, previous research has shown that lions preferentially hunt in areas of semi-dense vegetation and cover, such as tall grasses and open shrublands (Elliott et al., 1977; Scheel, 1992; Spong, 2002; Hopcraft et al., 2005; Fischhoff et al., 2007). This pattern is likely due to the fact that lions are primarily ambush-style predators, relying on vegetation that can hide their presence from prey species until the last possible moment while not restricting their view of potential prey individuals (Hopcraft et al., 2005; Valeix et al., 2009). Similarly, leopards prefer to hunt in areas with moderate woody plant cover, such as open mixed woodlands (Balme et al., 2007). However, substantially less is known about the behaviors of these carnivores in relation to encountering domestic prey. This is particularly true at the household scale (i.e., the scale of bomas; Montgomery et al., 2018a). It remains unclear however, the extent to which hunting behaviors of lions, leopards, or hyenas for wild prey might apply to the selection of livestock for depredation. Therefore, it is possible that the carnivores, in fact, respond to potential livestock prey in the boma randomly.

It is also likely that human presence and activity at the boma contributed to the inherent randomness in the spatial patterns in carnivore depredation of livestock. Livestock husbandry practices, the structural integrity of bomas, as well as cues of human presence including noises, lights, the presence of dogs, and many other elements can be deterrents to large carnivores (Ogada et al., 2003; Frank, 2010; Loveridge et al., 2017). Thus, humans have a capacity to intentionally or inadvertently disturb large carnivores intending to kill livestock at the boma. However, the exact combination of factors that might best deter advancing carnivores has not yet been identified. Importantly, our assessment was focused only on known attacks of livestock, not the other stages of the depredation process (Macarthur and Pianka, 1966; MacNulty et al., 2007; i.e., carnivore search and pursuit of livestock in the boma). To assess how human behavior influences the probability of attack, the rates at which carnivores encounter bomas and do not attack must be calculated. Within wild prey systems, encounter rates are one of the primary determinants of predation intensity (Hebblewhite et al., 2005; Balme et al., 2007). We identify the study of the rates at which carnivores encounter livestock at the boma and do not attack as a productive area of future research.

Finally, the spatial randomness that we observed may also be attributable, at least in part, to noise in the data collection system. Such noise would include issues in sampling, translation, misreporting of depredation events, or spatio-temporal dimensionality. For instance, we considered depredation data from 2009 to 2013, and collapsing the temporal extent of the data could have obscured fine scale temporal dynamics in the depredation patterns. Many studies have shown the importance of temporal resolution in revealing and predicting the mechanisms driving spatial patterning (Elliott et al., 1977; Van Orsdol, 1984; Stander and Albon, 1993). Examining the temporal dynamism associated with these data is part of a separate analysis in which we discovered strong effect of seasonality, with attacks being 2.84 times more likely to occur in the wet season than the dry season, aligning with a similar influence of seasonality found by Kuiper et al. (2015), Kissui et al. (2019). Additionally, our data showed substantial year-to-year variation in hyena depredation patterns (Kissui et al., 2019).

Our study emphasizes the importance of conducting model diagnostic tests of spatial autocorrelation in depredation risk models. Such tests provide the framework for meaningful application of conflict intervention efforts (Baruch-Mordo et al., 2008; Chakraborty, 2011; Miller, 2015). As the principles of spatial autocorrelation underlie the majority of risk model analyses (Chakraborty, 2011; Miller, 2015), without explicit examination of the autocorrelative patterns within the depredation datasets, the results may be misrepresentative of the processes occurring on that landscape. Spatial randomness may indicate that there is no clustering of livestock depredation events, when that result may in fact be due to the presence of other processes that exhibit spatially random patterns at the spatial or temporal scale of assessment. Consideration of such factors is essential for effective application and interpretation of livestock depredation risk models.

The outputs of these risk models are used to identify high-priority locations in which to apply conflict intervention or mitigation efforts around the world, thus informing preventative action to maximize impact and minimize cost (Marucco and Mcintire, 2010; Treves et al., 2011; Miller, 2015). Notably, the exact processes at play may differ depending on the ecological community, human culture, and environmental characteristics of the study location. However, the range of alternative spatial processes identified here are representative of the diversity of factors that should be considered within these examinations.

Therefore, such diagnostic approaches can be applied to other study systems to inform subsequent examinations of biotic and abiotic correlates of carnivore depredation of livestock. Without refined understanding of the potential sources of spatial randomness, the model output may not be well-aligned with the implementation of interventions meant to reduce depredation. This misapplication of intervention efforts could result in higher livelihood costs for local communities, increased rates of retaliatory killing of carnivores, and overall increase in conflict between the two (Dickman, 2010; Inskip et al., 2013). Such concerns are not limited to the East African system in which this study is situated, but are relevant to any location experiencing human-carnivore conflict over livestock depredation. The widespread and urgent nature of this threat underscores the necessity of effective use of all available resources and tools, and livestock depredation risk models are a valuable contribution to this effort (Treves et al., 2011; Miller, 2015; Miller et al., 2015). With attention to spatial processes such as those identified here, they are more likely to provide accurate management-relevant predictions of livestock depredation, thus increasing the impact of research-informed conservation efforts and the management practices derived therein.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The data examined herein was approved by the Tanzanian Committee on Science and Technology (COSTECH) and the Tanzanian Wildlife Research Institute (TAWIRI) and all requisite research permits were received. This study was carried out as part of the Tarangire Lion Project's long term monitoring program, did not comprise of any direct, or indirect interactions with wildlife, and did not collect any personal information from participating individuals. Thus, no additional ethics approvals were required.

AUTHOR CONTRIBUTIONS

All work within this manuscript is original research carried out by the authors. BK developed the original research design and field data collection. CH prepared the data for analysis, carried out the analysis, and drafted the article. RM contributed to the spatial analysis of the data and editing. All authors contributed substantially to the writing and proofing of the article, and read and approved the final submitted version.

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