The Integral Nature of Encounter Rate in Predicting Livestock Depredation Risk

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Carnivore depredation of livestock is one of the primary drivers of human-carnivore conflict globally, threatening the well-being of livestock owners, and fueling large carnivore population declines. Interventions designed to reduce carnivore depredation typically center around predictions of depredation risk. However, these spatial risk models tend to be informed by data depicting the number of livestock attacked by carnivores. Importantly, such models omit key stages in the predation sequence which are required to predict predation risk, or in this case depredation risk. Applying the classic predation risk model defined by Lima and Dill demonstrates that depredation risk is dependent upon quantifying the rates at which carnivores encounter livestock before attacking. However, encounter rate is challenging to estimate, necessitating novel data collection systems. We developed and applied such a system to quantify carnivore-livestock encounters at livestock corrals (i.e., bomas) across a 9-month period in Central Kenya. Concurrently, we monitored the number of livestock attacked by carnivores at these bomas. We calculated carnivore-livestock encounter rates, attack rates, and depredation risk at the boma. We detected 1,383 instances in which carnivores encountered livestock at the bomas. However, we only recorded seven attacks. We found that the encounter rate and attack rate for spotted hyenas were almost six and three times higher than that for any other species, respectively. Consequently, spotted hyenas posed the greatest depredation risk for livestock at the boma. We argue that better understanding of carnivore-livestock encounter rates is necessary for effective prediction and mitigation of carnivore depredation of livestock.

Keywords: conflict management, human-carnivore conflict, livestock depredation, predation risk, motion-activated camera

INTRODUCTION

Biodiversity loss is a wicked problem yielding a number of negative impacts on coupled human and natural systems around the world (Chapin et al., 2000; Pimm et al., 2014; Beck et al., 2019). In the dynamic and increasingly-globalized twenty-first century, drivers of biodiversity loss are varied, ranging from coarse processes including climate change and land conversion, to fine-scale ones

such as poaching (Chapin et al., 2000; Pimm et al., 2014). Loss of biodiversity in the order Carnivora is of particular concern given the influential role that these species tend to play in the apex and meso-predator positions of global ecosystems (Estes et al., 2011; Ripple et al., 2014; Dorresteijn et al., 2015). As these roles are often near the top of trophic systems, large carnivores can be key ecological regulators facilitating the maintenance of ecosystem health (Estes et al., 2011; Ripple et al., 2014). Despite their ecological importance, >75% of the world's remaining large carnivore populations have declining trajectories (Ripple et al., 2014, 2016; Wolf and Ripple, 2017) principally driven by habitat loss and fragmentation, overhunting, prey depletion, and conflict with humans (Dickman, 2010; Ripple et al., 2014; Eklund et al., 2017; Wolf and Ripple, 2017; Krafte Holland et al., 2018). Conflict between humans and carnivores tends to be associated with threats to human security and private property (Ripple et al., 2014; van Eeden et al., 2018a,b). Most common among these threats is depredation of livestock, where retaliatory killing of carnivores by affected livestock owners is a common response (Krafte Holland et al., 2018; van Eeden et al., 2018b). Consequently, carnivore depredation of livestock is an important challenge facing both biodiversity conservation and human wellbeing (Barua et al., 2013).

Carnivore depredation of livestock persists globally and has expanded with increasing human population growth (Wolf and Ripple, 2017). To date, there is minimal evidence of the effectiveness of most applied solutions to this conflict (Miller, 2015; Eklund et al., 2017; van Eeden et al., 2018a). This limited efficacy is attributable, in part, to evident disconnects between research effort and the implementation of conservation strategies (Sunderland et al., 2009; Montgomery et al., 2018a; Beck et al., 2019; Gray et al., 2019). One potential driver of this research-implementation gap involves the misalignment of research practice and conservation need (Linklater, 2003; Lawler et al., 2006; Stroud et al., 2014; Di Marco et al., 2017). This facet of the research-implementation gap is influenced by a range of factors including positive feedbacks in patterns of conservation funding (Stroud et al., 2014; Troudet et al., 2017) and taxonomic biases in publication review and editing decisions (Bonnet et al., 2002; Linklater, 2003; Martín-López et al., 2009). Further, research on carnivore depredation of livestock is often restricted to well-established methodologies such as fecal analysis and track transects because of the logistical constraints associated with remote study locations and dynamic animal behaviors (Van der Weyde et al., 2018; Prugh et al., 2019). Consequently, in many cases research practices have been slow in adapting to meet changing conservation needs (Lawler et al., 2006; Stroud et al., 2014). As a result, critical subjects remain unexplored in the human-carnivore conflict literature, one of which is the rate at which carnivores encounter potential livestock prey.

Predator-prey encounters are a fundamental stage of the predation sequence (Mech, 1970; Lima and Dill, 1990; MacNulty et al., 2007) and encounter rate is an integral parameter necessary to predict predation risk (see Holling, 1959; Lima and Dill, 1990; Abrams, 2000). In the predator-prey model originally presented by Holling (1959) and adapted by Lima and Dill (1990), predation

risk can be predicted as a function of:

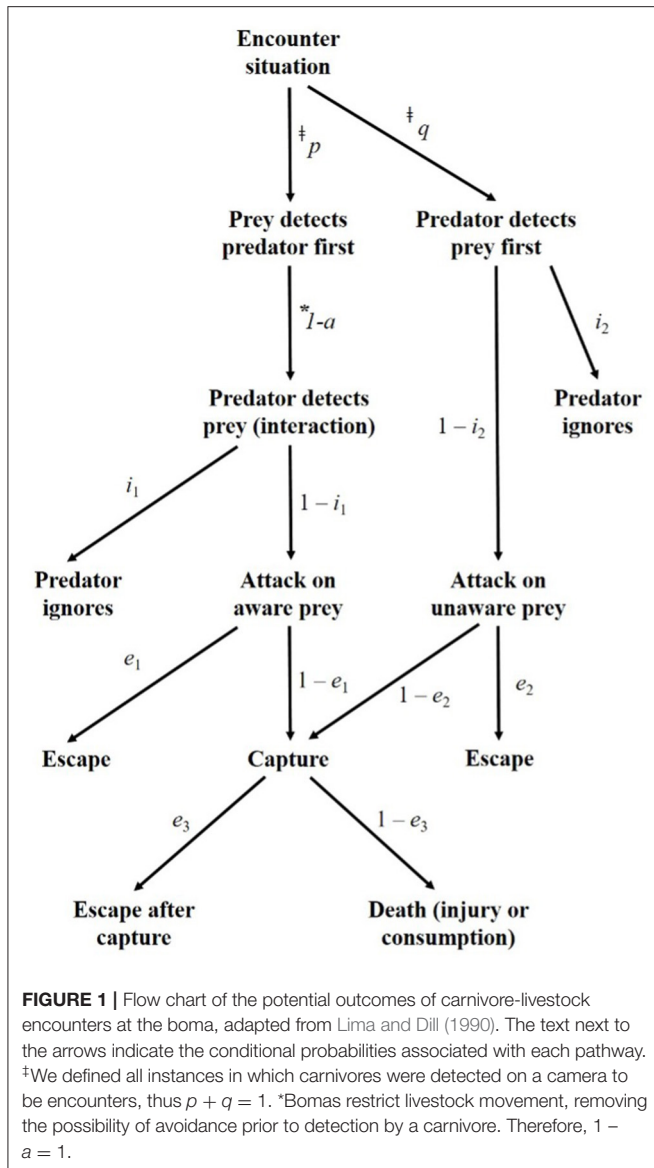$$P\left(\text{death}\right) = 1 - \exp(-\alpha dT) \qquad (1)$$

Where the probability of prey being killed $P(\text{death})$ is derived from the rate of encounter between predator and prey (α), the probability of death given an encounter (d), and the time spent vulnerable to an encounter (T; Lima and Dill, 1990). The probability of death given an encounter (d) is calculated by the conditional probabilities (i.e., "subcomponents" of predation risk) of various possible interactions between predator and prey (**Figure 1**). Specifically, d is defined as:

$$d = [p\left(1-a\right)\left(1-i_1\right)\left(1-e_1\right) + q\left(1-i_2\right)\left(1-e_2\right)](1-e_3) \qquad (2)$$

Here, a represents the probability of effective avoidance of the predator, which is not a possible outcome in the case of corralled livestock, i_1 and i_2 are attack subcomponents, and $e_{1,2,\text{and}3}$ are escape subcomponents. Importantly, this model predicting predation risk cannot be fit without an understanding of the rates at which predators encounter prey (Holling, 1959; Curio, 1976; Lima and Dill, 1990; Abrams, 2000; Prugh et al., 2019). Despite the importance of encounter rate, depredation risk is typically calculated without this integral parameter.

Depredation risk models are most often informed solely by successful carnivore attack on livestock data (Treves et al., 2004; Miller, 2015; Hoffmann et al., 2019). These models, often termed "spatial risk models," typically use the count of these attacks to associate abiotic and biotic conditions with depredation (Hebblewhite et al., 2005; Baruch-Mordo et al., 2008; Behdarvand et al., 2014; Miller et al., 2015; Broekhuis et al., 2017). Here, carnivore depredation data are collated across space and time to map spatial, and sometimes temporal, variation in depredation risk. The accuracy of these models is paramount given that the spatio-temporal predictions regularly inform interventions designed to reduce human-carnivore conflict (Miller, 2015; Mpakairi et al., 2018; Hoffmann et al., 2019). As described by Miller (2015), "spatial risk models quantify the realized predation risk...rather than the overall fundamental predation risk." Therefore, these models do not quantify depredation risk (sensu the predation risk equation of Lima and Dill, 1990), but instead use only the final step in the predation sequence of potential interactions and outcomes (**Figure 1**) as a proxy for depredation risk. Hereafter, we refer to depredation risk as defined by Lima and Dill (1990), not as this realized predation proxy. Notably, while studies relying on this proxy provide valuable insights that can inform livestock husbandry and carnivore management strategies, they may be limited in their ability to predict predation risk as they omit measures of encounter rate.

Carnivore-livestock encounters have likely not been widely estimated because of the challenges inherent to collecting these types of data. Efforts to collect encounter data are often hampered by the cryptic and wide-ranging nature of carnivores as well as the technological limitations in mapping contact points between carnivores and livestock (Lima, 2002; Breck, 2004; Gray, 2012; Krafte Holland et al., 2018). Consequently,

FIGURE 1 | Flow chart of the potential outcomes of carnivore-livestock encounters at the boma, adapted from Lima and Dill (1990). The text next to the arrows indicate the conditional probabilities associated with each pathway. ‡We defined all instances in which carnivores were detected on a camera to be encounters, thus $p + q = 1$. *Bomas restrict livestock movement, removing the possibility of avoidance prior to detection by a carnivore. Therefore, $1 - a = 1$.

novel means of data collection are required to overcome these constraints. We developed and deployed such a system to detect carnivore-livestock encounters. We applied this system to a region of Central Kenya that experiences high rates of carnivore depredation of livestock (Ogada et al., 2003; Frank, 2010). Concurrently, we also collected data on carnivore attacks on livestock, in the same manner as is traditionally used in the aforementioned spatial risk modeling. We estimated species-specific carnivore encounter rates, attack rates, and calculated depredation risk using the Lima and Dill (1990) equation. As rates of livestock depredation, and the resultant impacts on both humans and carnivores, are likely to continue to intensify, targeted examinations of the applicability of research practice to conservation needs are increasingly necessary. Our contribution to this effort here provides valuable insights into carnivore space use and habitat selection, mitigation efforts informed by those

behaviors, and recommendations for future studies to better elucidate the stochasticity that remains unexplored in patterns of carnivore depredation of livestock.
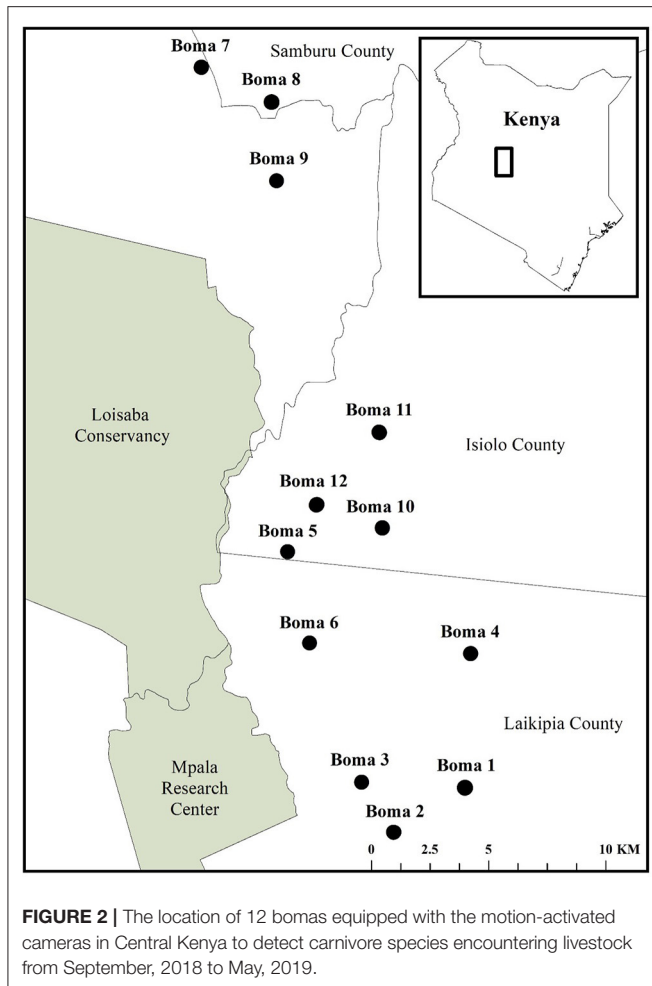
METHODS

Study Area

We positioned our study in Central Kenya, along the borders of Samburu, Isiolo, and Laikipia Counties (**Figure 1**). This landscape is predominantly semi-arid bushland divided among a matrix of privately-owned conservancies, commercial ranches, and agro-pastoralist community-owned conservancies (Frank et al., 2005; Frank, 2010; Bond, 2014; Yurco, 2017). Livestock-owners in this landscape keep cattle, sheep, and goats (collectively referred to as shoats), donkeys, and camels (Ogada et al., 2003; Frank et al., 2005; Frank, 2010; Unks et al., 2019). There are two rainfall seasons, with heavier rains from April-June and lighter rains from October-December. Total annual rainfall is highly variable, but often ranges from 500 to 750 mm (Mizutani, 1999a; Georgiadis et al., 2007). The landscape supports a carnivore guild of African lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), striped hyenas (*Hyaena hyaena*), black-backed jackals (*Canis mesomelas*), aardwolves (*Proteles cristata*), caracals (*Caracal caracal*), and African wild dogs (*Lycaon pictus*; Mizutani, 1999b; Ogada et al., 2003; Frank et al., 2005). All of these carnivore species, with the exception of aardwolves have been found to depredate livestock in this region (Frank et al., 2005; Frank, 2010).

Our 650 km² study area included the western units of Oldonyiro Community Conservancy, the southern units of Kirimon Community Conservancy, and the Koija and Il Motiok units within Naibunga Community Conservancy, which are subject to considerable levels of carnivore depredation of livestock (**Figure 2**). For instance, between March, 2018 and October, 2020; livestock-owners in these communities reported 2,390 livestock injured or killed by large carnivores, 67% of which were attacked at night while held in livestock corrals within homesteads, otherwise known as bomas (Pilfold and Ruppert, unpublished data). Therefore, we focused our data collection system on detecting carnivores encountering and attacking livestock at the boma.

Data Collection

We selected 12 bomas across our study site *via* a stratified random sample, with three bomas randomly chosen within each of the four communities (**Figure 2**). Upon identifying these bomas, we consulted the chairman of each community and met with the heads of all households to gain permission for their participation in our study. We equipped each boma with a suite of motion-activated cameras (Bushnell Trophy Cam HD Aggressor—No Glow, Model 119776C) attached to fence posts, and positioned them to be outward-facing. We placed all cameras 0.5 m off of the ground and evenly distributed around the outer wall of the boma so as to best detect approaching carnivores. Each boma had 6–7 cameras depending on the circumference of the perimeter wall, separated by an average distance of 27.1 m (**Figure 3**).

FIGURE 2 | The location of 12 bomas equipped with the motion-activated cameras in Central Kenya to detect carnivore species encountering livestock from September, 2018 to May, 2019.

FIGURE 3 | The location of the motion-activated cameras around the perimeter of one the 12 bomas in Central Kenya. The diagram indicates the position of the cameras in relation to the boma wall, the average distance between cameras, and the camera detection range and angle. The photographs show the placement of the cameras on the fence posts.

We programmed the cameras to record videos (15-s duration) with no delay period between triggers. The cameras were active between dusk and dawn, consistent with the time period in which livestock are vulnerable to carnivore depredation at the boma (Ogada et al., 2003; Frank et al., 2005; Kissui, 2008). We maintained these cameras across the duration of our study, between September, 2018 and May, 2019.

Over the same time period, we followed established protocols (see Ogada et al., 2003; Woodroffe et al., 2005; Kissui, 2008; Leflore et al., 2019) to map the frequency of carnivore attacks on livestock at these bomas. We documented attack records via a conflict reporting network composed of 19 community representatives selected by local leadership (see Ruppert et al., 2021). Livestock owners were asked to call their representative immediately following each conflict event involving carnivores. At the incident site, representatives used a structured questionnaire to gather data from the livestock owner and, when available, a witness. At each event, the representative recorded the; (i) date and approximate time of the attack, (ii) type and number of livestock injured or killed, (iii) carnivore species responsible, and (iv) GPS location of the attack. Identification of responsible carnivore species was
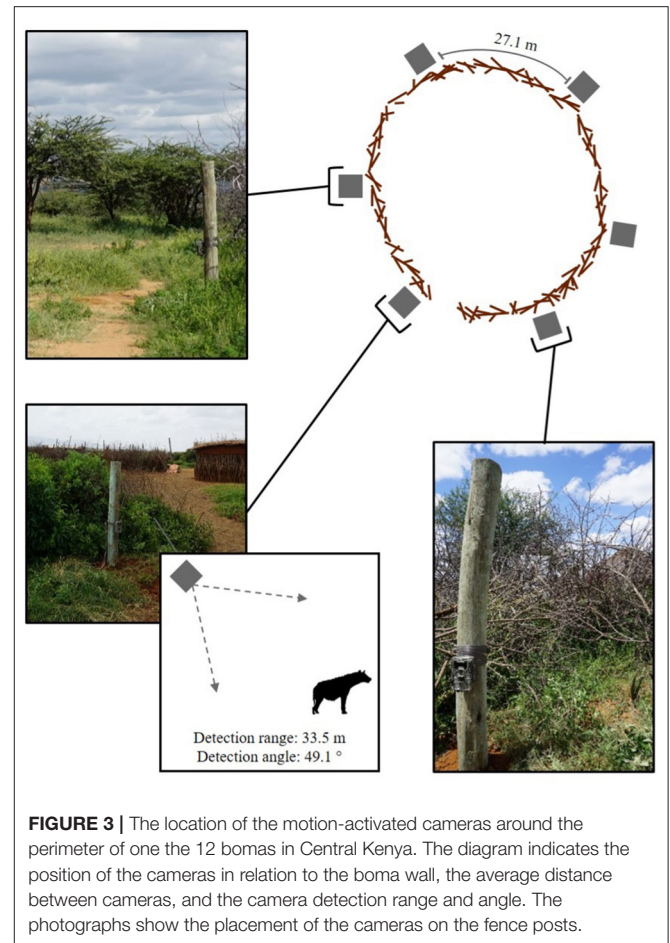
determined as soon as a representative could reach the site, with species determined via tracks, bite location and marks, and any other evidence associated with the incident site, with consensus reached among representatives, livestock owners, and a researcher or witness when available. We also confirmed the presence of the responsible species at the attacked boma via camera trap videos for each incident during the study period. Representatives were initially trained to administer the standardized form in March 2018, and guidance on the process and use of equipment were reinforced during monthly field visits by AL, LL, and IL. All representatives entered the data directly into Survey 123 software on Samsung Galaxy J1 phones while at the location of the attack. Ethical approvals for human subjects research were reviewed and approved by the Institutional Review Board (IRB #02555e) of Miami University, Ohio. Permission was granted by the Kenya National Commission for Science, Technology, and Innovation under Research License #690384, and Kenya Wildlife Services. Methods were also reviewed and approved by the Institutional Animal Care and Use Committee at San Diego Zoo Global (Protocol #18-017).

Data Analysis

For each video file returned from the motion-activated cameras, we recorded the: (i) carnivore species detected, (ii) number of

individuals of that species, (iii) date, and (iv) time the camera was triggered. We defined a carnivore-livestock encounter have occurred when at least one individual of a depredating carnivore species of was detected in the viewshed of the cameras (i.e., within 33.5 m of the boma wall, **Figure 3**). We considered instances when multiple individuals of the same species were present at the boma concurrently to be one encounter event. The detection extent is consistent with the chase initiation distance of the carnivore species (Kruuk, 1972; Elliot et al., 1977; Hayward et al., 2006) and thus, representative of an encounter (Lima and Dill, 1990). However, carnivore-livestock interactions are unique in comparison to free-ranging prey encounters due to the structural interference of the boma wall, which can influence attack dynamics. Regardless, the walls of the 12 bomas were all constructed with acacia thorn bush with highly variable structural integrity, often resulting in openings large enough to allow for visibility through the physical barrier (Lichtenfeld et al., 2015; Chaka et al., 2020). Further, carnivores regularly break into bomas to attack livestock, demonstrating they are aware of the presence of livestock within (Ogada et al., 2003; Kolowski and Holekamp, 2006; Kissui, 2008). Livestock also often stampede in an attempt to flee the boma when carnivores are near, indicating they are similarly aware of the presence of carnivores on the other side of the wall (Ogada et al., 2003; Frank, 2010). To limit pseudo replication, we consolidated all videos of one carnivore species triggered within 10 min of each other at the same boma into a single encounter. We constrained our encounters to a 10 min window, as previous examinations indicate that species detections decrease significantly outside of this time frame (Lepard et al., 2019).

We quantified the number of encounters and attacks per night, and examined variation in carnivore-livestock encounters by date, time, boma location, and carnivore species. We then calculated the species-specific depredation risk for livestock in the boma using Equations (1, 2). We based these calculations upon the rate of encounter, and the number of attacks by each carnivore species resulting in livestock escape (i.e., no injury), escape after capture (i.e., injury), and death. As noted above, we defined all instances in which a carnivore was detected on a camera to be an encounter. Consequently, we assumed $p + q = 1$, as all encounters progressed to the next stage of the predation sequence (see Lima and Dill, 1990; **Figure 1**). Similarly, we assumed $1 - a = 1$ because bomas constrain the movement of livestock (Frank et al., 2006; Frank, 2010; Chaka et al., 2020). When encounters occur with livestock corralled within a boma, they do not have the freedom of movement to avoid carnivores prior to detection. By the same logic, whether the livestock or carnivore detect the other first is likely to have little effect on subsequent progression through the stages of predation. Therefore, we made the following further assumptions: (i) depredation risk was equal for both orders of detection ($p = q$), (ii) risk of attack was equal regardless of whether or not the livestock are aware of carnivore presence ($1 - i_1 = 1 - i_2$), and (iii) risk of capture was equal regardless of whether or not the livestock were aware of carnivore presence ($1 - e_1 = 1 - e_2$; **Figure 1**).
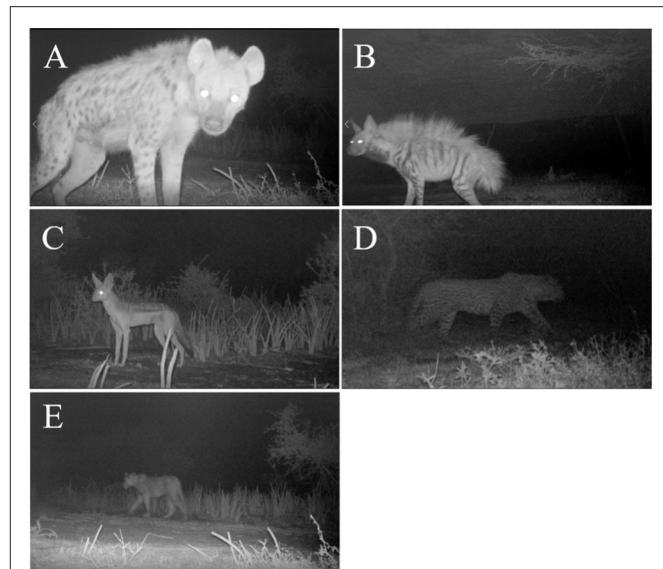
FIGURE 4 | The carnivore species detected on motion-activated cameras at 12 bomas in Central Kenya from September, 2018 to May, 2019. The five potentially depredating species recorded to encounter livestock were: **(A)** Spotted hyena (*Crocuta crocuta*), **(B)** Striped hyena (*Hyaena hyaena*), **(C)** Black-backed jackal (*Canis mesomelas*), **(D)** Leopard (*Panthera pardus*), and **(E)** African lion (*Panthera leo*).

RESULTS

Between September, 2018 and May, 2019 our motion-activated cameras recorded a total of 2,347 videos of carnivores detected at 12 livestock bomas, of which there were a total of 1,383 independent carnivore-livestock encounters. The five species identified among these carnivore-livestock encounters were spotted hyenas, striped hyenas, black-backed jackals, leopards, and African lions (**Figures 4**, **5A**, **6**). The most common carnivore species that we detected was the spotted hyena, which encountered livestock at the bomas in 76.1% ($n = 1,052$) of the detections. The next most detected species was the striped hyena (13.2%, $n = 183$), followed by black-backed jackals (10.1%, $n = 139$), leopards (0.5%, $n = 7$), and African lions (0.1%, $n = 1$; **Table 1**; **Figures 5A**, **6**). The number of carnivore-livestock encounters increased throughout the evening hours, peaking between 23:00 and 03:00 before declining to 06:00 (**Figure 5B**). Carnivore-livestock encounters also fluctuated throughout the study period, with peaks in November, 2018 and May, 2019 corresponding to the light and heavy rainy seasons, respectively (**Figure 5C**). The number of carnivore-livestock encounters also varied by boma, ranging from 26 to 472 (**Figures 5D**, **6**). Across the same time period, we recorded a total of seven carnivore attacks on livestock at the study bomas. Only two carnivores, spotted hyenas (71.4%, $n = 5$) and leopards (28.6%, $n = 2$), were responsible for these livestock attacks (**Tables 1**, **2**). The attacks resulted in the deaths of one dog and 21 shoats, and the injury of two additional shoats (**Table 2**).
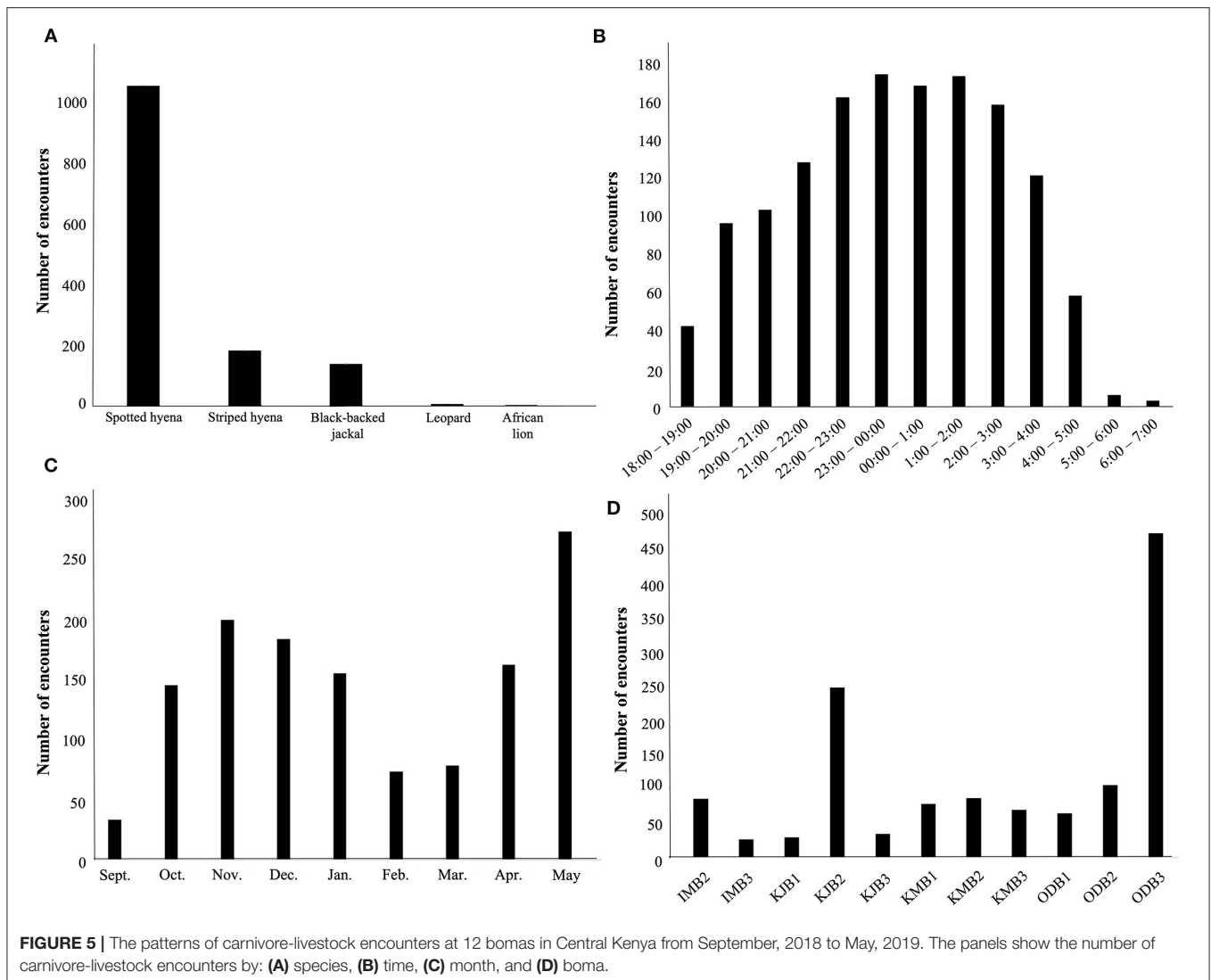
FIGURE 5 | The patterns of carnivore-livestock encounters at 12 bomas in Central Kenya from September, 2018 to May, 2019. The panels show the number of carnivore-livestock encounters by: **(A)** species, **(B)** time, **(C)** month, and **(D)** boma.

We recorded the highest encounter rate for spotted hyenas, with an average of 3.79 encounters/night (**Table 3**). Striped hyenas had the next highest rate (0.66 encounters/night), followed by black-backed jackals (0.51 encounters/night), leopards (0.03 encounters/night), and African lions (0.004 encounters/night; **Table 3**). Spotted hyenas and leopards were the only species with non-zero attack rates and calculated depredation risk. Spotted hyenas averaged 0.02 attacks/night, while leopards averaged 0.007 attacks/night. Depredation risk from spotted hyenas per boma was 0.01, and 0.007 for leopards (**Table 3**).

DISCUSSION

Assessments of the research-implementation gap regularly identify factors that diminish the impact of applied conservation practice (Knight et al., 2008; Miller et al., 2016). Within the context of human-carnivore conflict, effective alignment between

data collection and conservation need is of particular importance (Montgomery et al., 2018a; Beck et al., 2019; Gray et al., 2019; Hoffmann and Montgomery, 2022). Our study supports this broader research effort by demonstrating the integral nature of encounters in predicting carnivore depredation of livestock risk. We found that spotted hyenas had the highest encounter rate among all carnivores identified, with the average number of encounters per night almost six times higher than any other species. However, the depredation risk associated with spotted hyenas was only marginally higher than that of leopards, which were the next most common depredator. Therefore, our results indicate that carnivore species exhibit vastly different depredatory behaviors at the boma. Furthermore, we found that carnivores encountered livestock at the boma far more often than they attacked (**Tables 1**, **3**).

While the number of carnivore attacks of livestock was low overall, we recorded carnivore-livestock encounters at all study bomas, with some experiencing hundreds of encounters during the study period (**Figures 5D**, **6**). However, the fact that the direct
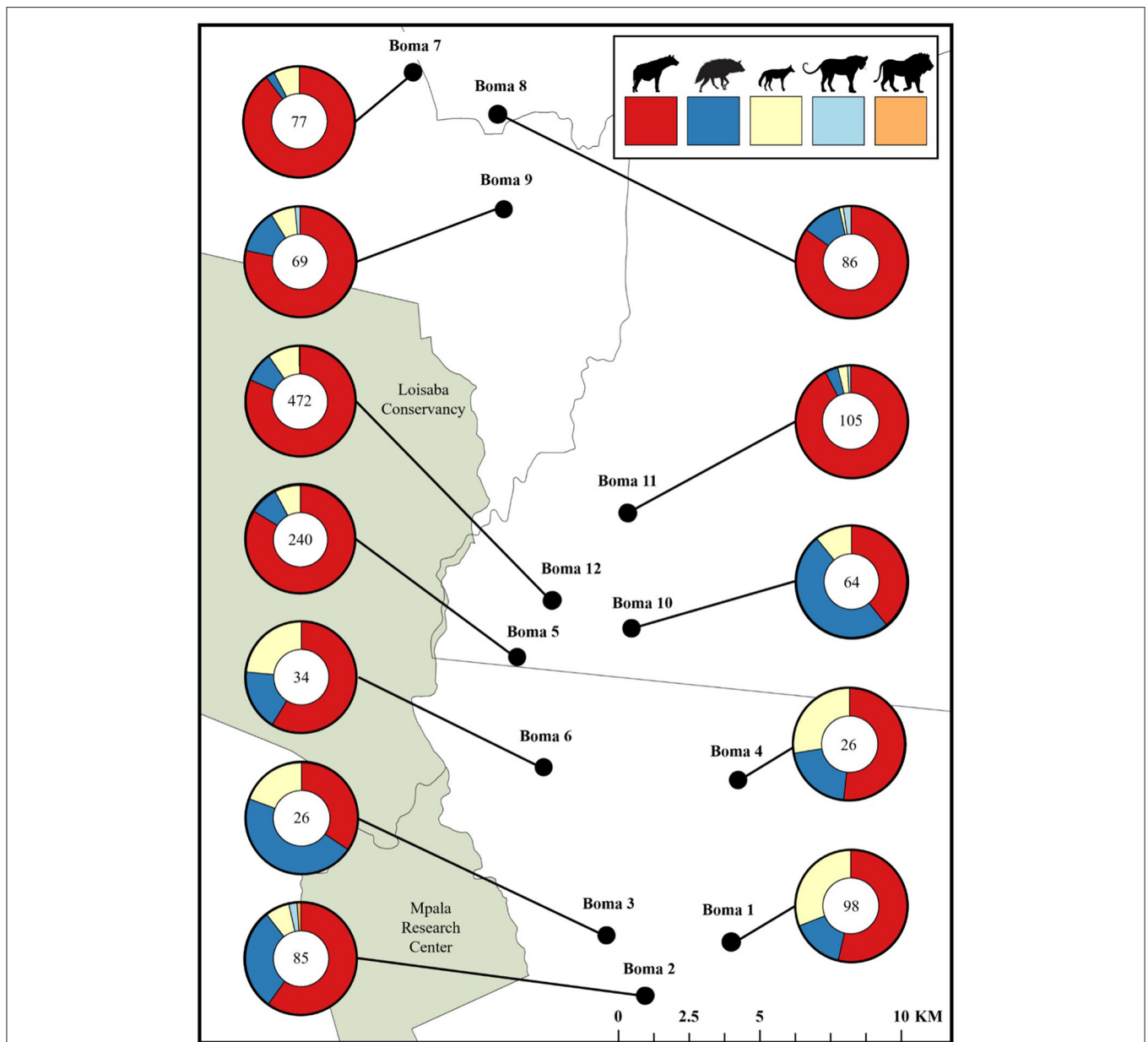
FIGURE 6 | The proportion of carnivore-livestock encounters attributed to each of the five recorded carnivore species at 12 bomas in Central Kenya from September, 2018 to May, 2019. Each chart also indicates the total number of carnivore-livestock encounters at the boma.

effects of carnivore depredation were low does not mean that the indirect effects of carnivore presence were inconsequential. Carnivore presence may have substantial effects on both the livestock and the overall conflict driven by livestock depredation. For instance, carnivore presence influences the behavior of cattle in Eastern African grazing landscapes, which may result in reduced foraging (Beck et al., 2020). Impacts such as these, often termed non-consumptive effects or risk effects, have been well-studied in both wild prey systems and grazing livestock herds (Fortin et al., 2004; Basille et al., 2015; Moll et al., 2017; Beck et al., 2020). Additionally, interactions with predators may increase

livestock stress levels and modify vigilance behavior, resulting in a range of impacts including reduction of body condition and decreased reproductive output (Lima, 1998; Creel et al., 2007; Creel and Christianson, 2008; Laporte et al., 2010). While we are not aware of any study that has examined these types of impacts at the scale of bomas (Montgomery et al., 2018b), it is likely that carnivore presence is similarly impacting the livestock corralled within these structures. As our study presents a limited sample of 12 bomas across 1 year, we offer the non-consumptive effects of carnivore-livestock encounters at the boma as a rich area of future inquiry.

TABLE 1 | The number of carnivore-livestock encounters and carnivore attacks on livestock at 12 bomas in Central Kenya from September, 2018 to May, 2019.

Boma #	Spotted hyena *Crocuta crocuta*		Striped hyena *Hyaena hyaena*		Black-backed jackal *Canis mesomelas*		Leopard *Panthera pardus*		African lion *Panthera leo*	
	Encounter	Attack	Encounter	Attack	Encounter	Attack	Encounter	Attack	Encounter	Attack
1	52	0	15	0	30	0	1	0	0	0
2	51	0	25	0	6	0	2	1	1	0
3	9	0	12	0	5	0	0	0	0	0
4	15	0	5	0	6	0	0	0	0	0
5	201	2	21	0	18	0	0	0	0	0
6	20	0	6	0	8	0	0	0	0	0
7	69	1	2	0	6	0	0	0	0	0
8	73	1	10	0	1	0	2	0	0	0
9	54	0	9	0	5	0	1	0	0	0
10	25	0	32	0	7	0	0	0	0	0
11	97	1	4	0	3	0	1	0	0	0
12	386	0	42	0	44	0	0	1	0	0
Total	1,052	5	183	0	139	0	7	2	1	0

The results are shown by boma for the five depredating carnivore species recorded.

TABLE 2 | The seven carnivore attacks on livestock reported at 12 bomas in Central Kenya from September, 2018 to May, 2019.

Attack	Month	Boma #	Carnivore responsible	Type of livestock attacked	Number of livestock killed	Notes
1	September 2018	7	Spotted hyena	N/A	0	One dog killed
2	November 2018	11	Spotted hyena	Shoat	0	One shoat injured
3	December 2018	5	Spotted hyena	Shoat	9	
4	January 2019	12	Leopard	Shoat	2	One shoat injured
5	February 2019	5	Spotted hyena	Shoat	1	
6	April 2019	8	Spotted hyena	Shoat	7	
7	May 2019	2	Leopard	Shoat	2	

We also detected substantial differences in encounter rates among the carnivore species recorded. Spotted hyenas accounted for over three quarters (76.1%) of recorded encounters (**Table 1**; **Figures 5A**, **6**). Similarly, they were responsible for 71.4% of attacks on livestock, resulting in the injury or death of 18 shoats, and had the highest calculated depredation risk (**Tables 1–3**). This finding aligns with those in other examinations of livestock depredation in both Laikipia County and sub-Saharan Africa more broadly, in which spotted hyenas are commonly reported to be the primary cause of livestock depredation (Ogada et al., 2003; Kissui, 2008; Frank, 2010; Mponzi et al., 2014; Kissui et al., 2019; Hoffmann and Montgomery, 2022). Relative carnivore population densities often provide a logical explanation for species-specific variation in livestock depredation (Kolowski and Holekamp, 2006). However, best estimates indicate that there is unlikely to be a significant difference in population density among the species we recorded encountering livestock at the boma (Frank, 1998; Frank et al., 2005; Wagner, 2006; Kinnaird and O'Brien, 2012; Prager et al., 2012; Bauer et al., 2016). Thus, the variation we identified among the rates of attack and encounter by carnivore species may be due to alternative drivers.

TABLE 3 | The average encounter rate, attack rate, and depredation risk at 12 bomas in Central Kenya from September, 2018 to May, 2019.

Species	Encounter rate	Attack rate	Depredation risk
Spotted hyena *Crocuta crocuta*	3.79	0.02	0.01
Striped hyena *Hyaena hyaena*	0.65	0.00	0.00
Black-backed jackal *Canis mesomelas*	0.50	0.00	0.00
Leopard *Panthera pardus*	0.03	0.007	0.007
African lion *Panthera leo*	0.004	0.00	0.00

The results are shown for each carnivore species, and all three are calculated over the time period of a single night (dusk to dawn).

One potential explanation for this species-specific variation comes from the foraging and movement behavior of each species. We found that leopards attacked livestock once out of every

four encounters at the boma, whereas spotted hyenas attacked only once out of every 211 encounters. Additionally, while we only recorded two leopard attacks, both resulted in the death of livestock. In contrast, livestock were killed in only slightly over half of the recorded spotted hyena attacks. Importantly, our small sample size precludes us from drawing any concrete conclusions related to these depredatory behaviors. However, our results provide a preliminary indication that the risk of death, given encounter (d in Equation 1), may vary substantially by carnivore species. Spotted hyenas are widely recognized as opportunistic feeders and are commonly recorded scavenging from human landscapes (Kolowski and Holekamp, 2006, 2007; Abay et al., 2011). They may approach bomas in search of refuse, subsequently attacking nearby livestock as those opportunities arise (Kolowski and Holekamp, 2007; Yirga et al., 2015; Chaka et al., 2020). It is therefore likely that spotted hyena-livestock encounters are driven not only by depredatory behaviors, but also by scavenging opportunities (Yirga et al., 2014). As spotted hyenas were the most common depredator of livestock in our study and many others, those scavenging opportunities are likely a key contributing factor to the depredation risk associated with that species. Consequently, the effectiveness of livestock depredation interventions for spotted hyenas may be improved *via* increased emphasis on reducing encounter rates. For example, efforts to minimize scavenging attractants for spotted hyenas at the boma (e.g., secure off-site butchering locations, better waste management infrastructure) may reduce encounter rates and thus depredation risk (Chaka et al., 2020).

Examination of temporal variation in carnivore-livestock encounters also revealed patterns relevant to the mitigation of depredation risk. We identified a peak in the frequency of carnivore-livestock encounters between the hours of 23:00 and 03:00, with a steep drop-off in the frequency of encounters in the early morning hours (**Figure 5B**). This result corresponds to trends in carnivore behaviors identified in other studies. For example, Cozzi et al. (2012) recorded a similar reduction in spotted hyena movement between midnight and sunrise. They identified nighttime light availability as the driving force of this trend, with the carnivores maximizing their activity during the darkest part of the night. The potentially depredating carnivores recorded in our encounters also are primarily nocturnal hunters (Hopcraft et al., 2005; Hayward et al., 2006; Van Cleave et al., 2018), and therefore are likely to exhibit similar activity patterns. Depredation risk is generally considered to be high between dusk and dawn, as most livestock are killed at night (Ogada et al., 2003; Yirga et al., 2012). The temporal variation we identified in carnivore-livestock encounters, however, shows that there may be fluctuations in depredation risk across that high-risk time period. The conditions associated with when a carnivore chooses to approach the boma may also correlate with prevailing biotic and abiotic conditions, including stochasticity in human behavior. Few households in this region have access to consistent electrical power, so human activity tends to closely align with natural light availability. Consequently, factors that have been shown to act as carnivore deterrents, such as human voices and dog vigilance (Ogada et al., 2003; Frank, 2010), are likely to be minimal between 23:00 and 03:00. However, the role of these fine-scale factors

in deterring carnivore encounters, and subsequent attacks on livestock, requires further investigation.

We also identified variation in carnivore-livestock encounters by season. For instance, there was one peak in carnivore-livestock encounters in November and another in June (**Figure 5C**). These peaks closely correlate with the timing of the two wet seasons in our study area. Specifically, the highest numbers of carnivore-livestock encounters aligned with periods of greatest mean rainfall (Mizutani, 1999a; Ulrich et al., 2012). The influence of seasonality on carnivore depredation of livestock has been examined extensively across sub-Saharan Africa (Patterson et al., 2004; Woodroffe and Frank, 2005; Kolowski and Holekamp, 2006; Valeix et al., 2009; Mukeka et al., 2019; Robertson et al., 2019). Consistently, rates of carnivore depredation of livestock have been shown to increase during rainy seasons (but see Pozo et al., 2020). This seasonality has been attributed to many potential drivers, including herding practices, wild prey migration, and prey switching driven by reduced predation success on wild prey (Patterson et al., 2004; Kolowski and Holekamp, 2006; Valeix et al., 2012; Mponzi et al., 2014; Kuiper et al., 2015; Loveridge et al., 2017; Kissui et al., 2019; Mukeka et al., 2019). As far as we are aware, however, this study provides the first evidence of seasonal variation in the frequency of carnivore-livestock encounters. This distinction is important, as it indicates that the well-established seasonal trends in rates of carnivore depredation of livestock are not just associated with the probability of death, given an encounter (d; Equation 1) or increased time spent vulnerable to an encounter (T), but are in fact likely associated with an increase in the rate of encounter itself (α).

CONCLUSIONS

Prediction of depredation risk is a fundamental strategy among studies seeking to mitigate carnivore depredation of livestock. Yet, logistical and ecological constraints have largely narrowed such approaches to the application of a proxy that cannot capture all aspects of depredation risk. Our effort to address this limitation highlights the important role of encounters in this predator-prey system. Encounter rate is an essential component of the prediction of depredation risk, and the subsequent development of interventions to minimize carnivore depredation of livestock. The evident variation in carnivore-livestock encounter rates and depredation risk by species further indicates the value of carnivore-livestock encounters in informing depredation mitigation efforts. However, there are many avenues of research that remain to be fully explored in relation to carnivore-livestock encounters. While the methods presented herein are limited to corralled livestock, recent advancements in animal-borne technologies such as proximity collars and neck-mounted cameras provide opportunities to explore encounter rates among mobile prey as well (Wilmers et al., 2015; Prugh et al., 2019). We advocate for further examination of encounters in multiple carnivore-livestock scenarios to develop more effective livestock protection efforts and continue to narrow the research-implementation gap.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Institutional Review Board (IRB #02555e) of Miami University, Ohio. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements. The animal study was reviewed and approved by Institutional Animal Care and Use Committee at San Diego Zoo Global (Protocol #18-017).

AUTHOR CONTRIBUTIONS

CH, NP, KR, and RM conceived the ideas and designed methodology. CH, NP, KR, AL, LL, and IL collected the data. CH analyzed the data. CH and RM led the writing of the manuscript. All authors contributed critically to the study and gave final approval for publication.

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