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RESEARCH ARTICLE

Maasai pastoralists kill lions in retaliation for depredation of livestock by lions

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Abstract

1. The borders of national parks in Kenya are hotspots for human–wildlife conflict. The deliberate killing of lions by Maasai pastoralists is illegal, but continues despite mitigation attempts. Currently, there is a somewhat pervasive opinion, within the human–wildlife conflict literature, that lions are killed by Maasai people either as cultural ceremony or indiscriminately in response to the loss of livestock.
2. We reconsider the indiscriminate reputation of lion-killing, using a combination of structured dialogue and quantitative analysis. Focus group discussions with Maasai pastoralists in three different pastoral regions, performed by in-country experts, minimized the risk of cross-cultural misinterpretation through a platform of shared Kenyan heritage.
3. In our survey of 213 Maasai pastoralist communities, we found universal agreement that humans and lions should coexist in Kenya.
4. Maasai communities distinguished among drought, disease, theft, loss and depredation as drivers of livestock losses. Maasai also distinguished among predatory species that take their livestock. The only cause of livestock loss that provoked increased killing of lions, was depredation by lions. Lion-killing was not provoked by other predatory species. We found regional variation in the baseline probability of lion-killing, and discuss the sources of this variation.
5. The probability of lion-killing increases as an act of retribution for predation of livestock that discriminates among species of carnivore. This, coupled with universal acceptance of coexistence between lions and Maasai pastoralists, should guide mitigation strategies for human–wildlife interactions in Kenya and beyond.

1 | INTRODUCTION

Large carnivores are of enormous conservation value, either in their own right (Weber & Rabinowitz, 1996), as contributors of important ecosystem services (Dobson et al., 2006), or as contributors to economies of developing nations via ecotourism (Dalerum, Somers, Kunkel, & Cameron, 2008). The killing of endangered carnivores by pastoralists ranks among the most important examples of human–wildlife conflict, globally (Treves & Karanth, 2003). This conflict risks the extinction of local populations of carnivores (Frank, Maclennan, Hazzah, Hill, & Bonham, 2006; Woodroffe & Frank, 2005; Woodroffe & Ginsberg, 1998). Understanding the reasons why carnivores are killed, and reducing the prevalence of this conflict, is therefore a high priority for conservation research.

One of the best-known examples of conflict between pastoralists and carnivores involves lions (*Panthera leo*) and the indigenous Maasai peoples of Kenya and Tanzania (Bruner, 2001). Lions roam freely in many of the African dry lands, but number only 16–35,000 individuals (Bauer & Van Der Merwe, 2004; Hazzah, Borgerhoff Mulder, & Frank, 2009; Ikanda & Packer, 2008), having suffered serious declines in recent decades (Nowell & Jackson, 1996). Kenya's lion population is estimated to number fewer than 2,500 individuals, with the Maasai rangelands harbouring over 800 of those (Kenya Wildlife Service, 2009; Riggio et al., 2016, 2013). Populations are concentrated in national parks, but the boundaries of these parks are porous to both wild animals and domesticated livestock (Woodroffe & Ginsberg, 1998). The endangerment of African lion populations is usually attributed to a combination of land-use change (Ray, Hunter, & Zigouris, 2005), and persecution by people (Linnell, Odden, Smith, Aanes, & Swenson, 1999; Woodroffe & Ginsberg, 1998). Much of this persecution has been blamed on indigenous pastoralists, partly due to the cultural significance of lion-hunting and -killing among them (Bruner, 2001; Kissui, 2008) and overlapping motivations that are simultaneously social, emotional and political (Goldman, De Pinho, & Perry, 2013). However, Maasai culture is changing rapidly, and while cultural killing remains a problem (Hazzah, Bath, Dolrenry, Dickman, & Frank, 2017; Hazzah et al., 2014), it is becoming much less common (Hazzah, Borgerhoff, & Frank, 2009; Hazzah, Kaplan, & Frank, 2013; McCabe, Leslie, & DeLuca, 2010).

More recently, lion-killing by Maasai has been ascribed to the act of retribution against the loss of livestock, particularly to predators (Kissui, 2008). Here we reconsider the perceived wisdom that the Maasai act indiscriminately against lions when other carnivore species are responsible for the depredation of livestock (Hazzah et al., 2009; Kolowski & Holekamp, 2006; Woodroffe & Frank, 2005). This builds on important work by Kissui (2008) who highlighted that Maasai pastoralists distinguish between lions and hyena as culprits of livestock depredation. Furthermore, recognizing that cultural perceptions of carnivores and the loss of livestock will vary among pastoralist groups and regionally (Manfredo & Dayer, 2004), we compare the relationship between lion-killing and livestock depredation among three geographical clusters of Maasai people in Kenya: Nairobi, Maasai Mara and Amboseli. These geographical regions aggregate across several important features of Maasai socioecology, including economic status, climate, engagement with conservation programmes and agricultural livelihoods.

The current work is focused on the analysis of interviews with Maasai pastoralists using methods that engage the local communities in a participatory manner. Kenyan and cultural goals of family and community sustainability were used as a framework by native Kenyan researchers to interview Maasai heads-of-households. We sought to determine (a) attitudes towards coexistence of humans and wildlife in Maasai land; (b) losses of livestock to multiple factors (depredation, theft, drought, disease and escape); (c) species of carnivore involved in the depredation of their livestock; (d) whether or not they had killed a lion. We considered the possibility that Maasai pastoralists actually favour the coexistence of humans and large carnivores, and hypothesized that the probability of lion-killing only increases with increasing depredation of livestock by lions. We also hypothesized that attitudes towards lions and retaliatory responses to livestock depredation might vary among geographical regions. We discuss how our results can inform approaches to lion management in the context of cultural and livelihoods of the pastoral communities.

2 | METHODS

2.1 | Study region

The study regions were (a) the dispersal areas of Nairobi National park (NNP), (b) community lands around Amboseli National Park and (c) community areas around the Maasai Mara National Reserve (MMNR) (Figure 1). These are three of the major conservation areas in Kenya, and also form part of the traditional lands of the Maasai people. The main land-use practice in the areas has been wildlife conservation and extensive livestock production but recently the region has experienced large-scale anthropogenic development activities such as roads, human settlements fences and large-scale crop production (Homewood et al., 2001; Osano et al., 2013). The research was conducted between October 2010 and March 2012.

Nairobi National Park encompasses an area of 117 km^2 in southwest Kenya and adjoins three geographic triangles that comprise the larger wildlife dispersal area for NNP, an area of 2,200 km^2. There is an increase in permanent human settlements, cash crop production and ecotourism facilities. The Mara Region is located in south western Kenya and borders the Serengeti National Park in Tanzania to the south. It encompasses 1,530 km^2 of the protected MMNR in which only wildlife conservation and tourism are permitted, as well as approximately 4,000 km^2 of the adjoining pastoral ranches in which the major forms of land use are traditional pastoralism by the Maasai people and pastoral settlements, some cultivation and wildlife tourism. Our study region in the Mara included the outer, more productive ranches in the east, and the inner ranches of the central and eastern part of MMNR (Bhola et al., 2012). In Amboseli, the research was conducted in six group (community-owned) ranches. Community ranching is a communal land tenure system where a group of closely related members are registered, jointly hold title to land, maintain agreed herd sizes and own livestock individually but herd them together (Kimani & Pickard, 1998). The group ranches are part of the 4,000 km^2 of community land around the park that acts a dispersal area for wildlife from the Amboseli National Park. The climate is highly variable spatially and temporally resulting in resource heterogeneity (BurnSilver, Worden, & Boone, 2008). The group ranches in our study site include Eselenkei, Kimana, Mbirikani, Kuku, Rombo and Olgulului. The group ranches closer to the base of Mt. Kilimanjaro (e.g. Rombo) experience about 1,250 mm annually while those closer to the Amboseli basin experience lower rainfall of about 500 mm annually (Ntiati,2002). In the recent past, the land use has changed from extensive livestock production and wildlife conservation to include irrigation agriculture (Okello & D'Amour, 2008).

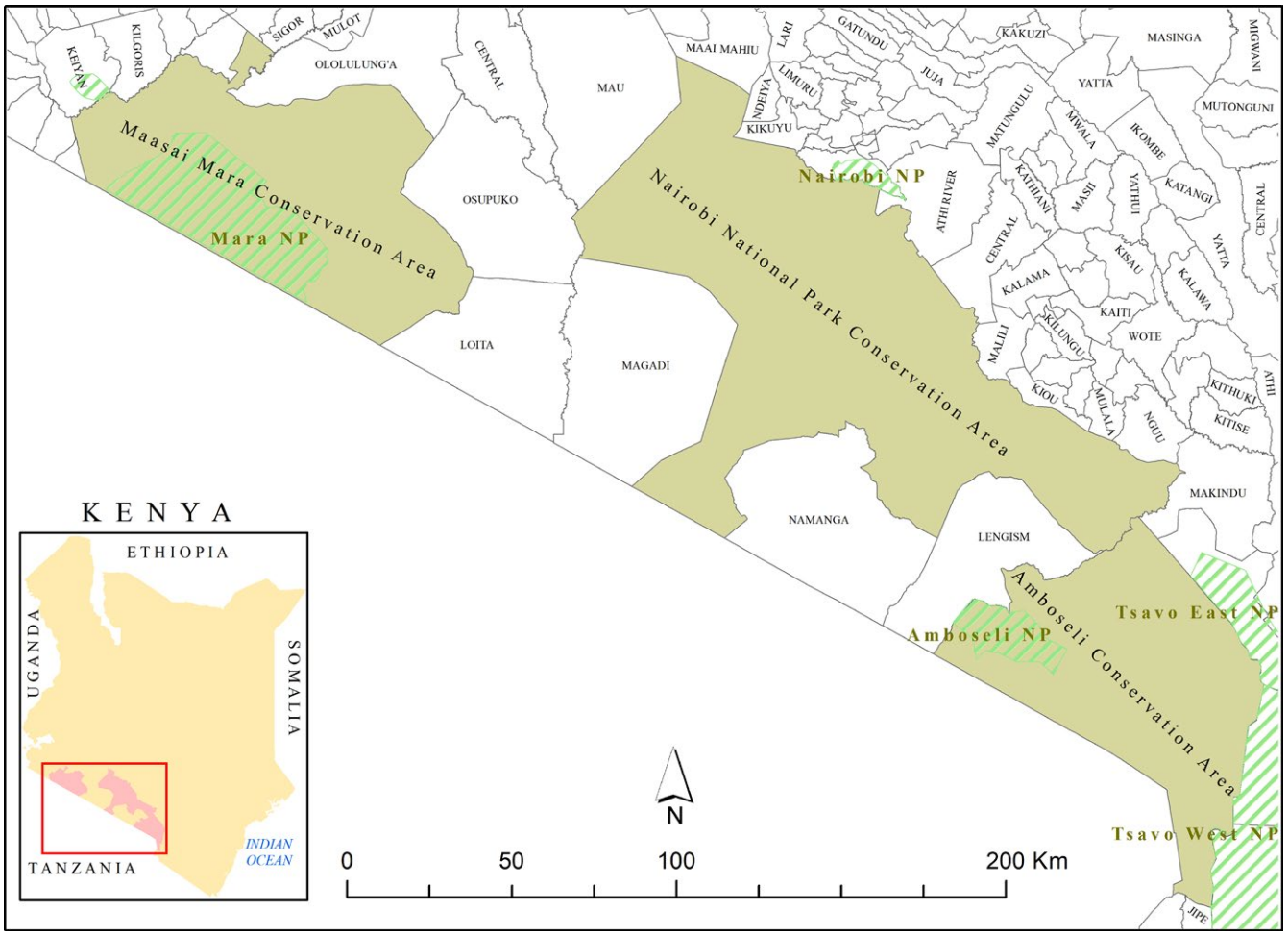

FIGURE 1 Map of the study area in Kenya (with inset showing broader geographical context). The Nairobi study Region included subdivisions Central, Ewuaso Kedong, Ngong, Isinya, Mashuru. The Amboseli study region included subdivisions Entonet, Oltiasika, Kimana, Central, Rombo and Chala. The Maasai Mara study region included subdivisions Lolgorian, Angata, Kirindoni and Mara

2.2 | Focus group discussions

The collection and analysis of evidence regarding sensitive cultural issues is best done through appropriate participatory approaches like focus group discussions (FGDs; Kitzinger, 1995). FGDs aid participatory appraisal by highlighting respondents' attitudes, priorities, language and framework of understanding. FGDs help identify group norms and values, encourage open conversation and provide insight into the articulation of knowledge, for example, through examination of what information is considered taboo or secret within the group (Kitzinger, 1995). Based on our prior collaboration with the communities in conservation work including Lion Guardians, Friends of NNP and the Ann Kent Taylor Fund, we were able to recruit focus groups across a broad geographical area and a large number of autonomous communities. Focus groups consisted of key informants, scouts and community members. Groups were chosen from communities who lived within or around hotspots of predation or lion–human conflict.

We compiled a checklist of questions to guide FGDs, based on the perceived major issues around human–lion conflict for the three study regions. Scouts helped the research team to profile communities and identify the best representation of all the people in FGDs. We determined participant-inclusion criteria based on demographics including age, gender, wealth, education, political power and location with reference to predation hotspots. The participants included men and women from the community. Due to a strong culture of women not speaking while in the same meeting with men, we intentionally separated male and female FGDs. Six preparatory meetings were convened, two in each study region, each numbering 10 participants. These preparatory meetings were used to optimize the sequence and structuring of questions, to identify sensitive and difficult aspects of the structured dialogue and to standardize the training of facilitators. During FGDs, facilitators guided participants to discuss the main issues around livelihoods, weather, wildlife, benefits and disadvantages of having wildlife around them. Participants prioritized the issues and the areas most affected. We provided maps of the region and asked participants to mark areas they considered important for their livestock during the day and where they felt most conflict occurred. This confirmed predation hotspots. To

test whether members knew each predator/wildlife species, photographs of various animals and paw print images were provided for them to identify.

2.3 | Semi-structured interviews

Responses from the preparatory meetings were used to adjust the structuring of the FGDs. We recruited and trained facilitators to conduct the FGDs, dividing them into four groups of three individuals with clear roles of moderator, note taker and observer. A pretesting exercise was conducted in one village in the Kitengela region in the southern border of NNP. This helped us to train FGD facilitators, and responses to initial questions were assessed to allow problematic questions to be rephrased or changed. Each group was then led by a local scout who was well known by the community and who had participated in community-based conservation initiatives. FGDs were conducted over a period of 6 months. A minimum of four individuals were targeted to take part in each FGD. Participants were visited in their manyattas or homesteads. In every village identified, an elder was contacted by phone in advance to mobilize the participants. Each of the facilitators' teams carried photographs of the main predators in the area to ensure the pastoralists identified the predators correctly. While FGDs allowed discussion throughout, the guides were structured so that groups of questions occurred in the following sequence:

1. *Demographics*. Participants discussed the ages, genders and distribution of livestock, wealth and power in their homesteads and communities.
2. *Livestock losses*. Participants discussed the loss of livestock to various sources, and in cases of depredation to various species of carnivore, during periods reducing sequentially from the preceding 10 years, to 5 years, to 2 years. Participants usually failed to remember numbers over periods longer than 2 years, therefore here we use 2-year data in our analyses.
3. *Response to livestock losses*. Participants discussed general attitudes towards the loss of livestock, and began to be probed about the possibility of retaliation against wild predators.
4. *Attitudes towards carnivores*. Participants discussed their perception of, and attitudes towards, wild carnivores, with increasing focus on the killing of wildlife by Maasai people.
5. *Lion-killing*. Participants were probed for information on the frequency of lion-killing, and the number of lions killed, during the preceding 10, 5 and 2 years. Admission of lion-killing is rare when short time periods are discussed, but participants were confident in their responses relevant to a 10-year history.
6. *Lion-killing methods*. Respondents discussed their preferred, and their chosen, methods of killing lions.
7. *Human–wildlife conflict*. Questions allowed respondents to identify possible mitigation strategies to reduce the intensity of lion–human conflict, including the possibility of carnivore extirpation.

We provide an empty datasheet as Table S1. The facilitators sought particularly to clarify and quantify the number of livestock the pastoralists had lost to various causes including disease, predation by wildlife, drought, theft and escape. They also sought to quantify the losses of livestock to various predatory species, and the frequency and magnitude of lion-killing in the last 2 years. Datasheets were filled out as a single outcome per FGD, hence each survey unit in our analyses represents a community rather than an individual. All data was reviewed by the researchers and the community scouts to authenticate and validate it. Any information that was suspected to be untrue or inconsistent was discarded (six interviews). This yielded 70 FGDs from the Nairobi region, 95 from the Amboseli region and 48 from the Maasai Mara region.

2.4 | Data handling

Data extracted from interviews suffer risks of human bias and exaggeration. During initial data exploration, we found that histograms of 'number of livestock lost' and 'number of lions killed' were extremely skewed, containing many zeroes and many questionably large numbers. We also note a mismatch in the span of years for the information on livestock losses (2 years) and on lion-killing (10 years). Any relationship we find between lion-killing and livestock loss should therefore be considered an association between admission to lion-killing and a proxy for the intensity of livestock losses due to various sources, rather than a predictive relationship. Throughout the forthcoming analyses, we use 'lion-killing' as our response variable, and regress it against explanatory variables that include numbers of livestock lost. To reduce the influence of outliers in the explanatory variables, we reduced skew using the natural logarithm of livestock losses. To reduce the exaggeration of lion-killing, make all analyses conservative and ease the choice of error structure for our response variable, we converted lion-killing from a count to a binary (yes/no) variable, recorded as 'yes' if there was any admission to the killing of lions over a 10-year period prior to the FGD.

2.5 | Statistical modelling

All of our analyses are GLM with a binary error structure (Crawley, 2012). We recognize that the survey units are geographically patterned, and that communities-within-regions tend to share similar socio-economic, cultural, climatic and political features, and tend to share similar levels of engagement with conservation charities and compensation or consolation schemes relevant to human–wildlife conflict. Hence we also modelled 'region' as a predictor, and in our discussion we consider reasons why regions might vary in the prevalence of lion-killing. Source region plays an important role in our hypotheses, and our explanatory variables (source of loss of livestock; species of carnivore) vary both within and among regions, hence we choose to study region as a fixed effect and consider our FGDs as independent survey units.

In order to understand the factors that motivate Maasai people to engage in lion-killing we use our GLMs to address the following questions:

1. Is the probability of lion-killing influenced by different causes of losing livestock (predation, drought, disease, theft and escape)?
2. Is the probability of lion-killing influenced by whether lions are identified as the species involved in livestock predation?
3. a Is the probability of lion-killing the same across different regions?
   b Do factors identified as important in predicting lion-killing vary across regions?

We used multi-model inference (Johnson & Omland, 2004) to compare two sets of candidate models. First, we analysed associations between the probability of lion-killing and the loss of livestock to predation, drought, disease, theft and escape. The full model was a logistic multiple regression of the binary response against region and log-transformed numbers of livestock lost to each cause. Multi-model inference tested all possible combinations of explanatory variables, yielding 64 logistic multiple regressions. We compared these models using ranked Akaike information criteria (AIC; Burnham & Anderson, 2003). Several models, of varying complexity, were found to be similarly informative. We used model-averaging to derive the AIC-weighted mean slopes associated with each source of livestock loss, and their 95% confidence intervals (Johnson & Omland, 2004). We consider each explanatory variable to be a useful predictor of lion-killing if their 95% CI does not cross zero.

Second, we asked whether the probability of lion-killing was influenced by the species of predatory carnivores. We used multi-model inference and model-averaging using AIC, with lion-killing as the binary response and categorical explanatory variables (yes/no) for each of the predatory species identified during FGDs (lion, leopard, hyena, jackal, cheetah, dog; 128 logistic multiple regressions).

Throughout these analyses we sought to understand whether the probability of killing lions varied among regions. All models and multi-model inference included region as an explanatory variable, and we considered the significance of interactions between region and the members of the most informative set of explanatory variables.

All statistical analyses were performed using program R 2.15.3 (R Core Team, 2018). Model averaging was performed using the R package 'MuMIn' (Barton, 2016). We tested the robustness of our analyses using standard frequentist model-simplification, which in all cases confirmed that the important predictors identified by model-averaging were the only statistically significant predictors of lion-killing. Predictors whose model-averaged parameters were not informatively different from zero, were also non-significant predictors of lion-killing.

This work was given ethical approval by the Kenya Wildlife Services, permit number KWS/BRM/5001. Prior to all FGDs, all participants were asked to provide informed consent. This consent was explained to them to mean that the information they provided would be used for primary research, and that they would receive no remuneration for their participation. Participants who did not provide this informed consent took no further part in the FGDs. Written consent was not received, indeed was not relevant to many participants; verbal consent was accepted by the ethics committee.

3 | RESULTS

3.1 | Coexistence of pastoralists and carnivores

A total of 213 FGDs were held in the three study regions. Among participants in all groups, there was unanimous agreement that solutions must be found to allow coexistence of pastoralists and large carnivores in Maasai land. None of the interviewees from the three regions indicated that large carnivores should be extirpated. Most of the participants said they respect wildlife in general because they generated tourism income. In the three study regions, pastoralists felt the competition for pasture between wild ungulates and livestock was a big challenge to their livelihoods. Although more livestock was lost to drought, the participants understood it as a natural calamity and they could do nothing about it. The youth and women demonstrate more negative attitude to wildlife than the older men and elders. In Amboseli, the people demonstrated more negative attitudes to elephants due to destruction of their crops. In this paper, we focus on our quantitative results, linked to our core hypotheses regarding links between lion-killing and the loss of livestock to carnivores, particularly lions.

3.2 | Summary of prevalence of lion-killing and predation of livestock

Admissions of lion-killing varied in prevalence across three regions, ranging from a quarter of communities in Nairobi to over half of communities in Amboseli (Table 1). The loss of livestock to carnivores was lowest in Nairobi and highest in the Maasai Mara. The prevalence of

TABLE 1 Summary statistics of the prevalence of admissions of lion-killing, number of livestock lost to carnivores and identification of lions as culprits of livestock depredation, in three regions of Kenya.

	Region		
	Nairobi	Maasai Mara	Amboseli
Focus group discussions	70	48	95
Admissions of lion-killing (%)	25.7	31.2	51.6
Lion identified as predator of livestock (%)	27.1	70.8	50.5
Average log(number of livestock lost to carnivores)	1.62	2.61	1.94

loss of livestock to lions in particular, was also lowest in Nairobi and highest (over 70%) in the Maasai Mara (Table 1).

3.3 | Lion-killing as a response to loss of livestock

We found that, among the various causes of livestock loss, the probability of killing lions was only influenced by loss to predation, and differed among regions. The logistic regression with minimum AIC included only depredation and region as predictors of lion-killing. Three other models had AIC values within two units of this 'best' model, but all of them included depredation and they shared no consensus regarding secondary predictors (Table 2). Model averaging revealed that the only predictors of lion-killing whose model-averaged 95% CI did not cross zero, were depredation and region (Figure 2b). The probability of lion-killing increased with increasing numbers of livestock lost to predators, in all three regions (Figure 3).

3.4 | Lion-killing in response to culprit species

Multi-model inference showed that livestock deaths due to leopards, hyena, dogs, jackals and cheetahs did not influence the probability of retribution against lions (Table 3). When lions were identified as the culprit of livestock loss, lions were more likely to be killed (Table 3; Figure 4a). The logistic regression with minimum AIC included lion, leopard and cheetah as predictors of lion-killing. However, 12 other models had AIC values within two units of this 'best' model. All rival models included region and depredation by lions as predictors of lion-killing. One interpretation is that the other species of carnivore cannot be dismissed as candidate predictors of lion-killing, because they appear in the set of similarly informative models. Model-averaged effects of non-lion carnivores suggested a decrease in the probability of retribution against lions when leopards or cheetahs were responsible for livestock loss, and an increase in probability of retribution against lion when jackals or dogs were responsible (and no effects when hyena were responsible). However, the set of candidate models shared no consensus regarding the influence of non-lion carnivores (Table 3), and the 95% confidence intervals for the model-averaged influence of non-lion carnivores all spanned zero, revealing them to be uninformative (Table 3; Figure 4b). Model averaging revealed that the only predictors of lion-killing whose model-averaged 95% CI did not cross zero, were regional differences (Figure 4a) and losses due to lions (Figure 4a,b).

3.5 | Regional variation

Livestock owners in Amboseli communities are overall more likely to kill lions than Maasai Mara and NNP communities, whose baseline probabilities of lion-killing are similar (Figures 2a, 3, and 4a). We found no variation among regions in the relationship between lion-killing and the loss of livestock to various sources, in particular the number of livestock lost to carnivores (test of interaction between Region and loss to carnivores; $\chi^2_2 = 3.612$, $p = 0.164$), and more specifically to lions (test of interaction; $\chi^2_2 = 2.465$, $p = 0.292$).

TABLE 2 Explanatory variables included in the 10 most informative models that regressed lion-killing against magnitudes of livestock losses to various sources. Models ranked by Akaike information criterion. ΔAIC describes the standard comparison of AIC: differences greater than two units suggest models are of considerably lower inferential quality. All models in this top-model set included livestock loss due to depredation and region as predictors.

Explanatory variables included	Disease	Drought	Loss	Depredation	Theft	Region	AIC	ΔAIC
				0.284		+	271.7	0
			−0.114	0.320		+	273	1.24
		−0.042		0.314		+	273.6	1.85
				0.280	0.104	+	273.6	1.88
	−0.015			0.289		+	273.8	2.07
			−0.108	0.316	0.079	+	275	3.24
		−0.026	−0.105	0.336		+	275	3.27
	0.004		−0.115	0.319		+	275.1	3.36
		−0.046		0.313	0.115	+	275.5	3.71
	−0.016			0.286	0.105	+	275.7	3.97

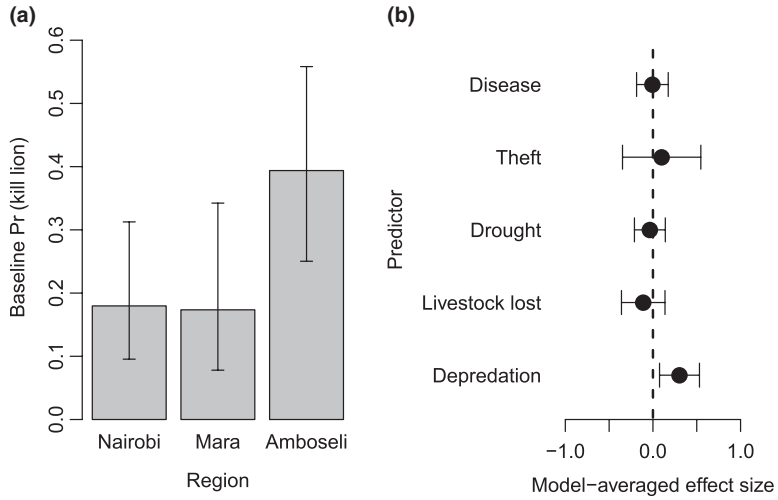

FIGURE 2 (a) Barplot of baseline probability of killing lion, estimated from GLM when number of livestock lost to predators is zero. The 95% confidence intervals reveal uncertainty in probabilities of lion-killing, but significantly higher probability in the Amboseli region. All parameters back-transformed from the logit link function used by GLM with binomial error structure. (b) Model-averaged regression slopes describing the relationship between probability of lion-killing and the number of livestock lost due to various sources. Whiskers describe model-averaged 95% confidence intervals. Any source of livestock loss is considered an informative predictor of lion-killing if its slope's confidence interval does not span zero. Slopes are linear on the logit scale; see Figure 3 for informative estimates on the probability scale

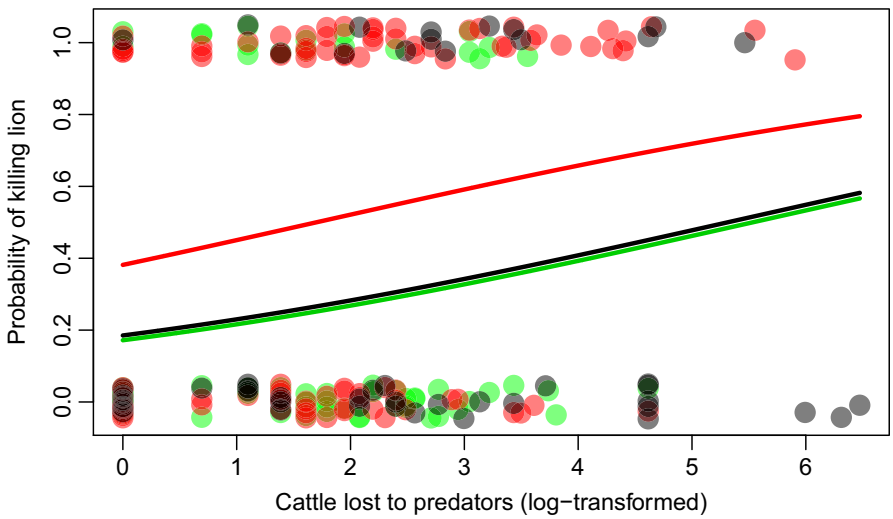

FIGURE 3 Relationship between lion-killing (data: yes/no; model fit: probability) and the log-transformed number of cattle lost to depredation. Data are jittered to reduce overlap of points. Regions are coloured: green = Nairobi; black = Maasai Mara; red = Amboseli

4 | DISCUSSION

The analysis of responses to 213 semi-structured interviews with Maasai pastoralists adds to the growing body of evidence that lion-killing is a retaliatory act motivated by the loss of livestock (Hazzah et al., 2009; Holmern, Nyahongo, & Roskaft, 2007; Kissui, 2008; Woodroffe & Frank, 2005). The key and novel finding here, however, is that retribution is not indiscriminate among species of carnivore. Maasai retaliate against lions when lions are perceived as the agents of livestock depredation. Depredation by other carnivores has no influence on the probability of lion-killing. We believe this is a major step forward in our understanding of the drivers of lion-killing, and helps to clarify the value of various conservation strategies to mitigate against it. Maasai communities unanimously rejected the idea that lions and other carnivores should be extirpated from the region. Lions are still a symbol of their identity and a source of cultural pride (Goldman et al., 2013). Compensation directed towards loss of livestock to lions should therefore be an important focus (Maclennan, Groom, Macdonald, & Frank, 2009), alongside incentivization schemes that help reduce the incidence of livestock depredation (Bulte & Rondeau, 2005). In the absence of compensation, public outcry against actual crop, livestock or property loss is believed to be related to locals' perception of potential risk and lack of control over addressing the problem (Nyhus, Osofsky, Ferraro, & Medden, 2009; Osano et al., 2013). Alternatively, pre-emptive reduction of lion depredation, for example using improvements to the security of livestock enclosures (bomas), could dramatically reduce the need for, and therefore the frequency of, retaliatory

TABLE 3 Explanatory variables included in the 13 most informative models that regressed lion-killing against the attribution of livestock depredation to various carnivore species. Models ranked by Akaike information criterion. ΔAIC describes the standard comparison of AIC: differences greater than two units suggest models are of considerably lower inferential quality. All models within two AIC units of the 'best' model all included 'lion' and 'region' as predictors

	Lion	Leopard	Hyena	Jackal	Cheetah	Dog	Region	AIC	ΔAIC
Explanatory variables included	1.200	−0.643		0.565	−1.222		+	262.8	0
	1.253	−0.568			−1.226		+	262.9	0.06
	1.160				−1.255		+	263.1	0.28
	1.254	−0.660		0.576			+	263.3	0.49
	1.310	−0.587					+	263.5	0.68
	1.205	−0.662		0.586	−1.438	1.884	+	263.5	0.74
	1.104			0.483	−1.247		+	263.5	0.74
	1.259	−0.583			−1.429	1.774	+	263.7	0.91
	1.218						+	263.9	1.14
	1.162				−1.464	1.69	+	264	1.22
	1.159			0.495			+	264.3	1.47
	1.104			0.500	−1.467	1.769	+	264.4	1.6
	1.259	−0.679		0.591		1.21	+	264.8	1.96

attacks (Ogada, Woodroffe, Oguge, & Frank, 2003; Woodroffe, Frank, Lindsey, Ole Ranah, & Romanach, 2007). We also suggest that training of herders, to identify the culprit of depredation with certainty, could help to minimize any possibility of unwarranted retaliation.

We found no difference in the relationship between livestock depredation and the probability of retaliatory lion-killing among Maasai groups around Nairobi, Maasai Mara and Amboseli, but clear differences in their baseline probability of lion-killing. Even in the absence of depredation of livestock, the probability that respondents admitted to killing lions was twice as high for Amboseli than for Maasai Mara and NNP. The prevailing contextual factors that distinguish among these regions include weather, wildlife management programs and the prevalence of cultural practices. Previous studies have shown that pre-emptive killing of lions is considered more likely to be experienced where communities view their livestock as economic banks, have no alternative sources of income and where authorities do not compensate for losses (Dickman, 2010). People in drier areas, such as Amboseli, are less able to tolerate losses of livestock and for this reason might be less tolerant of lions in the vicinity of their herds (Barua, Bhagwat, & Jadhav, 2013). Some cultural practices like *ola mayio*, the ritual killing of lions by young men graduating to adulthood, is more prevalent in northern Tanzania (Kissui, 2008) and parts of Amboseli (Muriuki, Ipara, & Kiringe, 2017). Although this practice is culturally regulated and now becoming less, thanks to education, we speculate that this may be the reason for high prevalence in baseline rates of admission of lion-killing, particularly in Amboseli. We recommend two important avenues of research, related to the prevalence of non-retaliatory lion-killing. First, it will be important to measure lion-killing empirically, to validate the information received from FGDs. Second, deeper understanding is required regarding the socio-economic and cultural factors that shape relationships between pastoralists and lions in different regions. Regions differ in the access of pastoralists to incentivization for conservation, consolation for loss of livelihood and compensation for loss of livestock. We will explore these regional differences in further, more qualitative, analyses of lion-killing.

We recognize that data sourced from interviews, even when validated by focus groups, contain several sources of bias (Robson, 2002). For example, Maasai elders are not familiar with Western counting systems, and might be prone to exaggeration. We minimized the influence of these exaggerations and biases by reducing skew in the respondents' estimations of numbers of livestock lost (using log-transformation), and by completely removing any quantitative assessment of lions killed (by converting this to a binary yes/no response).

Another possible concern with interview surveys is the difficulty in ascribing cause and effect. It remains possible that Maasai collectively 'engineered' the conclusions of this study by exaggerating or fabricating the culpability of lions for loss of livestock whenever they admitted to killing lions. Alternatively, respondents might falsely claim to have killed lions if the preceding interview questions helped to reveal lions as killers of their livestock. Furthermore, respondents

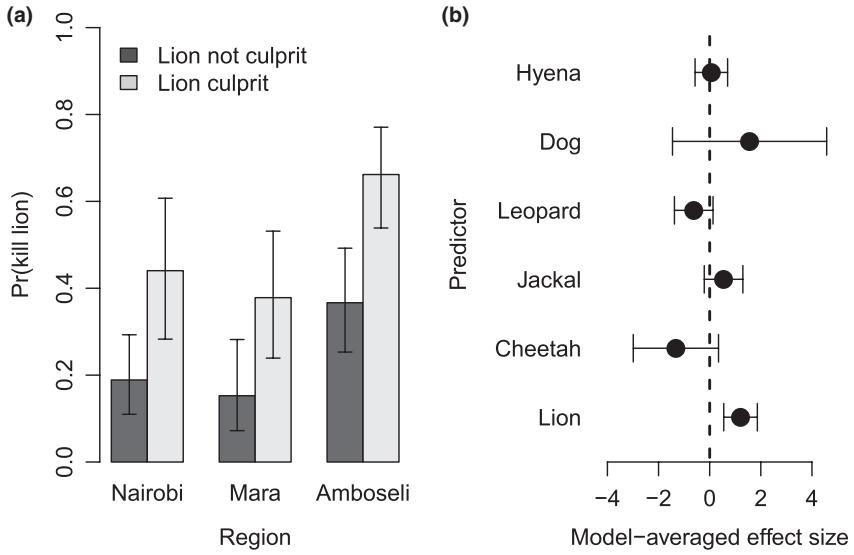

FIGURE 4 (a) Barplot showing estimates of the probability of lion-killing in the absence and presence of lion as culprit of depredation of livestock, in three regions of Kenya. Whiskers are 95% credible intervals. (b) Model-averaged regression slopes describing the change in probability of lion-killing when culprit species of carnivore were identified by focus group participants. Whiskers describe model-averaged 95% confidence intervals. Any culprit species is considered an informative predictor of lion-killing if its slope's confidence interval does not span zero

may have exaggerated the frequency or severity of livestock losses due to lions, in an attempt to receive better compensation.

We minimized the risk of biased responses in several ways. First, FGDs (Kitzinger, 1995) ensured the best identification of 'honest' and 'impartial' respondents at each homestead. The admission of an illegal activity such as lion-killing is never taken lightly by respondents. Second, we made certain that respondents felt neither threatened by the risk of prosecution, nor encouraged by the possibility of compensation. Third, interviews always explored questions in the following order: respondents were asked about the extent and sources of livestock losses; only then were they asked whether they had killed lions; finally, having admitted to the killing or not of lions, they were asked about their attitude towards coexistence of people and wildlife, and their preferred strategies to mitigate human–wildlife conflict. Fourth, early data handling allowed data recorders to identify outlying and 'unlikely' responses, und use contact with key informants (found during focus group meetings) to discard or adjust data. Adjustments were only ever applied to quantitative assessments of livestock losses and lion kills, not to attribution of sources of livestock losses. Finally, conduct of the interviews in Swahili by native Kenyan researchers minimized the risk of misinterpretation of responses and maximized the probability of honest responses.

Broadly, the current work supports a need to respect and include the ecocentric perspective (Watts, Custer, Yi, Ontiri, & Pajaro, 2015) of indigenous Maasai peoples in any balanced approach to lion management alongside cultural and livelihood sustainability. Unanimous agreement among pastoralists, that solutions must be found to allow the coexistence of people and lions, suggests that the inclusion of pastoralists in the decision-making and governance of human–lion conflict could be extremely beneficial. We hope that this evidence will prevent future allusions to 'indiscriminate' retribution against lions for the depredation of livestock by all carnivores. In further work, we aim to determine the Maasai pastoralists' attitudes towards the potential success of various strategies to mitigate against livestock depredation and retaliatory killings. We also aim to use participatory focus group outcomes to help understand sources of geographical variation in the probability of lion-killing, including differences in the availability and consistency of compensation or consolation schemes; climatic differences; difference in wealth and existence of alternative livelihoods; and differences in livestock husbandry.

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AUTHORS' CONTRIBUTIONS

E.O. and D.H. conceived the research and analysis. M.O., A.K., and P.K. assisted the data collection and synthesis. L.R. and T.C. advised on context edited the manuscript. E.O. and D.H. analysed the data and wrote the manuscript. All authors read and approved the final version of this paper.

CONFLICT OF INTEREST

Nothing to declare.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository http://doi.org/10.5061/dryad.qd504d9 (Ontiri et al., 2019)

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