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Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania

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Abstract

The African lion *Panthera leo*, spotted hyena *Crocuta crocuta* and leopard *Panthera pardus* are all killed in retaliation for livestock predation, but each species suffers differently from these impacts due to differences in predatory behavior and cultural attitudes of pastoralists. Using detailed data on livestock predation in the Maasai steppe landscape in Northern Tanzania, I investigated how prey preference, location and timing of livestock attacks contributed to the vulnerability of lions, leopards and spotted hyenas to retaliatory killing. Lions mostly preyed upon adult cattle and donkeys. In contrast, hyenas and leopards primarily killed small stock (goat, sheep and calves) and dogs. Hyenas and leopards mostly attacked livestock at night, whereas lions often attacked grazing livestock during the daytime. These behaviors made lions the most vulnerable to direct retaliatory killing, although some villages specifically targeted hyenas with poison, and the cultural traditions of pastoralists also exacerbate the retaliatory killing of lions. I highlight the complex interactions of social (human) and ecological dimensions of livestock predation and retaliation against predators. Any conservation intervention should strive to address human–carnivore conflicts at the appropriate social scale.

Introduction

Many ecological, biological and anthropogenic factors operate independently or interactively to cause the global decline of carnivore species (Purvis *et al*., 2000; Cardillo *et al*., 2004, 2005; Shivik, 2006). In mammals, species with slow life histories (smaller litters, slow growth rates, late sexual maturity), complex social structure, large home ranges, large body size and lower population densities are more vulnerable to population declines (McKinney, 1997; Purvis *et al*., 2000; Fisher, Blomberg & Owens, 2003; Cardillo *et al*., 2004). However, the most urgent threats to large mammalian carnivores result from human population growth and the associated impacts from habitat degradation, extirpation and disease (Fuller, 1995; Forester & Machlis, 1996; Nowell & Jackson, 1996; Weber & Rabinowitz, 1996; Kissui & Packer, 2004). Habitat loss and human population growth caused range contraction and the decline in grizzly bears *Ursus arctos horribilis*, gray wolves *Canis lupus* and mountain lions *Puma concolor* in Northern America (Clark, Curlee & Reading, 1996; Laliberte & Ripple, 2004). In Africa, habitat fragmentation and persecution by humans is linked to the disappearance of wild dogs *Lycaon pictus* and to the decline in cheetah *Acinonyx jubatus* and lions *Panthera leo* in most of their historical ranges such that current populations are largely restricted to isolated reserves (Woodroffe, 2001; Ogada *et al.,* 2003; Patterson *et al*., 2004; Packer *et al.,* 2005).

Conflicts caused by livestock predation lead to retaliatory killing of large carnivores. This is perhaps the most serious threat facing large carnivores amidst the ever-expanding human population. Most protected areas are too small to support wide-ranging carnivores. Such species must utilize adjacent dispersal areas for supplementary food (Woodroffe & Frank, 2005). Conflict-related mortality can be so high that reserve border areas could represent population sinks through an 'edge effect' (Woodroffe & Ginsberg, 1998; Macdonald & Sillero-Zubiri, 2002; Kolowski & Holekamp, 2006).

Livestock predation can cause significant economic losses among pastoralists. For example, Patterson *et al*. (2004) estimated livestock predation to represent 2.6% of the herd's economic value in a Kenyan ranch which incurred a loss of ~$8749 per annum. Similarly, Mishra (1997) reported an economic loss of $15 418 due to predation among the Indian-trans Himalayan communities equivalent to $128 loss per family per year, and Butler (2000) recorded economic loss averaging $13 or 12% of each household's net annual income in Zimbabwe. Due to such losses and sometimes due to perceived dangers, pastoralists have had a long

history of intolerance against large carnivores (Sillero-Zubiri & Laurenson, 2001). For example, the governments in Massachusetts Bay and Virginia paid bounties for wolf scalps in the 1630s, and many wolves were killed such that by 1850s, wolves were rare in the eastern USA (Dunlap, 1988). Red foxes in the UK are deliberately killed by farmers due to perceived threat to livestock (Baker & Macdonald, 2000). However, conservation efforts can be improved by raising the tolerance of pastoralists for wild carnivores through educational and economic incentives (e.g. cheetah on sheep ranches in Namibia) (Marker, Mills & MacDonald, 2003).

In regions with widespread livestock predation, pastoralists retaliate by indiscriminately killing predators (Woodroffe, 2001; Polisar *et al*., 2003; Treves & Karanth, 2003; Kolowski & Holekamp, 2006). While several studies have documented retaliatory killing of African carnivores (e.g. Ogada *et al*., 2003; Patterson *et al*., 2004; Kolowski & Holekamp, 2006), no previous study has empirically compared the relative vulnerability of sympatric carnivore species to retaliatory killing. I therefore investigated and compared how predation on different types of livestock, location and timing of livestock attacks contributed to the vulnerability of lions *P. leo*, leopards *Panthera pardus* and spotted hyenas *Crocuta crocuta* to retaliatory killing in the Maasai steppe, Northern Tanzania.

Lions are social carnivores living in territorial groups, but individual lions can capture prey twice their size. Lions can survive on a broad range of prey species that vary between habitats (Hayward & Kerley, 2005). Their most common prey are wildebeest *Connochaetes taurinus*, zebra *Equus burchelli* and buffalo *Syncerus caffer* (Schaller, 1972; Mills & Shenk, 1992; Scheel, 1993; Funston, Mills & Biggs, 2001; Kissui & Packer, 2004), and warthog (Scheel & Packer, 1991). Although lions are most active at night, they frequently hunt during the day (Schaller, 1972).

The spotted hyena is also a social carnivore living in territorial groups called clans (Kruuk, 1972). The main prey for hyenas includes wildebeest, zebra and Thomson gazelle *Gazella thomsonii* (Kruuk, 1972; Höner *et al*., 2002). Spotted hyenas are flexible in their behavior; they are active both during the day and at night (Kruuk, 1972; Frank, 1986). They are highly adapted to human settlement and do not appear to be afraid of humans especially at night (Kolowski & Holekamp, 2006, pers. obs.). Boydston *et al*. (2003) studied space use by spotted hyenas in Kenya and concluded that hyena behavior changed in response to human activities and suggested such plasticity conferred advantages in human-dominated environments.

Leopards are widely distributed; occupy a broad variety of habitat from forest to desert (Mizutani & Jewell, 1998) and they seem to do better in human-dominated areas than lions and hyenas (Nowell & Jackson, 1996). Leopards exhibit remarkable behavioral plasticity in terms of habitat selection, activity patterns and prey selection; they can adapt to a range of environmental and anthropogenic factors such as changes in prey base and land use (Woodroffe, 2000; Marker & Dickman, 2005).

The three carnivore species (lion, leopard and hyena) are sympatric in the Maasai steppe landscape and they all engage in livestock predation. I hypothesized that the species that killed the most livestock (and especially the most valuable livestock) would suffer the most retaliatory killing and that vulnerability to retaliation would depend on the location and time of day of livestock predation. Traditionally, the Maasai engage in ritual lion (but not hyena and leopard) hunts called *Ala-mayo* to express bravery and rite of passage to adulthood (Ikanda & Packer, in press). *Ala-mayo* features organized hunting parties mostly by young morani warriors. However, *Ala-mayo* is outlawed by the Tanzanian wildlife laws, and although it is still practiced, it is less common in the Maasai steppe. In the course of the study, every effort was made to verify livestock predation events and the associated incidences of retaliatory killing of predators.

Social–ecological systems such as the Maasai steppe are complex such that successful conservation outcomes are compromised by mismatches between social and ecological scales (Cumming, Cumming & Redman, 2006; Slotow & Hunter, 2008). Understanding how scale influences the nature of social–ecological system interactions enhances conservation outcomes (Cumming *et al*., 2006). Besides examining the context in which different species of predators are differentially vulnerable to retaliation due to livestock predation, I assess the social scale of decision making in retaliation and evaluate its significance in the success of large carnivore conservation.

Study area

The study was conducted in the Maasai steppe in Northern Tanzania (Fig. 1), one of East Africa's most important wildlife areas with large numbers of migratory ungulates, elephants *Loxodonta africana*, lions, leopards, cheetahs *A. jubatus*, hyenas and wild dogs *L. pictus*. Tarangire (2800 km^2) and Manyara (330 km^2) National Parks are the core protected areas within the Maasai steppe, which covers a total area of $>25\,000$ km^2 (Borner, 1985; Prins, 1987) (Fig. 1). The wildlife move seasonally between the National Parks and the adjacent dispersal areas (Fig. 1): during the dry season (June–November), the migratory species remain inside protected areas but move into dispersal areas outside protected areas (in communal village lands) for most of the wet season (November–May) (Lamprey, 1964; Kahurananga, 1981; Kahurananga & Silkiluwasha, 1997; TMCP, 2000).

The Maasai steppe contains the fourth largest lion population in Tanzania, but the two core protected areas only cover ~10% of the entire ecosystem. Hyenas and leopards are very common throughout the Maasai steppe, although their population sizes are unknown. The study area spans Monduli and Simanjiro districts in Arusha and Manyara regions, respectively. Maasai is the predominant ethnic group in Monduli and Simanjiro districts. They keep indigenous zebu cattle *Bos indicus*, small stock (sheep and goats) and donkeys, and most households have domestic

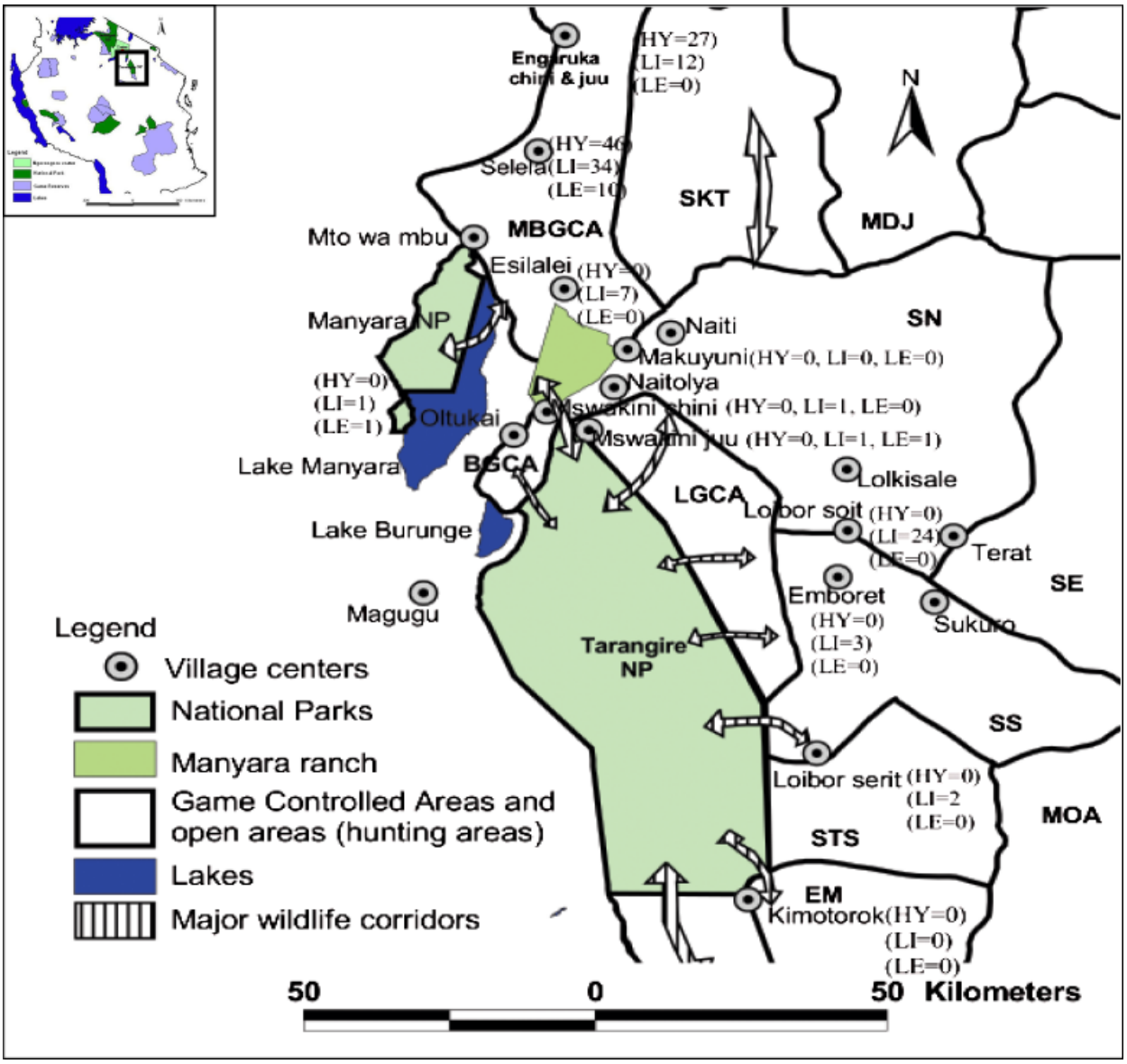

Figure 1 Map of the Maasai steppe showing Tarangire NP, Manyara NP and the surrounding village and hunting areas. Names of hunting areas shown: EM, East Mkungunero; STS, Simanjiro; MOA, Masai open area; SS, Simanjiro south; SE, Simanjiro east; SN, Simanjiro north; LGCA, Lolkisale game-controlled area; BGCA, Burunge game-controlled area; MBGCA, Mto wa mbu game-controlled area; SKT, Kitumbeine; MDJ, Monduli juu. Major wildlife corridors are mapped according to studies by Kahurananga & Silkiluwasha (1997); TMCP (2000). The number of predators killed due to retaliation in surveyed villages is shown in parentheses (HY, hyenas; LI, lions; LE, leopard). Insert is a map of Tanzania.

dogs (Sachedina, 2006). Other ethnic groups are Waarusha and Barbaig. While Barbaig have been in the Maasai steppe for many decades, most Waarusha have immigrated into the area from nearby towns, and they mostly engage in small-scale agriculture and livestock keeping.

An estimated 350 000 pastoralists inhabit the Maasai steppe, with about one million indigenous zebu cattle (Nelson, 2005; Sachedina, 2006). The human population growth is 4% for Arusha and 3.8% for Manyara regions for the inter-census period between 1988 and 2002 (Tanzania Population & Housing Census, 2002).

Figure 1 shows three types of protected areas in the Maasai steppe: National Parks have the highest level of wildlife protection and are patrolled by staff from the Tanzanian National Parks (TANAPA). Game-controlled areas and Open areas extend to village lands. Game-controlled areas are semi-protected by the wildlife laws, but authorities allow consumptive utilization through licensed trophy hunting and livestock grazing. Open areas are not protected by law, except for the requirement that all trophy hunting be licensed by the Tanzanian wildlife division. Lions, hyenas and leopards are all trophy-

Table 1 Percentage of livestock attack events by lions, hyenas *Crocuta crocuta* and leopards *Panthera pardus* classified by verification method in 12 villages during 2004 to July 2005 (see text for details)

		Verification method					
		Site visit		Herder/owner interview		Third party	
Village name	No. of events	*n*	%	*n*	%	*n*	%
Emboreet	72	13	18.06	52	72.22	7	9.72
Engaruka chini	41	9	21.95	30	73.17	2	4.88
Engaruka juu	13	3	23.08	8	61.54	2	15.38
Esilalei	29	6	20.69	20	68.97	3	10.34
Kimotorok	5	1	20.00	4	80.00	0	0.00
Loboir siret	5	2	40.00	1	20.00	2	40.00
Loibor soit	56	12	21.43	39	69.64	5	8.93
Makuyuni	14	2	14.29	10	71.43	2	14.29
Mswakini chini	8	3	37.50	5	62.50	0	0.00
Mswakini juu	11	3	27.27	7	63.64	1	9.09
Oltukai	47	9	19.15	33	70.21	5	10.64
Selela	95	18	18.95	67	70.53	10	10.53
Total	396	81	20.45	276	69.70	39	9.85

hunting species (Msoffe, 2003; Rodgers, Melamali & Nelson, 2003).

Methods

I recruited and trained 15 people, consisting of one to two persons resident in each of the 12 study villages across the Maasai steppe (Fig. 1) to maintain a detailed record of incidents (events) of livestock predation by lions, hyenas and leopards from January 2004 to July 2005. I presented a series of photographs of the targeted carnivore species to test the ability of incident recorders to discriminate between carnivore species. Lions, leopards and hyenas are the most common large carnivores in the Maasai steppe that engage in livestock predation (cheetah and wild dogs are very rare and only occasionally prey upon livestock). The three major species are well known by local language as *Orng'atuny* for lion, *Lugwaruu-kerii* for leopard and *Orngo'jine* for hyena. All assistants could accurately distinguish cheetah from leopard through morphology and behavior, and correctly described cheetah as primarily occupying open/sparsely wooded grassland and mostly attacking livestock during the day, while leopards reside in thicker wooded areas and attack livestock at night in bomas. A Maasai boma typically consists of several mud huts (homesteads) surrounding a central cattle enclosure (Supporting Information Plate S1), and each homestead may have a separate enclosure for their family's goats, sheep and calves. These shelters generally consist of wooden walls plastered with mud and cow dung. Other ethnic groups configure their households around a single homestead with a smaller cattle enclosure and/or a shelter for smaller stock. In either case, livestock enclosures are typically made from thorn bushes and occasionally from wooden poles. The boma walls averages 1.5 m high and 1–1.5 m thick. Livestock is taken out to grazing fields in the morning hours, between 08:00 and 10:00 h, and returned to bomas around 18:00 h. At night, livestock is kept in the bomas.

A livestock attack event was defined as an incident in which a predator killed or injured one or more livestock. Therefore, several livestock could be attacked in a single event. Livestock attacks were verified in two ways (Table 1). About 20% of attack events were verified by visiting the attack site (mostly at the bomas), while about 70% were confirmed in interviews with livestock herders/owners <24 h of the attack. The remaining 10% were recorded during interviews with a third person, therefore representing a less certain source of information. However, there is no compensation for livestock attack losses in Tanzania, so there is no incentive for intentional misrepresentation. Thus, the true extent of livestock attacks is probably underreported.

I revisited each village at fortnightly intervals to collate attack-event information and to interview affected livestock owners for detailed information and verification. Information recorded for each event included the type and number of livestock attacked, the location and context of the attack, whether the attack resulted in fatality or injury, the name of the livestock owner, the person responsible for the livestock at the time of the attack, the species, age and sex of the predator, and the response to the attack by the livestock owners/herdsmen and the general community. Retaliatory killings were carried out by many individuals up to 100 people from several communities (Supporting Information Plate S2).

Potential sources of bias

Although most studies of human–wildlife conflict have used similar techniques (e.g. Kolowski & Holekamp, 2006; Van Bommel *et al.*, 2007; Woodroffe *et al.*, 2007), these surveys suffer from three potential sources of bias. First, the

Tanzanian government does not compensate for losses to predation, so pastoralists lack incentive to report livestock losses, leading to a likely underestimate of the true extent of predation. Secondly, Maasai warriors engage in ritual lion killing, *Ala-mayo*, so it is possible that some of the lion killings might have been motivated by culture rather than retaliation. However, the ease and consistency with which livestock predation could be verified makes it very unlikely that reports of lion attacks were exaggerated. Ikanda (2006) was able to distinguish retaliation from *Ala-mayo* in the nearby Ngorongoro Conservation Area (which serves as a well-known destination for young Maasai warriors seeking an opportunity to kill a lion). In contrast, the Maasai in the Maasai steppe relied on livestock attacks as an opportunity for *Ala-mayo* rather than fabricated lion attacks to justify *Ala-mayo*. Third, survey respondents generally bias their memory toward recent events, so all analyses were specifically restricted to the most recent events. Note, though that the attack-events verification and follow-up interviews further improved the quality and reliability of the data collected for this study.

Data analyses

I used the χ^2-test to test the observed frequency of predation on different types of livestock and contexts of livestock attack events by the three carnivores. The differences in livestock predation between lions, hyenas and leopards were calculated according to the number of attack events on each type of livestock (because multiple prey may be captured in a single event). The lack of reliable information on total prey abundances precluded the determination of the actual prey preferences for each carnivore species.

I used the Wilcoxon (Rank sums) test to compare predation between the wet season (November–May) versus dry season (June–October). Spearman's correlations were used to examine the relationship across villages between the numbers of attacks on livestock versus the number of predators killed. All statistical tests were performed using SAS 9.1.

In assessing the probability and nature of pastoralists' responses to livestock predation, I defined retaliation as the active pursuit of a predator by organized hunting parties using weapons such as spears and arrows within 1 day of an attack event. This definition excludes occasions where poison was used to target predators. Under this definition, there was 100% probability of retaliation against lions ($n = 99$ attack events), but no retaliation against hyenas ($n = 231$) and leopards ($n = 66$).

Results

Impact of predation

Figure 2 shows the estimated loss of cattle, goats and sheep to predation compared with other causes of livestock loss in 38 well-studied bomas. Each boma contained an average of 198.27 ± 293.25 SD cattle (range 15–1500) and 240.38 ± 240.61 SD goats plus sheep (range 35–1000). Compared with predation, the impact of disease was >10 times greater for cattle and >5 times higher for goats and sheep.

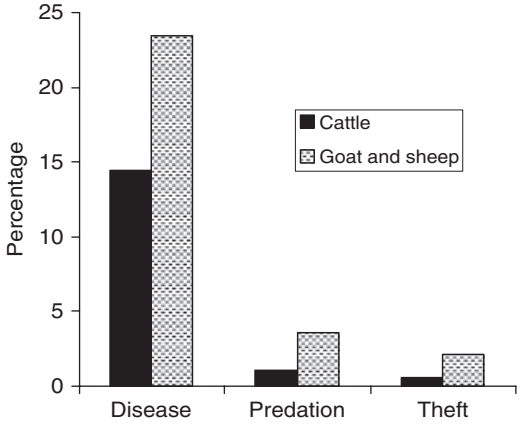

Figure 2 Major causes of cattle *Bos indicus*, goats and sheep losses in the Maasai steppe during 2004 to July 2005

Table 2 Number of attack events on different type of livestock by lions, hyenas *Crocuta crocuta* and leopards *Panthera pardus* over a period 2004 to July 2005

	Cattle	Goat and sheep	Donkey	Calf	Dogs	Baby goats and Sheep	Total
Lion	58	20	16	4	1	0	99
Hyena	9	186	18	12	4	2	231
Leopard	0	59	0	3	3	1	66
Total	67	265	34	19	8	3	396

Livestock predation tactics by lions, hyenas and leopards

A total of 396 attack events were reported on cattle, goats/sheep, donkeys and dogs during the 19-month study period: 58% ($n = 231$) were by hyenas, 25% ($n = 99$) by lions and 17% ($n = 66$) by leopards. Table 2 presents the number of attack events according to the type of livestock. Lions attacked an average of 1.7 cattle per event (range 1–6), 1.8 calves (range 1–3), 4.5 goats and sheep (range 1–16), 1.3 donkeys (range 1–3) and 1 dog. Hyenas attacked an average of 1.2 cattle (range 1–2) per attack event, 1.3 calves (range 1–2), 4.1 goats and sheep (range 1–50), 1.2 donkeys (range 1–4) and 4 dogs. Leopards attacked an average of 1.7 calves (range 1–3) and 2.3 goat and sheep (range 1–10) per event and 3 dogs.

The three carnivore species showed a significant difference ($\chi^2 = 190$, d.f. = 6, $P < 0.0001$, $n = 385$) in the number of attack events on each type of livestock (excluding dogs and baby goats and sheep because of small sample size). Lions mostly preyed on cattle, whereas hyenas and leopards

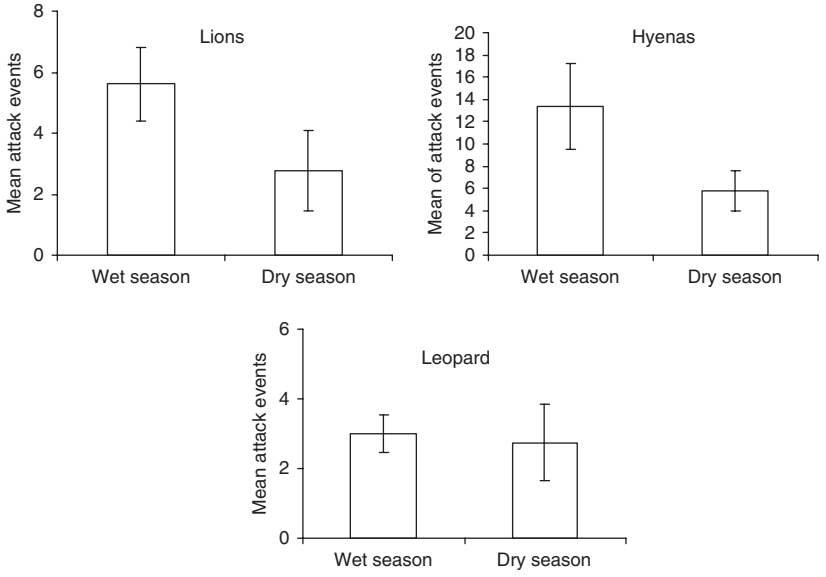

Figure 3 Seasonality of attack events on livestock by lions, hyenas *Crocuta crocuta* and leopards *Panthera pardus* in 12 villages. Values indicate village averages each season ± SE.

mostly took goats and sheep. Of the 67 attack events on cattle, 87% were by lions, 13% by hyenas and none by leopard. Hyenas were responsible for 70% of the 265 attack events on goat and sheep; 22% were by leopard and only 8% by lions. Hyenas also attacked the majority of calves, and hyenas and lions took similar numbers of donkeys. Leopards and hyenas were the primary predators on domestic dogs.

The larger wild herbivores move into dispersal areas outside the National Parks in the wet season (Lamprey, 1964; Kahurananga, 1981; Kahurananga & Silkiluwasha, 1997; TMCP, 2000), and lions attacked livestock significantly more often in the wet season than the dry season [Wilcoxon's (Rank sums) test, $z = 2.3395$, $P = 0.0193$, $n = 12$ villages] (Fig. 3), as did hyenas, although this difference was not statistically significant ($z = 1.5725$, $P = 0.1158$). Leopards attacked livestock at a similar rate in both seasons ($z = 1.2004$, $P = 0.2275$). Subsequent to the conclusion of this 19-month study, additional data over a 3 years period confirmed these seasonal patterns of livestock predation.

Context of livestock attack events

Livestock predation occurred in three distinct contexts: (1) while kept in bomas (enclosures) at night when lions and hyenas typically break through boma walls, while leopards can leap over short walls. In addition, lions either force their way inside or stampede the livestock, causing breakage of the boma walls; (2) in the grazing field during the day; (3) when separated from the herdsmen ('lost'). Comparing attacks in bomas versus grazing sites (the third category, 'lost' was excluded because of small sample size) lions were more likely to attack grazing livestock during the day while hyenas and leopards mostly attacked livestock at night ($\chi^2 = 48$, d.f. = 2, $P < .0001$, $n = 374$) (Fig. 4).

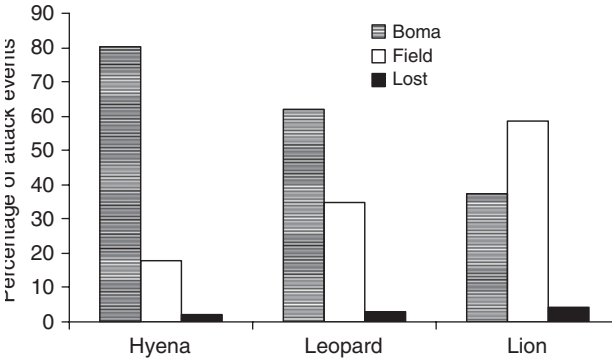

Figure 4 Principal contexts of livestock predation by lions ($n = 99$), hyenas *Crocuta crocuta* ($n = 231$) and leopards *Panthera pardus* ($n = 66$).

Livestock predation and retaliatory killing of predators

During the 19-month study period, 85 lions were killed in the 12 villages (mean 7.08 ± 10.81 SD, range 0–34 per village). Across villages, the number of lions killed was positively correlated with the number of cattle attack events by lions (Spearman's correlation, $r_s = 0.6385$, $P = 0.0254$, $n = 12$). Similarly, the number of lions killed was positively correlated with lion attack events on goats/sheep, although this relationship was not quite significant ($r_s = 0.5351$, $P = 0.0730$, $n = 12$) (Fig. 5). The sample size for hyenas and leopards were too small to test statistically. Hyenas were killed in a non-traditional manner: an estimated 71 hyenas were reported to have been poisoned in three villages (Engaruka juu, Engaruka chini and Selela); no other village was successful in killing hyenas. Only two villages successfully killed leopards: one leopard was killed in Oltukai village and another 10 in Selela village (Fig. 5).

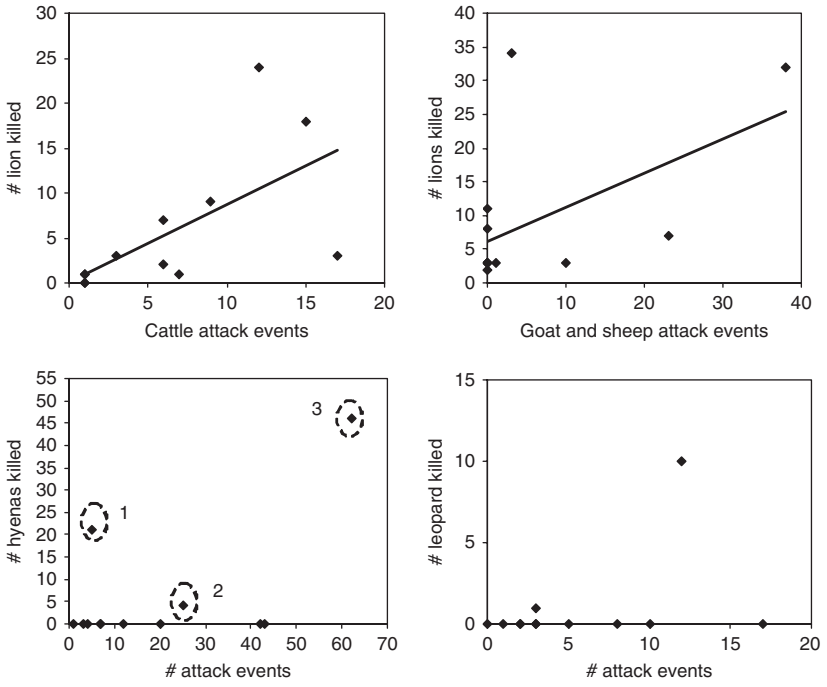

Figure 5 Relationship between the number of lions, hyenas *Crocuta crocuta* and leopards *Panthera pardus* killed by pastoralists in each village and the associated number of livestock attack events by each predator. Dotted circles indicate three villages (1 = Engaruka chini, 2 = Engaruka juu and 3 = Silale), which reported using poison against hyenas. The relationship for lion killed versus cattle attacks and lion killed versus goats/sheep attacks are shown with regression lines.

Discussion and conclusion

Impact of predation

In the Maasai steppe, disease claimed far more livestock than predation, yet the impact of predation was clearly high enough to provoke pastoralists into retaliating against lions, hyenas and leopards. In their review of livestock predation worldwide, Graham, Beckerman & Thirgood (2005) reported losses ranging from 0.02 to 2.6% per year. While the annual loss to predation of 1% for cattle in the Maasai steppe is comparable to other studies, the 4% loss for goats and sheep is relatively high. Kolowski & Holecamp (2006) reported an annual loss of 0.6% for cattle and 0.2% for goats and sheep in the Maasai Mara, Kenya. Patterson *et al*. (2004) reported annual losses of 2.4% for all livestock in ranches in south-eastern Kenya, and Butler (2000) reported 5% losses in Zimbabwe's Gokwe community lands.

Livestock predation tactics

Lions, hyenas and leopards showed divergent predatory behavior toward livestock with regard to the type of prey they attacked, time of day, season and site of livestock attacks. Lions generally captured cattle and donkeys, reflecting their preference for large prey in wildlife areas (Schaller, 1972; Kingdon, 1997; Kissui & Packer, 2004). In contrast, hyenas and leopards both attacked small stock (goats, sheep and calves) and dogs. Similar contrasts between the three carnivore species were recorded by Patterson *et al*. (2004) and, Kolowski & Holekamp (2006). Hyenas and leopards were mostly nocturnal in attacking livestock (as also noted by Kolowski & Holekamp, 2006), whereas lions frequently attacked grazing livestock during the daytime.

Livestock predation by lions and hyenas are more prevalent in the wet season while leopard attacks do not differ between seasons (Fig. 3). The wet-season migration of wild prey from protected areas onto communal village land (Lamprey, 1964; Kahurananga, 1981; Kahurananga & Silkiluwasha, 1997; TMCP, 2000) would be expected to decrease livestock predation if predators resided in these areas all year round. There are no estimates of resident predator populations in the communal village lands, but recent studies have suggested an overall decline in abundance and diversity of wildlife species in the Maasai steppe (e.g. Rodgers *et al*., 2003; Nelson, 2005) due to unsustainable harvests and deteriorating habitat. Lions are known to follow concentrations of migratory prey (Schaller, 1972), while hyenas commute over long distances during foraging trips (Kruuk, 1972). It is possible that the movement of lions and hyenas from National Parks into communal village lands lead to increased opportunities for livestock predation in the wet season. The lack of seasonal variation in leopard predation might suggest that leopards' propensity for attacking livestock remains unchanged with the presence of migratory prey. However, additional research is clearly needed to determine whether any of these three predators shows a consistent preference for wildlife prey versus livestock.

In this study, a number of dogs were victims of predation; though Woodroffe *et al*. (2007) found that dogs improved livestock security both in the day-time grazing fields and in the bomas at night. However, Ogada *et al*. (2003) found that the presence of dogs was only associated with reduced lion predation on cattle but not on goats and sheep nor by

leopards and hyenas. In other parts of Maasailand, dogs did not reduce nocturnal livestock predation by hyenas and lions, nor did predation rates depend on boma height, transparency or thickness of thorn brush walls (Kolowski & Holekamp, 2006; Ikanda & Packer, 2008).

Social (human)–ecological contextualization of retaliatory killing of predators

Hyenas were the most frequent predators on livestock followed by lions and leopards. If pastoralists retaliated by killing predators according to the overall frequency of attack events, hyenas should be the most vulnerable to direct retaliatory killing. Instead, lions were exceptionally vulnerable to direct retaliatory killing compared with hyenas and leopards except when poison was applied to target hyenas. Several factors could contribute to this vulnerability: first, differences between predators in their livestock predatory behavior. Lions are more likely to defend a livestock carcass against humans, exposing themselves to frequent confrontations – which they inevitably lose. In contrast, hyenas are shy of people and run long distances immediately after a livestock attack event, moving well beyond the reach of humans; leopards are secretive, successfully hiding themselves after a livestock attack. Second, lions kill more cattle than hyenas and leopards; cattle have more value to Maasai pastoralists than the small stock typically attacked by hyenas and leopards, thus engendering more resentment against lions. The value of cattle referred here is not merely in monetary terms but also cultural. Cattle are the center of identity and the primary symbol of wealth and respect in the Maasai culture (Galaty, 1982). The loss of cattle arouses a much stronger emotional response than the loss of small stock.

With regard to the main reason to retaliate, clearly livestock predation by lions was the major drive toward retaliation (Fig. 5). All predation events by lions recorded during this study were followed by retaliatory lion hunts. The decision to retaliate against hyenas and leopards did not appear to be driven by livestock predation: if the three outlier villages are excluded in the analysis of hyena attack events (Fig. 5), the correlation is essentially flat. Although the impact of livestock predation occurred at the boma (household) level, retaliatory lion hunts involved many people in a community outside the affected family (Supplementary Material Plate S2). Therefore, there is a mismatch in scales at which predation by lions and retaliation against lions occurs. The confounding effect of Maasai culture and traditions related to *Ala-mayo* could explain this apparent mismatch in the scale of lion predation and the decision of pastoralists to participate in retaliatory lion hunts. The fact that 100% of predation events by lions were followed by retaliatory lion hunts confound a fair assessment of the alternative hypothesis that lion killing is driven by Maasai culture (*Ala-mayo*) and that livestock predation is used as pretext for lion hunting. Killing a lion with a spear is indicative of bravery (*Ala-mayo*) and has traditionally been used as a rite of passage to adulthood (Maddox, 2003, Ikanda & Packer, in press), greatly increasing the incentive to participate in a retaliatory lion hunt. Such cultural sentiment is not associated with hyenas or leopards. However, the illegality of *Ala-mayo* by the Tanzanian wildlife laws makes it less attractive for Maasai to organize frequent unprovoked lion hunting parties. Thus, livestock attacks by lions trigger a swift response by the Maasai, and most lion hunting parties in the Maasai steppe appear to be driven by livestock attacks by lions. The lions' behavior renders them relatively easy to locate and kill, further encouraging retaliatory lion hunts.

Maasai do not actively hunt hyenas and leopards in the same way as lions, instead only killing these species opportunistically, although poison seems to be the most effective strategy for targeting hyenas. Retaliatory responses against predators have been reported in some areas [e.g. Ogada *et al.* (2003) in Kenyan Maasai land], but not in others: Zimmermann, Walpole & Leader-Williams (2005) found that the propensity of Brazilian ranchers to kill jaguars was not related to the number of livestock lost.

This study highlights the social–ecological complexity of the livestock predation problem and the subsequent retaliatory killing of predators. The broader success for conserving carnivores in the Maasai steppe will depend on how the social drivers (such as *Ala-mayo*) are incorporated into an ecological framework (Cumming *et al.*, 2006; Slotow & Hunter, 2008). While improving livestock husbandry of individual households could potentially reduce predation, tackling social drivers will be more difficult. Specifically, issues related to *Ala-mayo* will require education and economic strategies that address attitudes and behaviors of the entire Maasai community.

Conclusion

This study provides insights into the dynamics of livestock predation among three large African carnivores and factors related to retaliatory killings. The following are possible approaches for effective long-term conservation of large carnivores in the Maasai steppe:

(1) Because livestock predation is an important motivation for killing predators, human–carnivore conflicts could be reduced by improving livestock husbandry. For example, well over half of all livestock attacks occurred at night while livestock were kept in bomas. All three predators were able to surmount the simple thorn brush/wooden barriers. Chain-link fencing can be purchased locally for the price of a few livestock, providing a cost-effective material for reducing the impact of large carnivores on pastoralists.

(2) Because lions are subject to retaliatory killing when they venture into communal lands, information on their spatial–temporal movements would identify important wildlife refuge areas. Incorporating such information into village land-use plans would help pastoralists to avoid herding their livestock in areas frequently utilized by lions.

(3) Community outreach programs by the Tanzanian wildlife authorities (TANAPA) and Wildlife Division hold great potential to promote carnivore conservation by incorporating

research findings and directly involving communities in conflict mitigation programs, primarily through improved livestock husbandry that promote livestock security and through social economic programs that provide incentives to promote carnivore conservation. In addition, outreach programs should strive to address human–carnivore conflicts and *Ala-mayo* at the appropriate social scale.

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Supporting Information

Additional Supporting Information may be found in the online version of this article

Plate S1. Design of a typical Maasai boma with several homesteads around a central thorn bush cattle corral where livestock from all homesteads are kept. Small stocks (goat, sheep, calves) are kept in separate small enclosures for each homestead. Each homestead owns a portion of the existing livestock herd.

Plate S2. Retaliatory lion hunting party following a lion attack on two cattle in a boma in Oltukai village in Jan. 2007.

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