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Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya

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Abstract

Lion depredations on livestock are largely responsible for their conflicts with humans and for the historic collapse of their geographic range. Understanding of patterns associated with such predation can be used to mitigate its effects and promote more stable coexistence of lions and humans. We analyzed attacks on livestock over a four-years period on two neighboring arid-land ranches adjoining Tsavo East National Park, Kenya. A total of 312 attacks claiming 433 head of stock were examined. Lions were responsible for 85.9% of the attacks; hyenas and cheetahs were the other predators responsible. Lions and hyenas attacked mainly cattle and did so at night, whereas cheetahs almost exclusively took smaller sheep and goats. There was no temporal autocorrelation of daily losses, suggesting that the attacks are independent events. Both number of attacks and number of stock killed showed significant seasonal differences, and their monthly totals correlated positively with precipitation. Intensified predation in the wet season differs from patterns of lion predation elsewhere but reinforces the pattern that large carnivores take more livestock when native prey are most difficult to find and kill. On average, wildlife attacks claimed 2.4% of range stock annually, and livestock represented ca. 5.8% of the diet of ranch lions. This predation represented 2.6% of the herd's estimated economic value, and cost the ranch $8749 per annum. Each lion cost ranchers approximately $290 per year in depredations.

Keywords: Lion; Predator; Conflict; Cattle; Kenya; Seasonality

1. Introduction

Across the globe, human activities have caused declines in carnivore population levels and contraction of their geographic ranges (Woodroffe, 2000). Even where carnivores are not directly persecuted, they are often vulnerable to incidental declines owing to their large area and energy requirements and hence small population sizes (Gittleman, 1993). However, it is their reliance on other animals for food that commonly brings carnivores into direct conflict with humans, especially in areas where native wildlife has been extirpated and replaced by domesticated stock (Ramakrishnan et al., 1999; Saberwal et al., 1994; Seidensticker et al., 1999). When carnivores attack humans and livestock, campaigns to eradicate them are inevitable (Seidensticker et al., 1999; Woodroffe, 2000; Young and Goldman, 1946). Understanding the circumstances surrounding carnivore attacks and mitigating them is a crucial issue for conserving and managing many apex predators (Frank, 1998; Herrero, 1985).

Few carnivores have suffered more dramatic reductions of range and population sizes than the lion (*Panthera leo*). Before humans colonized the Western Hemisphere, the lion was perhaps the most widespread terrestrial mammal, ranging from southern Africa to northern Europe, across all of Asia and North America, extending south as far as Peru (Kurtén and Anderson, 1980; Turner and Antón, 1997). Lions remained

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widespread into historic times, persisting in most of Africa, and parts of Europe and Asia. Recently, loss of habitat, shrinking prey populations, and direct persecution has resulted in dramatic contraction of their range and lions now persist in a small fraction of the area they occupied just a century ago (e.g., Kingdon, 1997). Lion populations can recover quickly if accorded adequate space and protection (Hunter, 1998; Stuart-Hill and Grossman, 1993), but this is seldom possible near human settlements because of the continual threat that lions pose to rural communities and their livestock (Frank, 1998).

Protected areas offer a potential solution to lion conservation but may fall short if they are too small or are surrounded by human populations (Woodroffe and Ginsberg, 1998). Kenya's largest park system, Tsavo (Tsavo East National Park and Tsavo West National Park), includes ca. 20,000 km^2 of arid savanna and is large enough to sustain viable populations of elephants, rhinos, lions, and many other species of wildlife (e.g., Armbruster and Lande, 1993). But because the parks' boundaries were drawn to exclude prior settlements in Voi and the Taita Hills, nearly 250,000 people now live on the park's borders, most in the central zone where they are virtually surrounded by wildlife populations (Fig. 1).

Conflicts between humans and wildlife in Tsavo are inevitable, given this geography. The Community Office of the Kenya Wildlife Service (KWS) and regional medical clinics compile these incidents. Analyses of them (Kusimba, in review) reveal that elephants (*Loxodonta africana*) cause the most complaints, mostly in raids on farms. Next are lions, which raid the livestock herds and occasionally also attack herders. Beside the human tragedies, such conflict may also cause environmental degradation – where predators make ranching grossly unprofitable, rangelands that support countless native species may be converted to sterile sisal plantations or herders may resort to snaring or poisoning of predators (Patterson, 2004a). More detailed information on the ecology and intensity of predation on livestock is key to developing strategies for conserving both carnivores and wildlands (Polisar et al., 2003).

2. Methods

2.1. Study area

This study was conducted in southeastern Kenya on Taita and Rukinga ranches, two privately held, neighboring properties that encompass 68,800 ha (690 sq km) along the Nairobi–Mombasa Highway (3°34′ to 3°53′S, 38°40′ to 39°02′E; Fig. 1). The ranches lie adjacent to the southwestern boundary of Tsavo East National Park (11,747 sq km) and are an integral part of the Greater Tsavo Ecosystem, which extends into neighboring

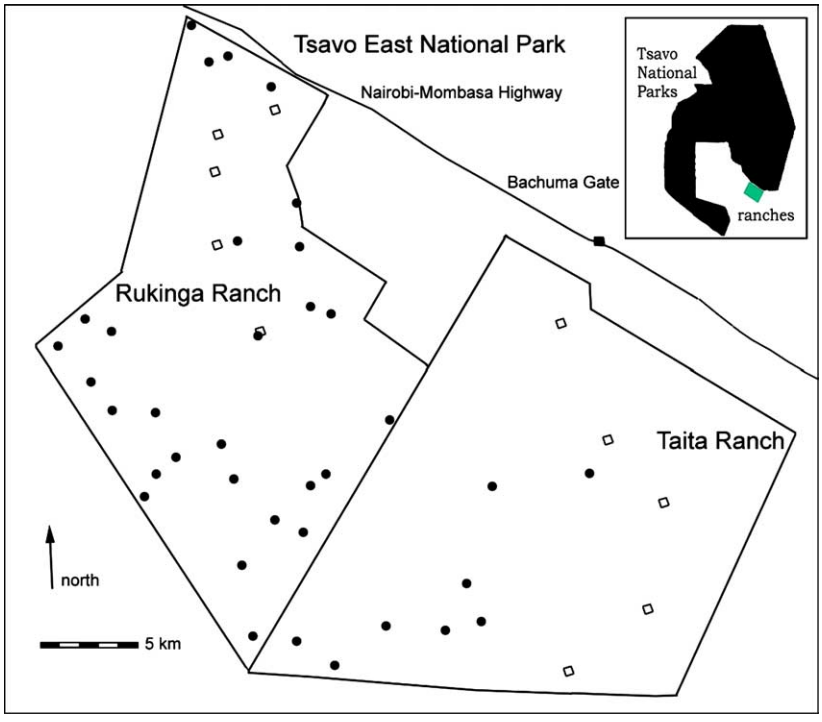

Fig. 1. Map of Rukinga and Taita Ranches, operated by the Galana Cattle Company between 1996 and 1999. The northern boundary of the ranches abuts the Nairobi–Mombasa Highway, and Taita Ranch (the eastern one) is directly opposite Bachuma Gate of Tsavo East National Park. Circles identify man-made excavations ("dams") that serve as seasonal reservoirs for rainwater, while diamonds identify concrete tanks that provided pipeline water.

Tanzania (e.g., Coe et al., 1999). The ranches support arid savanna woodland, with dense *Acacia–Commiphora* thickets in moister lateritic soils that give way to grassland and thorn-scrub in drier, sandier regions. Although the ranches lack permanent rivers or lakes, they contain scattered artificial reservoirs or dams, which hold seasonal rainfall through some or all of the extended dry season. In addition, during this study, 10 concrete tanks (8-m diameter) received water pumped from Mzima Springs, 100 km away in Tsavo West National Park, which broadened the foraging of livestock and also provided water to wildlife (Fig. 1).

2.2. Herd sizes and livestock attacks

The Taita and Rukinga ranches are now managed as part of a wildlife conservancy that serves as a buffer to the parks; today, only 500–1000 head stock both ranches. However, during 1996–1999 they were home to 4000–5000 head, mainly cattle, but also including goats and sheep as well as a few camels and donkeys. All belonged to the Galana Cattle Company, Ltd., which was under the management of Terrance Hopkins. Throughout the study period, livestock residing on the ranches were joined by transient herds brought into graze for a few weeks or months enroute to slaughterhouses in Mombasa. The dynamics of stocking limits the specification of herd sizes and their composition to annual totals derived by census and prevents calculating instantaneous predation rates. Ranch records indicate that the company had 5165 head in 1996, 4847 in 1997, 4261 in 1998, and 3990 in 1999. Declining prices of beef and rising prices of pipeline water for the tanks accounted for the secular decline in stocking rates (M. Prettejohn, personal commun.).

Attacks on livestock and losses to predators were observed and reported by herders, who tended stock in pairs, both day and night. At night, up to five herds each containing ca. 200 head were gathered into a *boma* or corral, where thorn enclosures and human attendants could protect livestock. Different bomas were used concurrently, each supervised by a man responsible for as many as 1000 head and 10 herders associated with his corral. Headsmen reported attacks to the ranch headquarters, which logged them under Hopkins' supervision. In all, 307 attacks reported between 1996 and 1999 included the originating *boma*, while 89 of these (29%) recorded the component herd. But because bomas were regularly relocated to maintain availability of water and forage, they could not be analyzed spatially, temporally, or by boma design.

Managers used several age–sex categories for their observations: calf, a nursling of either sex; weaner, a weaned animal less than a year old; heifer, a young cow that has had no more than one calf; cow, a female that has had two or more calves; steer, a castrated male; and bull, a breeding male. Analyses uncovered monthly variation in predation that suggested possible associations with climate. Accordingly, we assembled available local records for temperature and precipitation, collected at the ranch headquarters: rainfall totals by month for 1991–1992 and 1994–1998 and maximum and minimum temperatures for most days during 1998. Chi squared and Fisher exact tests were done with STATISTICA (StatSoft, 1997). Analysis of the temporal autocorrelation of the attacks were done with the autocorrelation function of SPSS (SPSS, 2001) in both daily and monthly intervals, with time lags of 365 days and 12 months, respectively. We plotted the correlations between monthly rainfall and temperatures vs. monthly attacks using the cross-correlation analysis of SPSS, and time lags of 0–6 months. Simple bivariate correlations were done with SPSS. Because assumptions of normality were not met by our temporal data, we used non-parametric tests whenever possible.

2.3. Livestock biomass and value estimates

Information on the weights and retail economic value of the various age-classes of livestock were obtained from butchers in Voi during March and April 2003. Their estimates of mass (all in kg) were: bulls, 167; steers, 75; cows, 71; heifers, 50; weaners, 30; calves, 20; goats and sheep, 16.3. Approximate food requirements of lions were derived from Schaller's (1972) estimates. Costs of pipeline water and estimates of sustainable losses of livestock were obtained from Michael Prettejohn, who currently manages the Galana Cattle Company.

2.4. Lion censuses

The number of lions living on the ranches during the study period is unknown. During 2002, censuses were undertaken of lions on Taita Ranch (38,800 ha or 56% of the property managed by Galana Cattle Company), in 10 12-day sessions throughout the year. Two vehicles cruised 30–70 km of tracks twice daily in two 4-h shifts that spanned the period from late-afternoon to mid-morning. Tracking, observation, radio-tracking, and acoustic playbacks were used to locate lions (Kays and Patterson, 2002; Ogutu, 1994). All lions seen were located, observed, individually distinguished by whisker patterns, coloration, and scars, and photographed.

3. Results

3.1. Number of attacks and livestock killed

The company logged 312 different attacks on its livestock over the four-years period: 69 during 1996, 103 during 1997, 85 during 1998, and 55 during 1999,

respectively corresponding to 22.1%, 33.3%, 27.2% and 17.6% of the four-years total. These attacks claimed the lives of 102, 146, 140, and 45 head of livestock, respectively, representing 23.6%, 33.7%, 32.3%, and 10.4% of the 433 killed; additional livestock were sometimes injured in these attacks (23, 13, 15, and 17 head, respectively), but those costs are ignored in the balance of this paper. Considering stocking rates over this period, each year attacks claimed the lives of 2.4% of all stock on the ranches: 2% in 1996, 3% in 1997, 3.3% in 1998, and 1.1% in 1999.

The marauding species was determined in all but 8 attacks, which together claimed 36 cattle in 1998. Three carnivore species were determined to be responsible for fatal and injurious attacks on livestock: lions accounted for 277 attacks (ranging from 83.5–95.7% of those annually), spotted hyena 16 (0–9.1%), and cheetah 9 (0–4.9%). Elephants were responsible for 2 (0–3.6%) fatal attacks, but these were aggressive assaults on cattle, not predation events, and are not considered further. Lion attacks claimed the lives of 372 livestock (70–97.1% of those annually), spotted hyena 14 (0–4.8%), cheetah 9 (0–3.4%), and elephants 2 (0–4.4%).

The timing of most attacks was unspecified, but records noted that 16 were daytime attacks and 42 took place at night. Lions ($n = 52$) and hyenas ($n = 4$) did not differ in their penchant for diurnal and nocturnal attacks (Fisher two-tailed exact probability = 1.0); three-quarters of the attacks by both species occurred at night. Records for 14 attacks (all in 1999) noted the sex and group size of the attacking lions: nine involved attacks by lone male lions, four by lone female lions, and one by a male–female pair.

The number of livestock taken in individual attacks varied from 0 to 13. Of 314 attacks producing injury or death, 24 (7.6%) caused only injuries, while a single victim died in 211 (67.2%) and two died in 50 others (15.9%). Lions averaged 1.36 victims per attack, and at least twice killed as many as six individuals. Attacks by hyenas and cheetahs typically claimed a single victim (averaging 1.07, and 1.0 individuals, respectively), but the three deadliest attacks – two claiming eight victims and one 13 – could not be attributed to predator species (''unknown'' attackers claimed 4.5 victims per attack). Differences among predators in livestock killed during attacks were significant (Median test: $\chi^2 = 8.95$, df = 3, $p = 0.0300$).

3.2. Prey selection

Carnivore species also differed in their selection of prey. We compared their attacks on goats and sheep (average adult weights 16.3 kg ± SD 4.9) with those on cattle (135.6 kg ± SD 59.1). Cattle were targeted in 266 of 277 (96%) attacks involving lions and 15 of 16 (94%) attacks by hyenas; these proportions did not differ significantly (Fisher two-tailed exact probability = 0.47). However, 8 of 9 (89%) attacks by cheetahs targeted goats or sheep. Lions and cheetahs differed significantly in targeted prey (Fisher two-tailed exact probability <0.0001). Combining sheep and goats with young cattle (calves, weaners, and heifers) and then comparing attacks on smaller stock with those on cows, bulls and steers, lions (116 attacks on small stock, 146 attacks on large ones) and hyenas (6,9) again did not differ significantly, while lions and cheetahs (9,0) did (Fisher two-tailed exact probability, $p < 0.001$).

3.3. Temporal patterning of attacks

Attacks over the four-year period claimed 1.4 animals per attack or about two head per week. The autocorrelation function values of daily lion predation events were marginally significant ($p < 0.05$) at a number of lag intervals. However, none of these correlation values were greater than ACF = 0.10 and therefore are probably not biologically significant. Monthly averages of lion attacks were not significantly autocorrelated at any time-lag interval. Thus, we considered lion attacks to be independent events across both daily and monthly time intervals.

There was substantial variation in the number of attacks and stock killed (Fig. 2). On average, attacks peaked in November and were high in January, April, and May – typically rainy-season months in the region's bimodal climatic regimen. We tested for correlation between temperature and precipitation with livestock attacks and kills over the 36 months (1996–1998) in which both data types are available. Marginal or significant positive rank-correlations were found between actual precipitation with both attacks ($r_s = 0.30$, $p < 0.08$; Fig. 4) and livestock killed ($r_s = 0.33$, $p < 0.05$), but neither measure of predation was correlated with average monthly precipitation ($r_s = -0.11$ and 0.15, respectively; $p > 0.1$), minimum temperature ($r_s = -0.2$, $r_s = -0.53$), or maximum temperature ($r_s = -0.33$, $r_s = -0.01$; all $p > 0.05$). Considering each year independently, the data for 1996 – the driest year – had the strongest relationship with rainfall ($r_s = 0.70$, $p < 0.0005$), while correlations involving the El Niño event of 1997 and 1998 were not significant ($r_s = -0.09$ and 0.05 respectively, $p > 0.1$). Evaluating potential time-lags between rainfall and predation events, we found no significant cross-correlations for lags of 1–6 months ($p > 0.1$).

3.4. Lion censuses

In 2002 surveys, 15 adults were identified on Taita Ranch, 7 males (3 with 3 prides, a pair, and 2 loners) and 8 females (all in prides; unpublished data), yielding

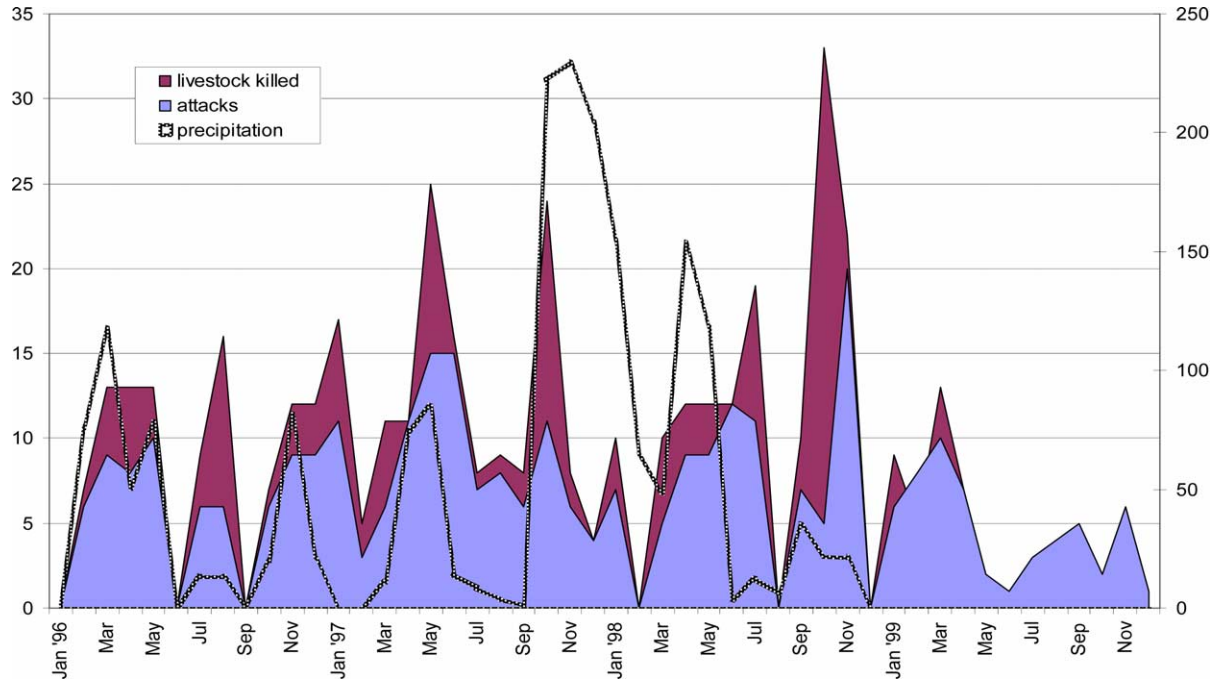

Fig. 2. Monthly plot of attacks and livestock killed over the 36-months span for which climate data (temperature and precipitation) are available. Both the number of attacks and number of livestock killed are positively correlated with monthly precipitation, although the former correlation is only marginally significant.

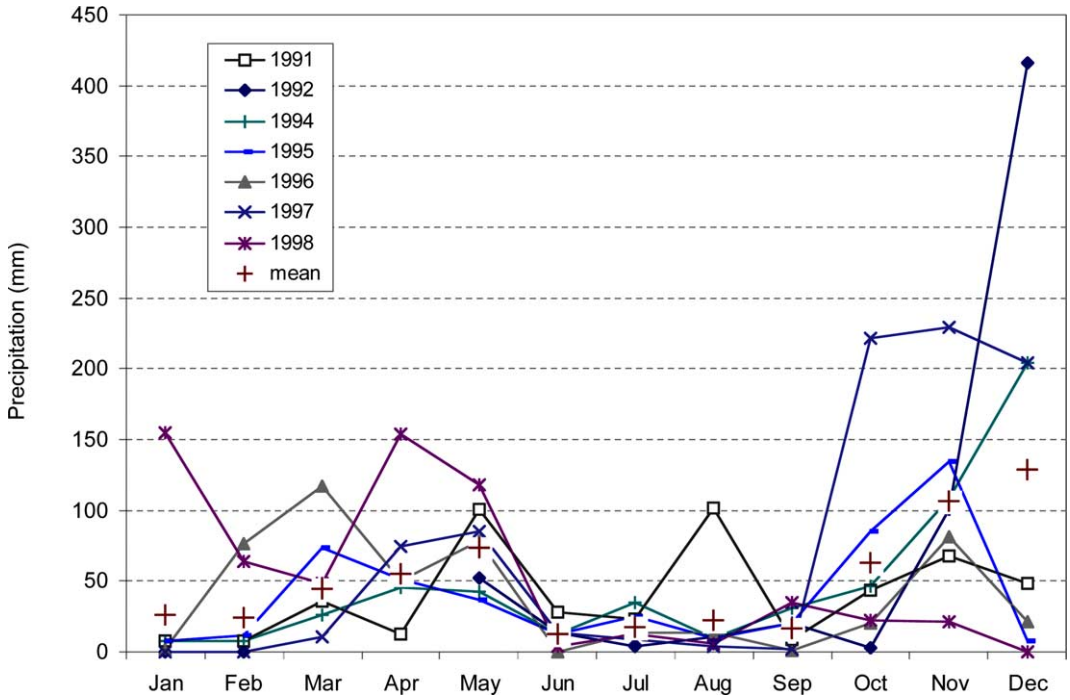

Fig. 3. Seven years of precipitation records for Taita Ranch, showing annual variation in monthly rainfall, pronounced increases in rainfall during the El Niño event, and the predictable four-month drought (June–September) each year. Changes in space-use behavior by lions and their native prey in response to this seasonal drought appear to trigger the increased rainy-season attacks.

a density of 0.04 adult lions per square kilometer. Surveys also documented spotted hyena (*Crocuta crocuta*), striped hyena (*Hyaena hyaena*), cheetah (*Acinonyx jubatus*), and leopard (*Panthera pardus*) on the ranches, but population estimates were not possible. If lion density remained constant between the study period and 2002,

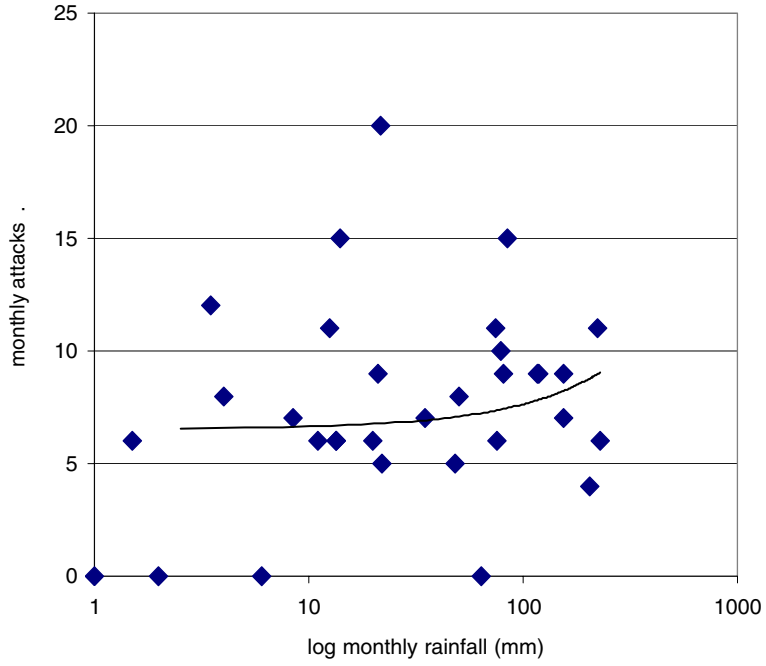

Fig. 4. Monthly rainfall (logged) vs. attacks on livestock for 36 months. The black line shows the marginally significant linear correlation ($r_s = 0.30$, $p < 0.08$). No non-linear or threshold relationships are obvious in these data.

as well as across Taita and Rukinga Ranches, roughly 26 adult lions would have utilized the properties during study years.

3.5. Ecological and economic significance

Over this study, lions and other wildlife averaged livestock attacks every 4 or 5 days and claimed 2.1 livestock weekly. Using local estimates of stock weight, the biomass lost in the four years of attacks can be estimated and allocated to species: lions, 19,694 kg; cheetahs, 150 kg; hyenas, 1187 kg; elephants, 146 kg; unspecified, 1919 kg. Our surveys suggest that the ranches supported a resident population of about 26 adult lions (12 males, 14 females). Using Schaller's estimates that males and females require 3813 and 2724 kg of live prey, respectively (Schaller, 1972), the 93 livestock taken annually by lions weighed 4924 kg, less than the amount needed by a single pair of lions consuming only livestock. The annual toll of livestock on the ranches represents 5.9% of the ca. 83,892 kg of prey needed by the estimated lion population. The tally of livestock killed by other predators is much smaller (Table 1).

Table 1
Attacks on livestock of the Galana Cattle Company, 1996–1999, by attacker and toll (numbers of individuals killed)

Livestock killed in attack	Lions	Hyenas	Cheetahs	Elephants	Unknown	Totals
0[a]	23	1	0	0	0	24
1	180	14	9	2	4	209
2	49	1	0	0	0	50
3	9	0	0	0	1	10
4	10	0	0	0	0	10
5	4	0	0	0	0	4
6	2	0	0	0	0	2
8	0	0	0	0	2	2
13	0	0	0	0	1	1
Total toll	277	16	9	2	8	312
Percentage	88.8%	5.1%	2.9%	0.6%	2.6%	100%
Average toll	1.36	1	1	1	4.5	1.41

[a] Tallies only those unsuccessful attacks that resulted in reports of one or more injured animals.

Table 2
Four-years tally of economic toll exacted by attacks on livestock, by attacker and livestock class

	Unit value (US $)	Lions	Cheetahs	Hyenas	Elephants	Unknown	Age-class total
Bull	$135.14	$1216 (9)	$0	$541 (4)	$0	$405 (3)	$2162
Steer	$94.60	$9082 (96)	$0	$189 (2)	$95 (1)	$189 (2)	$9555
Cow	$94.60	$9460 (100)	$0	$284 (3)	$95 (1)	$757 (8)	$10,595
Heifer	$94.60	$1230 (13)	$0	$189 (2)	$0	$757 (8)	$2176
Weaner	$67.57	$2297 (34)	$0	$0	$0	$0	$2297
Calf	$67.57	$6419 (95)	$68 (1)	$135 (2)	$0	$1014 (15)	$7635
Sheep	$16.90	$118 (7)	$118 (7)	$17 (1)	$0	$0	$254
Goat	$16.90	$304 (18)	$17 (1)	$0	$0	$0	$321
	4-year total	$30,127 (372)	$203 (9)	$1355 (14)	$189 (2)	$3122 (36)	$34,995
	% of total	86.1%	0.6%	3.9%	0.5%	8.9%	100.0%
	Annual cost	$7532	$51	$339	$47	$780	$8749

Numbers in parentheses represent numbers of individuals killed.

Livestock depredations can also be evaluated in economic terms. Table 2 tallies the representation of various age-classes among the victims and calculates associated economic costs. Calves, cows, and steers were most frequently lost in attacks and represented the largest components of economic loss. Lions were responsible for 86.1% of the total economic losses to all wildlife, estimated at $8749 annually. Thus, each adult lion cost the ranchers approximately $290 per year in depredations.

4. Discussion

4.1. Number of attacks

The attacks analyzed here represent occasions when lions and other predators attacked and injured or killed livestock. In virtually all of these cases, humans were attending these herds, overseeing their movements and foraging by day or defending their corrals at night. Vigilance in herd attendance and active defense are essential features of animal husbandry in East Africa. That herds can be maintained at all in the presence of large predators such as lions and spotted hyenas is a testament to the effectiveness and fearlessness of the herders, who do not hesitate to challenge groups of lions with nothing more than a spear, a knife, a firebrand, or even pots and pans. However, company data were not collected in a fashion that would enable us to analyze factors that contributed to effective herd defense.

Most timed attacks took place at night, when livestock are quartered in thorn stockades or bomas. In this region, bomas are constructed to control livestock, not to exclude predators (see also Frank, 1998), and are commonly no more than 1.5 m tall – it is the job of human attendants to confront and repel the predators (Patterson, 2004b). Most nocturnal attacks were by lions and hyenas, which are nocturnal even in protected areas (Mills and Biggs, 1993) and tend to become more strictly nocturnal outside them (Smithers, 1971). Although the timing of cheetah attacks was unnoted, diurnal attacks are probable (Caro, 1994).

Most documented attacks by ranch lions involved lone males (9 of 14 attacks; 64%), yet males comprised half (47%) of the adult lions documented in 2002 surveys on Taita Ranch. Nearby, 19 of 29 (66%) lions shot over the last decade near Voi (70 km NW of ranch headquarters) for attacking livestock or humans were males (Kerbis Peterhans and Gnoske, 2002). Often, ''problem lions'' tend to be young adults (3–5 years of age), often born within parks or other prime habitats, which have dispersed into game-poor areas where they become marauders (Patterson et al., 2003; Woodroffe and Ginsberg, 1998). However, it is not known whether males take livestock disproportionately to native prey in Tsavo, where lion social biology is poorly known. Males are frequent and successful hunters in the woodlands of South Africa (Funston et al., 2001) and are regularly observed hunting native prey in Tsavo. On the Laikipia Plateau of central Kenya, adult males comprise 66% of the animals culled annually in ranch control operations, but males and females appear equally likely to attack livestock (Frank, 1998).

Most wildlife attacks claimed only a single victim, and only lions were documented as taking more than two victims in an attack. The three costliest attacks – claiming 8, 8 and 13 victims – exceeded tolls for any attack here attributed to lions, but such attacks are otherwise well documented. On 6 June 2002, a lone lioness entered a boma outside of Voi and killed 54 goats in a single night (pers. obs.). Although it is tempting to attribute the costliest attacks in the dataset (which are unspecified) to lions, elephants or conceivably even rival humans might have been responsible. Spotted hyenas are common in the Tsavo area, but are generally seen in much smaller groups than in the Serengeti (Holekamp et al., 1997).

4.2. Prey selection

Prey selection by ranch predators was obviously biased by body size. Cheetahs differentially attacked smaller prey, and were the only carnivore to take more goats and sheep than cattle. In fact, the only *Bos* attacked and killed by a cheetah was a calf. This parallels their selection of native prey, mainly smaller antelopes (gazelles and impala) and even here preferring neonates and calves (Caro, 1994). The larger and more social hunters, lions and hyenas, attacked both large and small prey and at approximately equivalent frequencies. No records of leopard predation were recorded, although leopards occur on the ranches and probably claim some livestock there, as elsewhere (Mizutani, 1993).

Between 1994–1998, the Kenya Wildlife Service recorded 121 incidents near Voi involving carnivore attacks, including a fraction of these Galana Cattle Company incidents: 112 (93%) by lions, 4 (3%) by leopards, 2 (2%) by hyenas, and 3 (2%) by cheetahs (Kerbis Peterhans and Gnoske, 2002). These proportions are comparable to our findings, and likely reflect regional abundances of both predators and their native prey. Elsewhere in Kenya, rankings of depredations by these species differs substantially, so that in Masai Mara, for example leopards, lions, and hyenas accounted for 50.1%, 31.1% and 18.9%, respectively, of kills and injuries to livestock (Karani, 1994). In a three-year study in Zimbabwe, baboons were responsible for more than half of the 241 livestock kills (Butler, 2000).

4.3. Temporal patterning

Folk wisdom and anecdote mark the rainy season in Tsavo as one of heightened attacks on humans and livestock by lions and other predators (e.g., Hunter, 1952), but our study is the first to quantify a positive association of rainfall and attacks. Recently, Kerbis Peterhans and Gnoske (2002) found no evidence for a rainy-season increase in carnivore–human conflicts in the region near Voi. However, their conclusion rested on a smaller dataset (39% as many incidents) pooled over a longer time and larger area, used monthly averages for precipitation, and lacked analyses of variance. Annual variation in amounts and timing of rainfall in Tsavo make monthly averages poor predictors of biological responses over several years – we also found no correlation of predation with averaged values for precipitation or temperature. However, actual monthly rainfall over a 36-month period was correlated with both measures of predation intensity (Fig. 2), and correlations were particularly strong in the driest year (1996), before the anomalous El Niño event of 1997–1998. The differential strength of this relationship between years raises the possibility of non-linearity, and a threshold response by predators, although these are not obvious in our data (Fig. 4).

Contrary to prior studies, we found that lions are *more* likely to attack livestock after rains. In central and western Kenya, carnivores raid livestock more frequently during the dry season (Karani, 1994; Rudnai, 1979), and heightened dry-season risk characterizes stock-rearing in Zimbabwe (Butler, 2000) and other parts of East Africa. This pattern appears to rest on seasonal movements of native ungulates that alter prey availability for resident large predators. Mass migrations of native ungulates following vegetation stimulated by rains may leave non-migratory predators hungry in the dry season, and thus increase the vulnerability of resident livestock in Kenya's Masai Mara (Karani, 1994) and in the Kenyan central highlands (Rudnai, 1979).

In Tsavo, a four-month drought from June to September is predictable (Fig. 3) and most native species display adaptations to seasonal droughts (Patterson, 2004a). During droughts, lion prides in Tsavo spend most of their time near the few dependable water sources, where they can readily find and kill prey that also rely on these same water sources (Kays and Patterson, 2002). But, when seasonal rains fill ephemeral pools, prey disperse into the previously parched scrublands (Ayeni, 1975; Eltringham et al., 1999; Hunter, 1952) and lions must leave the reservoirs. If native ungulates scatter as soon as temporary pools become filled, there should be no lag between precipitation events and attacks on livestock, as would be expected if rainfall stimulated fast vegetative growth that in turn offered cover to ambush-dependent predators (Butler, 2000). Indeed, our cross-correlation analyses of monthly data identified no significant time lags.

Like other large carnivores, lions target livestock when native prey is inaccessible, whenever and wherever that may be. Availability may be governed by annual cycles as in the African cases cited or to human-caused depletion of prey populations (Singh and Kamboj, 1996). Varying intensity of livestock predation by large carnivores with availability of native prey has been documented spatially for big cats in Venezuela (Polisar et al., 2003) and temporally for carnivores in Zimbabwe (Butler, 2000), Kenya (Karani, 1994; Rudnai, 1979), and Europe (Meriggi and Lovari, 1996; Vos, 2000). Heightened attacks on livestock and humans may also result from altered cropping patterns in surrounding areas (Vijayan and Pati, 2002). For proper management, it is imperative that wildlife managers appreciate and understand regional variation in local ecological conditions and factors that influence livestock risk – an excellent study conducted in one region may be worthless for managing others.

Relationships between climatic factors and prey availability for lions vary widely between sites, and must be evaluated locally before livestock management plans can be adjusted to account for seasonal changes in

predation risk. Our analyses identified the onset of rains as a time of heightened vulnerability for livestock in Tsavo. Given the proximity of our ranches to meat-processing facilities in Mombasa, and the strongly seasonal pattern of loss, a seasonal stocking plan is suggested. By quartering stock only during dry-season months, and taking them to market before the annual rains, herders could harvest the annual grasses and herbaceous growth but avoid the majority of losses to predators. However, cattle could profitably be grazed only as long as the reservoirs held rainwater. Pipeline water to recharge depleted holding tanks now costs 50 times its value in 1990, rendering year-round maintenance of cattle currently impractical (M. Prettejohn, pers. commun.).

4.4. Ecological and economic significance

Estimates of lion population size and annual toll suggest that livestock comprise a small fraction of their annual diet, amounting to only 5.8%. Other prey taken by the ranch lions include zebra (*Equus burchelli and E. grevyi*), warthog (*Phacochoerus africanus*), giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), gerenuk (*Litocranius walleri*), oryx (*Oryx beisa*), buffalo (*Syncerus caffer*), and elephant. Maintenance of healthy populations of native ungulates on the ranches likely contributes to low levels of depredation on livestock (Polisar et al., 2003).

Annually, lions and other predators claimed 2.4% (1.1–3.3%) of the livestock on the ranches. Annual predation rates in the Tsavo area are comparable to those reported elsewhere for large felids in Kenya: Masai Mara, 0.4–1.6% (Karani, 1994); Laikipia, 0.8–2.0% (Mizutani, 1993); and Nairobi, <2.8% (Rudnai, 1979). Rates in Tsavo are certainly lower than the 12% reported for tigers in India (Madhusudan, 2003), but higher than in Zimbabwe, where lions claimed only ~1% of donkeys and cattle (Butler, 2000). Where overall mortality estimates for livestock are available, depredation rates on African livestock can be dwarfed by losses to disease and parasites. In the Masai Mara, losses to disease were an order of magnitude higher than to predators (Karani, 1994), while in Laikipia, losses to large predators represent 20–25% of total losses (Frank, 1998; Mizutani, 1993).

Annually, the Galana Cattle Company lost 2.4% of its livestock to wildlife attacks, about half the total loss that Kenyan ranchers consider sustainable (M. Prettejohn, pers. commun.). Losses to predators represented an estimated cost of $8749 annually. While Kenya's GNP per capita is only $320 (World Bank 2003), the ranches were publicly held and represent an instance of shared resources and losses in contrast to subsistence ranching. The 18,263 head of livestock on the ranches 1996–1999 had a market value of roughly $1,370,000 (estimated at $75 per head), and the annual loss to wildlife represented 2.6% of their annual $343,431 value.

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References

Armbruster, P., Lande, R., 1993. A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? Conservation Biology 7, 602–610.

Ayeni, J.S.O., 1975. Utilization of water holes in Tsavo National Park (East). East African Wildlife Journal 13, 305–323.

Butler, J.R.A., 2000. The economic costs of wildlife predation on livestock in Gokwe communal land, Zimbabwe. African Journal of Ecology 38, 23–30.

Caro, T.M., 1994. Cheetahs of the Serengeti Plains: Group Living in an Asocial Species. University of Chicago Press, Chicago.

Coe, M., McWilliam, N., Stone, G., Packer, M. (Eds.), 1999. Mkomazi: The Ecology, Biodiversity and Conservation of a Tanzanian Savanna. Royal Geographical Society, London.

Eltringham, S.K., Cooksey, I.A., Dixon, W.J.B., Raine, N.E., Sheldrick, C.J., McWilliam, N.C., Packer, M.J., 1999. Large mammals of Mkomazi. In: Coe, M., McWilliam, N., Stone, G., Packer, M. (Eds.), Mkomazi: The Ecology, Biodiversity and Conservation of a Tanzanian Savanna. Royal Geographical Society, London, pp. 485–504.

Frank, L.G., 1998. Living with lions: carnivore conservation and livestock in Laikipia District, Kenya. US Agency for International

development, Conservation of Biodiverse Resource Areas Project, 623-0247-C-00-3002-00, pp. 1–63.
Funston, P.J., Mills, M.G.L., Biggs, H.C., 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. Journal of Zoology 253, 419–431.
Gittleman, J.L., 1993. Carnivore life histories: a re-analysis in the light of new models. In: Dunstone, N., Gorman, M.L. (Eds.), In Mammals as Predators. Clarendon Press, Oxford, pp. 65–86.
Herrero, S., 1985. Bear Attacks: Their Causes and Avoidance. Lyons and Burford Publication, New York.
Holekamp, K.E., Smale, L., Berg, R., Cooper, S.M., 1997. Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). Journal of Zoology 242, 1–15.
Hunter, J.A., 1952. Hunter. Harper & Brothers Publishers, New York.
Hunter, L., 1998. Pride of Phinda. Bringing back lions to South Africa's coastal plain. BBC Wildlife 16 (10), 20.
Karani, I.W., 1994. An assessment of depredation by lions and other predators in the group ranches adjacent to Masai Mara National reserve. Department of Wildlife Management, Moi University, p. 70.
Kays, R.W., Patterson, B.D., 2002. Mane variation in African lions and its social correlates. Canadian Journal of Zoology 80, 471–478.
Kerbis Peterhans, J.C., Gnoske, T.P., 2002. The science of man-eating among lions *Panthera leo* with a reconstruction of the natural history of the man-eaters of Tsavo. Journal of East African Natural History 90 [''2001''], 1–40.
Kingdon, J., 1997. The Kingdon Field Guide to African Mammals. Academic Press, San Diego, CA.
Kurtén, B., Anderson, A., 1980. Pleistocene Mammals of North America. Columbia University Press, New York.
Kusimba, C., in review. The conservation conundrum: human-wildlife interactions in Tsavo, southeastern Kenya. Fieldiana: Anthropology.
Madhusudan, M.D., 2003. Living amidst large wildlife: livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, south India. Environmental Management 31, 466–475.
Meriggi, A., Lovari, S., 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? Journal of Applied Ecology 33, 1561–1571.
Mills, M.G.L., Biggs, H.C., 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. In: Dunstone, N., Gorman, M.L. (Eds.), In Mammals as Predators. Zoological Society of London, London, pp. 253–268.
Mizutani, F., 1993. Home range of leopards and their impact on livestock on Kenyan ranches. In: Dunstone, N., Gorman, M.L. (Eds.), In Mammals as Predators. Clarendon Press, Oxford, pp. 425–439.
Ogutu, J.O., 1994. Test of a call-in technique for estimating lion (*Panthera leo*, Linnaeus 1758) population size in the Masai Mara National reserve, Kenya, Department of Wildlife Management, Moi University, p. 69.
Patterson, B.D., 2004a. The Lions of Tsavo: Exploring the Legacy of Africa's Notorious Man-eaters. McGraw-Hill, New York.
Patterson, B.D., 2004b. Maneless and misunderstood. Earthwatch Institute 23 (2), 2–15.
Patterson, B.D., Neiburger, E.J., Kasiki, S.M., 2003. Tooth breakage and dental disease as causes of carnivore-human conflicts. Journal of Mammalogy 84, 190–196.
Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., Eisenberg, J.F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biological Conservation 109, 297–310.
Ramakrishnan, U., Coss, R.G., Pelkey, N.W., 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. Biological Conservation 89, 113–120.
Rudnai, J., 1979. Ecology of lions in Nairobi National Park and the adjoining Kitengela Conservation Unit in Kenya. African Journal of Ecology 17, 85–95.
Saberwal, V.K., Gibbs, J.P., Chellam, R., Johnsingh, A.J.T., 1994. Lion-human conflict in the Gir Forest, India. Conservation Biology 8, 501–507.
Schaller, G.B., 1972. The Serengeti lion; a study of predator-prey relations. University of Chicago Press, Chicago.
Seidensticker, J., Christie, S., Jackson, P. (Eds.), 1999. Riding the Tiger: Tiger Conservation in Human-dominated Landscapes. Zoological Society of London and Cambridge University Press, Cambridge, UK.
Singh, H.S., Kamboj, R.D., 1996. Predation pattern of the Asiatic lion on domestic livestock. The Indian Forester 122, 869–876.
Smithers, R.H.N., 1971. The mammals of Botswana. Museum Memoir No. 4. The Trustees of the National Museums of Rhodesia, Salisbury.
SPSS, 2001. SPSS for Windows. Release 10.1. Chicago, IL: SPSS Inc.
StatSoft, 1997. STATISTICA 5.1 for windows. Tulsa, OK: StatSoft Inc.
Stuart-Hill, G., Grossman, D., 1993. Parks, profits and professionalism: lion return to Pilanesberg. African Wildlife 47, 267.
Turner, A., Antón, M., 1997. The Big Cats and Their Fossil Relatives: An Illustrated Guide to Their Evolution and Natural History. Columbia University Press, New York.
Vijayan, S., Pati, B.P., 2002. Impact of changing cropping patterns on man-animal conflicts around Gir Protected Area with specific reference to Talala Sub-District, Gujarat, India. Population and Environment 23, 541–559.
Vos, J., 2000. Food habits and livestock depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. Journal of Zoology 251, 457–462.
Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3, 165–173.
Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science 280, 2126–2128.
Young, S.P., Goldman, E.A., 1946. The Puma, Mysterious American Cat. The American Wildlife Institute, Washington, DC.