Limiting Depredation by African Carnivores: the Role of Livestock Husbandry

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Abstract: *Most large carnivore species are in global decline. Conflict with local people, particularly over depredation on livestock, is a major cause of this decline, affecting both nominally protected populations and those outside protected areas. For this reason, techniques that can resolve conflicts between large carnivores and livestock farmers may make important contributions to conservation. We monitored rates of livestock depredation by lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), and spotted hyenas (*Crocuta crocuta*), and retributive killing of these species by farmers in livestock-producing areas of Laikipia District, Kenya. Farmers killed more lions, leopards, and spotted hyenas where these predators killed more livestock. Livestock husbandry had a clear effect on rates of depredation and hence on the numbers of predators killed. Cattle, sheep, and goats experienced the lowest predation rates when attentively herded by day and enclosed in traditional corrals (bomas) by night. Construction of the boma, the presence of watchdogs, and high levels of human activity around the boma were all associated with lower losses to predators. Although most of this work was carried out on commercial ranches, local Maasai and Samburu pastoralists have practiced nearly identical forms of husbandry for generations. Our study shows that traditional, low-tech husbandry approaches can make an important contribution to the conservation of large carnivores.*

Limitando la Depredación de Carnívoros Africanos: El Papel de la Crianza de Ganado

Resumen: *La mayoría de los carnívoros mayores están en declinación global. El conflicto con habitantes locales, particularmente por la depredación de ganado, es una de las mayores causas de tales declinaciones, lo que afecta tanto a poblaciones nominalmente protegidas como a aquéllas afuera de áreas protegidas. Por esta razón, las técnicas que resuelvan conflictos entre carnívoros mayores y ganaderos pueden constituir importantes contribuciones a la conservación. Analizamos las tasas de depredación de ganado por leones (*Panthera leo*), leopardos (*Panthera pardus*), chitas (*Acinonyx jubatus*) e hienas manchadas (*Crocuta crocuta*), y la matanza en represalia de estas especies por granjeros en áreas productoras de ganado en el Distrito Laikipia, Kenia. Los granjeros mataron más leones, leopardos e hienas donde estos depredadores mataron más ganado. La crianza de ganado tuvo un claro efecto sobre las tasas de depredación y, por lo tanto sobre el número de depredadores muertos. Reses, ovejas y cabras presentaron las tasas de depredación más bajas cuando eran cuidadas de día y encerradas en corrales tradicionales (bomas) por la noche. La construcción de la boma, la presencia de perros guardianes y altos niveles de actividad humana alrededor de la boma estuvieron asociados con menores pérdidas por depredadores. Aunque la mayor parte de este trabajo se llevó a cabo en ranchos comerciales, pastores Massai y Samburu locales han practicado formas casi idénticas de crianza por generaciones. Nuestro estudio muestra que las técnicas de crianza tradicionales, de baja tecnología, pueden constituir una contribución importante a la conservación de carnívoros mayores.*

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Introduction

Most large carnivore species are experiencing ongoing global declines caused almost entirely by human activities. Large carnivores have disappeared from areas of high human density, and the species most exposed to conflicts with people are the most prone to extinction (Woodroffe, 2001).

Africa's large carnivores have declined over the last 30 years (Ginsberg & Macdonald 1990; Nowell & Jackson 1996; Mills & Hofer 1998), with several species listed as threatened by the World Conservation Union (Ethiopian wolf [*Canis simensis*], critically endangered; African wild dog [*Lycaon pictus*], endangered; African lion [*Panthera leo*], vulnerable; cheetah [*Acinonyx jubatus*], vulnerable; World Conservation Union 2002). In addition to their intrinsic value, Africa's large carnivores are important generators of income in developing countries through tourism and hunting (e.g., Western & Henry 1979). Conservation of large carnivores may therefore make economic sense, particularly in dry rangelands of limited value for agriculture.

Conflict between people and large carnivores undermines the viability of populations that are nominally protected and those living outside reserves. Where large carnivores have been studied in reserves, most of the recorded mortality has been caused, deliberately or accidentally, by people (Woodroffe & Ginsberg 1998). These deaths—due to shooting, poisoning, accidental snaring, and road accidents—occur mostly on or outside the borders of unfenced reserves and are particularly common where reserves are surrounded by areas supporting high densities of people (Harcourt et al. 2001). This mortality creates population "sinks" around protected areas; the resulting edge effect appears strong enough to cause local extinction (Woodroffe & Ginsberg 1998).

Only a handful of Africa's reserves are large enough to maintain viable populations of wide-ranging carnivores in the face of such strong edge effects (Brashares et al. 2001; Loveridge et al. 2001). For reserves to provide effective conservation in the long term, it will be necessary—for some species at least—to reduce human-induced mortality on and around reserve borders. Resolving human-wildlife conflicts may also permit viable populations to persist outside protected areas. Although some carnivore deaths occur by accident (e.g., in road traffic accidents, by capture in snares set for other species), a high proportion involve predators being deliberately killed by people who perceive large carnivores as a threat to livestock. For this reason, reducing depredation on livestock may lower the mortality of large carnivores that results from their depredations. Here, we report the results of a preliminary study of the effectiveness of livestock husbandry in mitigating the impact of predators on human livelihoods and the impact of humans on predator mortality.

Methods

Study Area and Species

Our study area was in the Laikipia District of northern Kenya (lat $37°2'$E, long $0°6'$N), an area of semiarid bush land and savanna used for commercial ranching, subsistence pastoralism, tourism, and small-scale agriculture. None of the area is formally protected, but tolerance for wildlife is generally high, though this varies between properties (Frank 1998). Ratios of livestock to wild ungulates are markedly lower in Laikipia than in neighboring districts (Georgiadis & Ojwang' 2001), though this also varies among properties and land uses. At the time of the study, the region supported populations of five species of large carnivore: lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), spotted hyenas (*Crocuta crocuta*), and striped hyenas (*Hyaena hyaena*). All these predators may be legally killed in defense of human life or livestock. African wild dogs were occasional vagrants at the time of the study but have since recolonized the area (Woodroffe, 2002). On commercial ranches, 0.8% of cattle and 2.1% of sheep and goats were lost annually to predators (with 2.5% and 8.2%, respectively, lost to disease; Frank 1998). On pastoralist "group" ranches, 0.9% of cattle and 2.5% of sheep and goats were lost annually to predators (Frank 1998; no data available on losses to disease).

Relationships between Predation on Livestock and Killing of Predators

One of us (L.G.F.) gathered data on rates of predation on livestock in 1995–1996 and numbers of predators killed in the same years through examination of ranch records and interviews with ranch managers and pastoralists on 17 ranches (14 commercial ranches, 3 community group ranches). Frank also received additional data from 7 commercial ranches and 2 group ranches via a postal questionnaire. Several ranches did not keep separate records on spotted and striped hyenas, so we considered the two species together. Available data suggest, however, that the (much more common) spotted hyena is responsible for the majority of hyena attacks on livestock (L. Leakey, unpublished data).

Effects of Husbandry on Livestock Depredation

Following the baseline survey, we initiated a more intensive study of the effects of husbandry on livestock depredation. This study was carried out on 10 properties (9 commercial ranches, 1 community area), covering 1443 km² in Laikipia. Each property was monitored for 2–17 months between January 1999 and May 2000. Properties were visited regularly each month to gather data on the number of livestock killed by wild predators and the circumstances surrounding the attacks. Most attacks
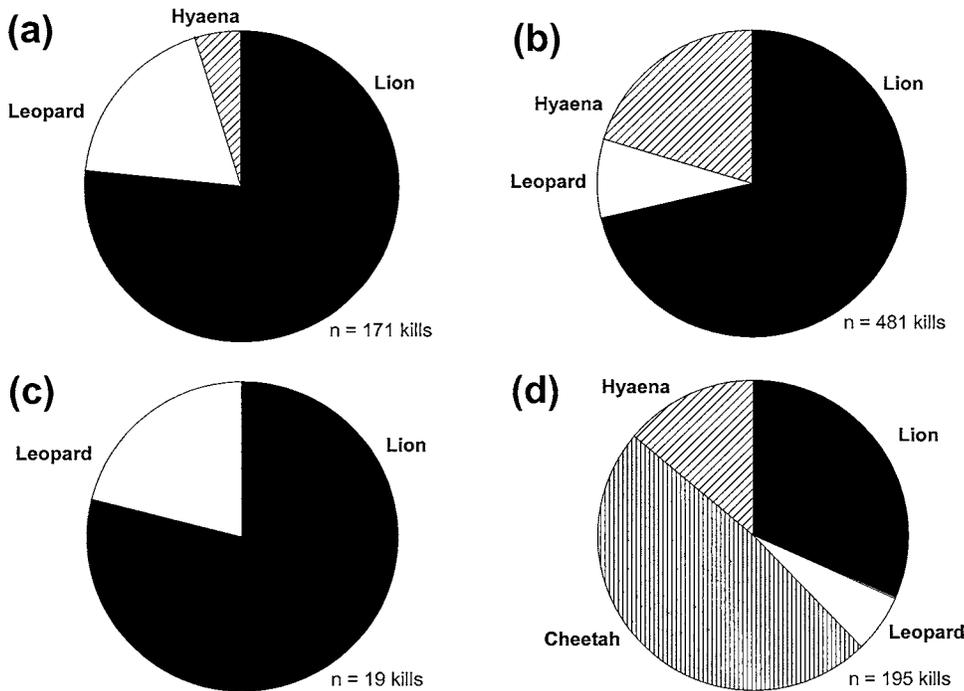
Figure 1. Variation in depredation rates of four predator species. Proportions of recorded livestock kills attributed to lions, leopards, cheetahs, and hyenas for (a) cattle and (b) sheep and goats by night at bomas (nighttime corrals) and for (c) cattle and (d) sheep and goats by day away from the boma.

were directly witnessed by herders, who have extensive experience with identifying predators, predator tracks, and feeding signs. On commercial ranches, ranch managers usually verified such reports by tracking and examination of carcasses. These data were gathered routinely by ranch managers to monitor livestock production. Because compensation is not available in Kenya, herders and herd owners had little incentive to misrepresent loss rates.

We gathered data on two types of livestock attack. About 75% of kills occurred at night, when livestock were taken from *bomas* (night time corrals), and about 25% occurred by day, when predators attacked livestock while they were out grazing (Fig. 1). Some livestock were killed when predators entered the boma. Others (particularly cattle) were killed when they stampeded out of bomas in response to the presence of predators (usually lions) outside. We monitored livestock losses at 84 bomas on the 10 properties. Information on daytime kills was gathered opportunistically on regular monthly visits to the properties.

Data Gathered at Bomas

We gathered baseline data on the construction of each boma, the type of livestock kept, the level of human activity, and the presence of various measures intended to deter predators. Intercorrelations among these measures are shown in Table 1.

We classified bomas used to keep cattle as "solid" (made of stone or wooden posts), "acacia" (made from *Acacia* brush), or "open" (no fencing; consisting only of a patch of ground where cattle were bedded down). We classified bomas used to keep sheep and goats as "solid" (made of stone or wooden posts), "acacia" (made from *Acacia* brush), "wicker" (branches woven around cedar poles), or "wire" (made of 10 × 10 cm wire mesh. We measured the height of boma walls in all cases, with the expectation that higher walls would be more difficult for both predators and livestock to penetrate. Additionally, we measured the thickness of *Acacia* brush walls, because this influences both the strength and the opacity of the wall. Some bomas—particularly those constructed of *Acacia* brush—consisted of several "rooms" separated by internal brush walls. These internal walls separate herds within the enclosure and strengthen the boma, making it less likely that panicked livestock will escape. We scored bomas as having one or two "rooms" or three or more "rooms."

Several predator deterrents were used at bomas within the study. Of these, the most common were dogs and guns. Dogs are not trained as guards and do not chase predators; rather, they serve to alert people of the presence of predators. Likewise, firearms were rarely used to shoot predators (most were shotguns loaded with bird shot) but were used to scare predators away—usually by shooting in the air—if they approached the bomas too closely. Guns were usually kept in the possession of a headman, often responsible for guarding several herds brought to a single boma each night. For this reason, the possession of a gun at a boma was associated with the presence of larger numbers of people (Table 1).

People themselves may also act as deterrents to predators. We measured human activity both as the typical

Table 1. Intercorrelations among characteristics of bomas (nighttime corrals) used in analyses of depredation rates.[a]

	Height	*Thickness*	*Log(people)*	*Houses*	*Cover*	*Dog present*	*Gun present*	*Complexity*
Thickness	$r = 0.46$ $n = 15,$							
Log(people)	$r = 0.098$ $z = 1.7$ $n = 53,$ $z = 0.70$	$r = -0.098$ $n = 14,$ $z = -0.33$						
Houses	$r = 0.056$ $n = 22,$ $z = 0.242$	$r = 0.567$ $n = 8,$ $z = 1.44$	$r = 0.718*$[a] $n = 23,$ $z = 4.04$					
Cover	$r = 0.15$ $n = 21,$ $z = 0.55$	$r = -0.30$ $n = 10,$ $z = -0.83$	$r = 0.046$ $n = 24,$ $z = 0.21$	$r = 0.238$ $n = 19,$ $z = 0.97$				
Dog present	$t_{51} = 4.77*$	$t_{13} = 1.82$	$t_{65} = 0.28$	$t_{22} = 0.38$	$t_{22} = 1.13$			
Gun present	$t_{31} = 0.54$	—	$t_{42} = 6.64*$	—	-	$\chi^2 = 0.2,$ $df = 1$		
Complexity	$t_{13} = 0.58$	$t_{13} = 0.64$	$t_{14} = 2.32***$	$t_{8} = 1.70$	$t_{10} = 0.22$	$\chi^2 = 1.9,$ $df = 1$	—	
Boma type	$F_{3,48} = 10.84*$	—	$F_{4,61} = 8.49*$	$F_{3,12} = 10.7*$	$F_{4,18} = 1.9$ $df = 4$	$\chi^2 = 33.4*,$	$\chi^2 = 17.8**,$ $df = 1$	—

[a]*Dashes indicate correlations that could not be calculated because of insufficient variation (e.g., thickness and complexity were measured only at Acacia bomas so could not be compared with boma type). Data comes from all bomas monitored for more than 6 months. Not all measures were available for every boma, and not all bomas were used to house both cattle and sheep and goats, so in some cases the sample sizes used for particular analyses differed somewhat from those presented here. Probability: $*p < 0.0001$, $**p < 0.005$, $***p < 0.05$; values without p value are not significant.*

number of people present (log-transformed) and as the number of houses at a boma. However, these two measures were closely correlated with one another (Table 1; $r = 0.718, n = 23, p < 0.0001$), so analyses included only the number of people present.

Predators' willingness to approach bomas may be influenced by the availability of cover. We therefore measured the distance to the nearest bush cover at each boma. Other forms of cover (e.g., rocks) were available in the study area but rarely in close proximity to bomas.

Livestock Kills Away from the Boma

When predators attacked livestock by day, we collected herders' reports of the number of predators present, the size of the herd, the number of herders present, and the habitat in which the attack occurred (dense or open bush). A handful of herds were accompanied by dogs, but the numbers were too small to permit analysis.

Statistical Analysis

We calculated livestock loss rates separately for cattle and small stock (sheep and goats combined). For each property, we calculated the numbers of predators reported killed in 1995–1996, and the numbers of livestock recorded as having been killed by those predators in the same years, expressing each as the number killed per square kilometer to correct for variation in the size (and thus in the approximate predator and livestock population) of each property.

For each boma, we calculated a monthly rate of depredation in 1999–2000 for each predator species by dividing the number of stock reported killed during the monitoring period for that boma by the number of months monitored. In addition, we calculated a total monthly depredation rate for each boma by considering attacks by all predators together. These monthly loss rates had a highly skewed distribution, with a preponderance of zeroes (e.g., 18/52 cattle bomas suffered no attacks). Residuals from analysis of variance (ANOVA) and regression models were likewise highly skewed, indicating that the use of parametric statistics would be inappropriate. To permit parametric multivariate analysis, we therefore classified each boma according to whether or not any livestock had been lost. When the full data set was used, these measures of loss rate were related to the period for which each boma was monitored, with bomas monitored for shorter periods less likely to record losses (Spearman rank correlation between period monitored and monthly loss rate: cattle, $r_s = 0.387, n = 52, p < 0.01$; sheep and goats, $r_s = 0.115, n = 49, p > 0.4$; logistic regression of the probability of loss on period monitored: cattle $\chi^2 = 3.22, df = 1, p < 0.1$, sheep and goats, $\chi^2 = 7.45, df = 1, p < 0.01$). These relationships disappeared when we excluded from the analysis bomas monitored for more than 6 months (Spearman rank correlation between period monitored and monthly loss rate: cattle, $r_s = -0.144, n = 39, p > 0.3$; sheep and goats, $r_s = -0.141, n = 45, p > 0.3$; logistic regression of the probability of loss on period monitored: cattle $\chi^2 = 0.00004, df = 1, p > 0.9$, sheep and goats, $\chi^2 = 2.32, df = 1, p > 0.1$). We

therefore included only those bomas monitored for more than 6 months in analyses of loss rates. These subsets of the loss rate data still showed highly skewed distributions.

We explored relationships between livestock loss rates and boma characteristics by univariate nonparametric analyses. In addition, logistic regression allowed us to make multivariate comparisons between boma characteristics and the probability of any livestock being lost, although this was necessarily a more coarse-grained analysis than consideration of actual loss rates.

Livestock loss rates while away from the boma could not be compared among herds because it was impossible to measure the denominators—how many livestock herds were not attacked on each property during the period each was monitored. Analyses were therefore restricted to comparisons of the number of livestock reported lost at each attack.

Results

Relationships between Predation in Livestock and Killing of Predators

The number of predators killed by farmers was related to the number of livestock killed by those predators (expressed as animals killed per square kilometer). The number of lions killed in 1995–1996 (mean 2.63 ± 4.66 SD, range 0–19, per property) was positively correlated with the number of livestock killed by lions on those properties (cattle, $r_s = 0.555$, $n = 17$ properties, $p < 0.05$; sheep and goats, $r_s = 0.604$, $n = 14$ properties, $p < 0.05$). During the same period, the number of hyenas killed (mean 6.17 ± 10.88 SD, range 0–40, per property) correlated with the number of sheep and goats killed by hyenas ($r_s = 0.848$, $n = 16$, $p = 0.001$), although not with the number of cattle killed by hyenas, which was low ($r_s = -0.195$, $n = 17$, not significant). The number of leopards killed (mean 0.23 ± 0.53 SD, range 0–2, per property) per square kilometer correlated with the number of cattle killed by leopards ($r_s = 0.573$, $n = 17$, $p < 0.05$), though not with the number of sheep and goats killed ($r_s = 0.444$, $n = 14$, not significant). There was no significant correlation between the number of cheetahs killed (mean 0.36 ± 1.41 SD, range 0–7, per property) per square kilometer and the number of sheep and goats killed by cheetahs, although the result suggested a positive trend ($r_s = 0.528$, $n = 13$, $p = 0.068$). No properties lost cattle to cheetahs.

Rates of Depredation by Four Predator Species

Lions were the most serious predator of cattle at bomas (Fig. 1a) and in the field (Fig. 1c). Lions also killed the largest number of sheep and goats at bomas (Fig. 1b), but cheetahs killed a larger number in the field (Fig. 1d). Cheetahs made no attacks on bomas.

Monthly depredation rates at bomas differed among lions, leopards, and hyenas both for cattle and for sheep and goats (Friedman test, corrected for ties: cattle $\chi^2 = 40.7$, df $= 2$, $p < 0.0001$; sheep and goats, $\chi^2 = 25.2$, df $= 2$, $p < 0.0001$). In each case, lions were the most serious predator. Within cattle, rates of depredation on calves versus adults at bomas varied among predator species, with lions taking a high proportion of adults and leopards taking calves exclusively ($\chi^2 = 86.5$, df $= 2$, $p < 0.0001$).

Within bomas, some rates of depredation by different predator species were correlated with one another, such that a boma with a high rate of sheep and goat depredation by lions also suffered high rates of loss to hyenas (Spearman rank correlations corrected for tied data: lions vs. hyenas, $r_s = 0.45$, $n = 45$ bomas, $p < 0.005$; lions vs. leopards, $r_s = 0.246$, $n = 45$, $p < 0.1$; leopards vs. hyenas, $r_s = 0.27$, $n = 45$, $p < 0.08$). Loss rates of cattle were not so correlated (lions vs. leopards, $r_s = 0.03$, $n = 39$ bomas, not significant; lions vs. hyenas, $r_s = -0.03$, $n = 39$, not significant; leopards vs. hyenas, $r_s = 0.02$, $n = 39$, not significant).

At some bomas, sheep and goats were kept together with cattle. At these bomas, depredation rates on the two livestock types were correlated with one another (correlations between kill rates of sheep and goats and of cattle: kills by lions, $r_s = 0.57$, $n = 14$, $p < 0.05$; kills by leopards, $r_s = 0.87$, $n = 14$, $p < 0.005$; kills by hyenas, $r_s = 0.56$, $n = 14$, $p < 0.05$). However, the presence of cattle per se did not appear to influence depredation rates on sheep and goats (comparing rates of attack on sheep and goats at bomas with and without cattle, Mann-Whitney U tests: lions, $U_{31,14} = 245.5$, $z = -0.71$, $p > 0.4$; leopards, $U_{31,14} = 231.5$, $z = -0.42$, $p > 0.7$; hyenas, $U_{31,14} = 243.5$, $z = -0.68$, $p > 0.4$), and the presence of sheep and goats did not influence depredation on cattle (lions, $U_{25,14} = 181$, $z = -0.18$, $p > 0.8$; leopards, $U_{25,14} = 185$, $z = -0.44$, $p > 0.6$; hyenas $U_{25,14} = 203$, $z = -1.56$, $p > 0.1$).

On all occasions where predators attacked cattle herds away from the boma, only a single animal was taken. There was no significant difference between predator species in the number of sheep and goats killed on each field attack (Kruskal-Wallis test $H_{75,45,25,8} = 5.26$, not significant). The median number of sheep or goats taken on each attack was 1 for all four predator species, although the range varied (maxima of five for lions [$n = 45$ attacks] and cheetahs [$n = 75$ attacks], three for leopards [$n = 8$ attacks], two for hyenas [$n = 25$ attacks]). For group-living predators, the number of livestock killed was correlated with the number of predators reported seen by herders (Spearman rank correlations: lions, $r_s = 0.631$, $n = 45$ attacks, $p < 0.0001$; cheetahs, $r_s = 0.518$, $n = 75$, $p < 0.0001$; hyenas, Mann-Whitney U test, $U_{23,2} = 46$, $p < 0.0001$).
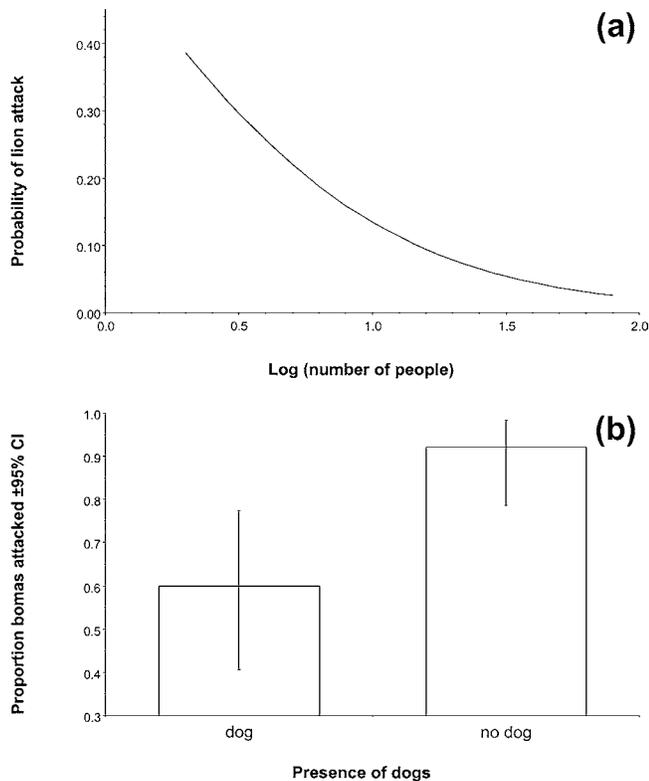
Figure 2. Characteristics of bomas (nighttime corrals) associated with probabilities of any attack by lions, based on multivariate logistic regression: (a) effect of log(people) and (b) effect of presence of domestic dogs. Overall $r^2 = 0.28$. Effect of log(people): $\chi^2 = 8.36$, p < 0.005. Effect of dog presence: $\chi^2 = 8.22$, p < 0.005.

Effects of Husbandry on Rates of Depredation at Bomas

MULTIVARIATE ANALYSES OF LOSS PROBABILITIES

Multiple logistic-regression analyses, comparing boma characteristics with the probability that any livestock (cattle, sheep or goats) were lost to predators, showed that lions were less likely to take any livestock from bomas with both dogs and large numbers of people present (Fig. 2; overall $r^2 = 0.28$; effect of dogs' presence, $\chi^2 = 8.22$, $p < 0.005$; effect of log(people), $\chi^2 = 8.36$, $p < 0.005$). None of the other measures made significant contributions to the model fit, so they were dropped from the analysis. A similar analysis showed that hyenas were more likely to take livestock from wire bomas ($\chi^2 = 4.76$, $p < 0.05$). Univariate analysis suggested that dogs' presence reduced the probability of hyena attack ($\chi^2 = 4.21$, $p < 0.05$), but this effect disappeared after boma type was controlled for ($\chi^2 = 1.93$, $p > 0.15$), with which dogs' presence was intercorrelated (Table 1). Logistic regression showed no significant effects of boma characteristics on the probability of leopard depredation.

BOMA CONSTRUCTION

A nonsignificant trend suggested that rates of lion depredation on sheep and goats could be influenced by boma type (Kruskal-Wallis test: $H_{18,10,8,6} = 6.80$, $p < 0.08$), although there was no similar effect for lion predation on cattle ($H_{14,13,8} = 0.34$, $p > 0.8$). Hyena depredation showed a similar pattern (sheep and goats $H_{18,10,8,6} = 6.96$, $p < 0.08$; cattle $H_{14,13,8} = 0.31$, $p > 0.8$), but there was no such relationship for leopard predation (sheep and goats $H_{18,10,8,6} = 0.74$, $p > 0.8$; cattle $H_{14,13,8} = 0.57$, $p > 0.7$). These relationships combined to show a significant effect of boma type on total monthly losses (all predators combined) of sheep and goats, with wire bomas performing especially poorly ($H_{18,10,8,6} = 8.11$, $p < 0.05$; Fig. 3a), but not of cattle ($H_{14,13,8} = 0.95$, $p > 0.6$).

The height of boma walls showed no significant correlation with rates of depredation by either lions (cattle, $r_s = 0.221$, $n = 25$, $p > 0.2$; sheep and goats, $r_s = -0.163$, $n = 41$, $p > 0.3$) or hyenas (cattle, $r_s = 0.195$, $n = 25$, $p > 0.3$; sheep and goats, $r_s = -0.297$, $n = 41$,
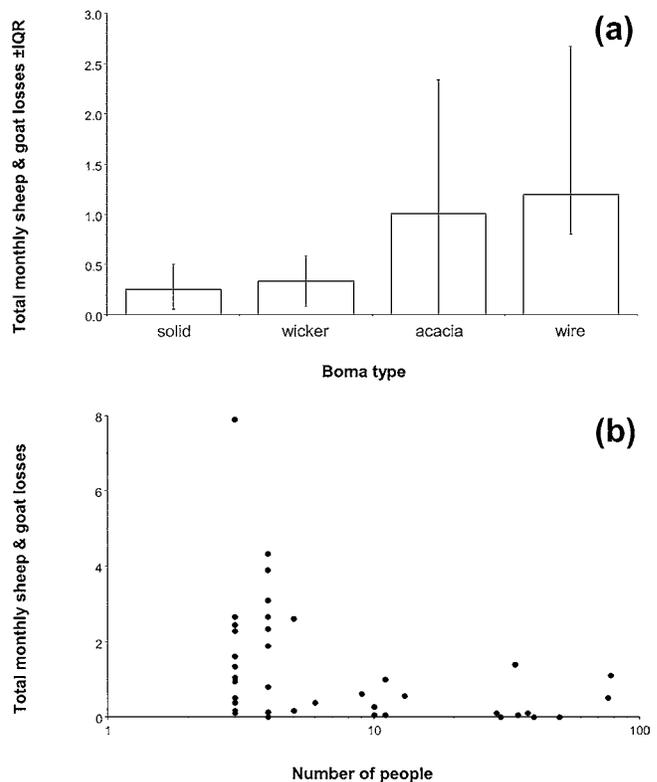

Figure 3. Characteristics of bomas (nighttime corrals) associated with variation in depredation on sheep and goats (all predator species combined) by univariate nonparametric analyses: (a) boma type (median and interquartile range [IQR]; Kruskal-Wallis test: $H_{18,10,8,6} = 8.11$, p < 0.05) and (b) log(people) (Spearman rank correlation: $r_s = -0.477$, n = 44, p < 0.005).

$p < 0.05$). However, somewhat paradoxically, higher boma walls were associated with higher rates of leopard depredation on cattle ($r_s = 0.436$, $n = 25$, $p < 0.05$), though not on sheep and goats ($r_s = 0.254$, $n = 41$, $p > 0.1$). This led to an overall positive relationship between wall height and total monthly loss rates of cattle to all predators ($r_s = 0.427$, $n = 25$, $p < 0.05$), although there was no such effect for sheep and goats ($r_s = -0.145$, $n = 41$, $p > 0.3$).

Wall thickness was also measured at *Acacia* bomas: there was no significant correlation between wall thickness and any measure of depredation rate (Spearman rank correlations: $|r_s|$ values all ≤0.70, all $p > 0.05$), although sample sizes were small. *Acacia* bomas were further classified as simple (1–2 "rooms") or complex (3 or more rooms). There was no significant relationship between boma complexity and any measure of depredation rate (Mann-Whitney U tests: $|z|$ values all ≤1.28, all $p > 0.15$). These results are comparable with the multivariate analysis presented above, which showed an effect of boma type (on hyena depredation) but no effects of wall height, thickness, or complexity.

PRESENCE OF DETERRENTS

Presence of dogs was associated with reduced rates of lion depredation on cattle (Mann-Whitney U test; $U_{29,10} = 241$, $z = -3.1$, $p < 0.005$) but not on sheep and goats ($U_{25,18} = 245.5$, $z = -0.511$, $p > 0.6$). There was no relationship between presence of dogs and depredation rates by either leopards (cattle, $U_{29,10} = 147.5$, $z = -0.12$, $p > 0.9$; sheep and goats $U_{25,18} = 239$, $z = -0.40$, $p > 0.6$) or hyenas (hyenas $U_{29,10} = 166$, $z = -1.28$, $p > 0.15$; sheep and goats $U_{25,18} = 239.5$, $z = 0.37$, $p > 0.7$), but the lion effect was strong enough to drive an association between presence of dogs and reduced total monthly loss rates of cattle (Fig. 4(a); $U_{29,10} = 224$, $z = -2.56$, $p < 0.05$), although this did not hold for sheep and goats ($U_{25,18} = 258$, $z = -0.81$, $p > 0.4$).

The presence of firearms at bomas appeared to deter lions from predation on sheep and goats (Mann-Whitney U test: $U_{21,6} = 97$, $z = -2.01$, $p < 0.05$) but not cattle ($U_{19,4} = 43$, $z = -0.41$, $p < 0.6$), although the sample of bomas with guns was small. Guns were not associated with reduced predation on livestock by either leopards or hyenas (all $U < 42$, all $|z| < 0.4$, all $p > 0.6$); hence, there was no detectable impact on overall monthly loss rates of either cattle ($U_{19,4} = 44$, $z = -0.49$, $p > 0.6$) or sheep and goats ($U_{21,6} = 88.5$, $z = -1.49$, $p > 0.1$).

The typical number of people present at a boma correlated strongly with rates of attack on livestock. Larger numbers of people were associated with lower rates of lion predation on both cattle ($r_s = -0.327$, $n = 38$ bomas, $p < 0.05$) and sheep and goats ($r_s = -0.493$, $n = 44$, $p < 0.005$). Leopard predation on cattle was likewise lower where more people were present ($r_s = -0.329$, $n = 38$,
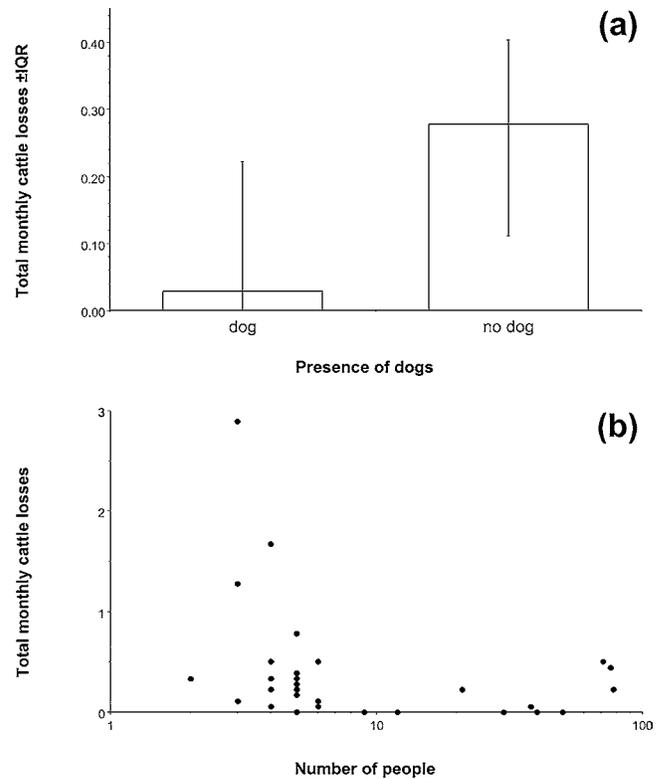

Figure 4. Characteristics of bomas (nighttime corrals) associated with variation in depredation on cattle (all predator species combined) by univariate nonparametric analyses: (a) presence of domestic dogs (median and interquartile range [IQR]; Mann-Whitney U test: $U_{29,10} = 224$, z = −2.56, p < 0.05) and (b) log(people) (Spearman rank correlation: $r_s = -0.388$, n = 38, p < 0.05).

$p < 0.05$), though there was no such effect for sheep and goats ($r_s = -0.103$, $n = 44$, $p > 0.5$). Conversely, hyena depredation on sheep and goats was less frequent where more people were present ($r_s = -0.322$, $n = 44$, $p < 0.05$), with no effect on cattle depredation ($r_s = 0.139$, $n = 38$, $p > 0.3$). These effects combined to generate significantly lower overall monthly loss rates to predators at bomas where more people were present (cattle, $r_s = -0.388$, $n = 38$, $p < 0.05$, Fig. 4(b); sheep and goats, $r_s = -0.477$, $n = 44$, $p < 0.005$, Fig. 3(b)). These results are roughly comparable with the multivariate analyses presented above, which showed significant effects of both dogs and people on lion predation.

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The distance to the nearest cover was inversely correlated with the rate at which sheep and goats were taken by hyenas ($r_s = -0.567$, $n = 18$ bomas, $p < 0.05$), indicating that hyenas were more likely to take small stock from bomas close to bushy cover. There were no

significant correlations between distance to cover and rates of depredation on sheep and goats by other predators (lions $r_s = -0.377$, $n = 18$, $p > 0.1$; leopards $r_s = -0.222$, $n = 18$, $p > 0.3$) or between this measure and attack rates on cattle (all $|r_s| \leq 0.195$, $n = 17$, all $p > 0.4$). Distance to cover was not associated with depredation probabilities in the multivariate analyses presented above.

Effects of Husbandry on Depredation away from the Boma

Effects of husbandry on depredation away from the boma concerned only sheep and goats because no field attacks on cattle involved the loss of more than one animal. A smaller number of sheep or goats was lost to predators on each attack where the ratio of herders to livestock was high (all predators combined, Spearman rank correlation: $r_s = -0.193$, $n = 166$ attacks, $p < 0.05$). Lions and cheetahs were less likely to take more than one sheep or goat when the number of herders per sheep or goat was higher (Mann Whitney U tests: lions, $U_{34,12} = 290$, $z = -2.19$, $p < 0.05$; cheetahs, $U_{62,13} = 538$, $z = -1.97$, $p < 0.05$). There was no significant effect of the herder-to-livestock ratio on the probability that hyenas or leopards took more than one sheep or goat (hyenas, $U_{23,2} = 38$, $z = -1.52$, $p > 0.1$; leopards, $U_{5,3} = 11.5$, $z = -1.2$, $p > 0.2$).

The overall number of sheep or goats killed on each attack was higher in open bush than in thick bush (all predators combined, Mann-Whitney U test, $U_{84,82} = 4016$, $p < 0.01$). Both cheetahs and hyenas were more likely to take multiple sheep or goats when attacks took place in open bush (cheetahs, $\chi^2 = 5.34$, df $= 1$, $p < 0.05$; hyenas, $\chi^2 = 4.26$, df $= 1$, $p < 0.05$). There were no such effects for lions ($\chi^2 = 0.38$, df $= 1$, not significant) or leopards ($\chi^2 = 0$, df $= 1$, not significant).

Discussion

Our results indicate that depredation on livestock is, to some extent, preventable. In general, livestock that were closely herded by day and kept at night in bomas with watch dogs and high levels of human activity were less likely to be killed by wild predators. Other factors—including the density of predators, the availability of wild prey, and the behavior of individual predators—are clearly important influences on rates of depredation (e.g., Stander 1991; Linnell et al. 1999; Thirgood et al. 1999). However, good husbandry may have the dual effects of reducing livestock losses in the short term and, in the long term, preventing predators from developing a "taste" for killing livestock. Our data indicate that reducing livestock losses in this way should have conservation benefits by reducing the numbers of predators killed by farmers.

Our analyses were hampered by the skewed distribution of the data on depredation rates at bomas and by intercorrelation among explanatory variables. However, the results of the multivariate analyses of loss probabilities tended to support the more fine-grained univariate analyses of loss rates, with effects of human activity, domestic dog presence, and boma type being detected by both approaches. Some results of the univariate analyses were not supported by the multivariate analyses, including effects of firearms on lion depredation, boma height on leopard depredation, and habitat on hyena depredation. A relationship between lion depredation and the presence of firearms was detected by univariate logistic regression ($\chi^2 = 6.83$, $p < 0.01$), but it became nonsignificant and was dropped from the model when the effects of people and dogs were included. The fact that the presence of guns was associated with large numbers of people at bomas (Table 1) probably explains this. The relationship between hyena depredation and distance to cover was fairly weak and might not have been detectable by the coarse-grained logistic-regression analysis. The relationship between boma height and leopard depredation was paradoxical (with predation risk increasing with wall height) and might have been caused by intercorrelation between boma height and boma type (Table 1; although boma type was not related to leopard predation rates). An ongoing case-control study, comparing "case" bomas attacked on a particular night with "control" bomas that are not, should overcome the problem of skewed data on depredation rates, permitting more extensive multivariate analyses and perhaps confirming or refuting these findings.

The approaches taken to livestock husbandry in Laikipia and other semiarid rangeland areas of East Africa are fundamentally different from those operating in southern Africa and other more developed regions of the world. Although people and predators coexist (admittedly uneasily) in several East African rangelands (Kruuk 1981), in southern Africa large carnivores have been eliminated from most livestock areas, and cattle in particular graze unaccompanied by herders. This latter approach has economic benefits: fewer staff are needed, and cattle may graze at night, potentially increasing their growth rates. This abandonment of herding traditions can lead to severe conflicts between people and predators, especially on the borders of protected areas and in regions where predators have recovered after a period of local extirpation (e.g., Mech 1995; Marker et al. 1996; Hemson, 2001). Traditional husbandry has persisted in East African rangelands—even in areas such as Laikipia, where some of the properties and livestock are owned by wealthy foreigners—in part because of the high probability that livestock that are not tended will be stolen (Frank 1998). In addition, unemployment is high and there is an unbroken tradition of livestock herding, creating a pool of cheap labor willing to work as herders. This threat

of stock theft—which applies equally to local pastoralists and foreign-born commercial ranchers—has, perhaps more than any other factor, indirectly reduced the perceived need to completely eradicate large predators. The predators discussed here are under varying degrees of legal protection in Kenya, but effective poisons are widely available and local people could eradicate most of the large carnivores were they strongly inclined to do so.

Husbandry measures that effectively limit depredation on commercial ranches—in particular, intensive herding of livestock and bomas with high levels of human activity—closely resemble the traditional practices of local Maasai and Samburu pastoralists (see also Kruuk 1981). The wire bomas found to be ineffective on commercial ranches are rarely if ever used in pastoralist areas. However, acacia bomas built on commercial ranches are often of stouter construction than those in pastoralist areas, partly because ranch staff have access to tractors for hauling branches and small trees. Kruuk (1981) concluded that construction of stouter bomas would help pastoralists in northern Kenya reduce their rates of livestock loss to predators. Although our results do not support Kruuk's conclusion, with no detectable effects of either boma height or thickness, in an ongoing case-control study (see above) we will test this hypothesis on a larger data set from community areas.

The strongest effects of livestock husbandry on rates of livestock depredation were found for lions. This is doubtless in part because lion attacks were the most common and thus dominated the data set. It is the experience of local pastoralists, however, that attacks by leopards can be particularly difficult to guard against because they can climb through or over the stoutest boma. Our results tend to support this observation.

The presence of domestic dogs may have equivocal consequences for local conservation. Some commercial ranches prohibit dogs, to avoid their being used to hunt wildlife. Moreover, although dogs appeared to reduce depredation, they may also act as reservoir hosts for diseases such as rabies and distemper that can cause catastrophic mortality among wild carnivores (e.g., Cleaveland & Dye 1995; Roelke-Parker et al. 1996). The density of domestic dogs on commercial ranch land in Laikipia at the time of the study ($0.15/km^2$ across six ranches in 1999; R.W., unpublished data) was substantially lower than that needed to sustain endemic rabies infection in dogs alone (Cleaveland & Dye 1995). Modeling suggests, however, that domestic dogs may play a role in maintaining infection in populations of alternative hosts such as jackals (Rhodes et al. 1998) and in transmitting such infections to endangered wildlife (Haydon et al. 2002). With black-backed jackals (*Canis mesomelas*) and bat-eared foxes (*Otocyon megalotis*) common in the study area, increasing the density of domestic dogs could make it more likely that endemic rabies or distemper infection could become established, unless the dogs were vaccinated regularly.

More research is needed in this area before we can judge whether the effect of domestic guard dogs on the conservation of wild carnivores is positive or negative.

High levels of human activity around bomas appeared effective in limiting depredation by all species. Such activity need not necessarily involve employing more staff: more human activity was apparent where herders' families were permitted to live with them at the boma. However, several managers of commercial ranches preferred to have only their own staff living at bomas, for reasons of security and environmental impact.

Our results indicate that depredation by large African carnivores can be mitigated through livestock husbandry. This has demonstrable conservation benefits in that fewer predators were killed where predators killed fewer livestock. In these circumstances, decisions concerning approaches to livestock husbandry are largely economic ones, depending on the local costs and relative benefits of intensive husbandry. However, the fact that simple, effective, low-technology solutions can make substantial contributions to the resolution of conflicts between people and predators is encouraging. Such measures could be implemented particularly effectively around the borders of reserves. Where necessary, subsidy of such practices might provide a cost-effective means of increasing the capacity of reserves to protect wide-ranging carnivores.

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Queries

Q1 Author: Kruuk 1981: please spell out UNEP-MAB and IPAL; please provide publisher and place of publication.

Q2 Author: "Et al" found in reference where it is not correct style. Please correct the author list (in reference "Roelke-Parker, et al., 1996").