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Do anthropogenic sources of food increase livestock predation in the area surrounding Ruaha National Park?

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Research Paper

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Summary

Wild carnivores are threatened by human activities, particularly by lethal responses to livestock predation. As natural prey populations decline, predation of livestock and consumption of discarded livestock 'waste' (carcasses and body parts) should increase. We investigated whether parameters linked to the production of livestock waste affected the likelihood of livestock predation. We interviewed 160 households near Ruaha National Park in Tanzania to obtain information on households, livestock ownership, predation and parameters linked to livestock waste production. Our analysis identified parameters that affected the likelihood of predation on cattle, sheep and goats. When these parameters were controlled for, we found an increased likelihood of cattle predation as waste from diseased and slaughtered cattle increased. Sheep predation was more likely and cattle predation was less likely as sheep deaths from starvation increased. Goat predation was more likely in medium-sized than smaller or larger villages, suggesting a trade-off to predators between the increasing benefit of more livestock waste and the costs of higher human disturbance and diminishing natural prey abundance as village size category increased. Our findings suggest that improved disposal of livestock waste from slaughtered cattle and measures to decrease cattle deaths from disease should reduce predation of highly prized cattle.

Introduction

Human activities have substantially reduced the size and range of carnivore populations worldwide (Treves & Karanth 2003), which has resulted in wide-ranging ecological consequences (Estes et al. 2011, Ripple et al. 2014, O'Bryan et al. 2018). The perceived threat of livestock predation is a major challenge to carnivore conservation as it can result in fatal outcomes for carnivores (Treves & Karanth 2003, Patterson et al. 2004, Kissui et al. 2019). A reduction in natural prey (e.g., as a result of extensive bushmeat hunting; Hofer et al. 1996) may lead to an increase in livestock predation and human–carnivore conflict (Odden et al. 2013, Wolf & Ripple 2016, Soofi et al. 2019). Alternatively, high livestock predation may occur when high densities of natural prey support high densities of wild carnivores (Stahl et al. 2002, Suryawanshi et al. 2017). Although high human population growth, coupled with a rising demand for meat, is likely to intensify human–carnivore conflict (Crist et al. 2017), effective legal protection has helped some wild carnivore populations to expand (Chapron et al. 2014, Kuijper et al. 2016).

The consumption of anthropogenic sources of food is increasing in some carnivore species (Oro et al. 2013, Hopkins et al. 2014, Newsome et al. 2015), including waste from slaughtered livestock (Yirga et al. 2012, Ćirović et al. 2016). Reliance on food provided by humans can alter evolutionary and demographic processes in carnivores and lead to broad ecological changes (Oro et al. 2013). Although numerous studies have investigated factors affecting livestock predation in Africa (Ogada et al. 2003, Patterson et al. 2004, Kolowski & Holekamp 2006, Holmern et al. 2007, Sutton et al. 2017, Weise et al. 2018), the effect of discarded carcasses and body parts (together described here as 'livestock waste') on livestock predation is rarely investigated. In Ethiopia, the reduced production of livestock waste during periods of religious fasting can increase livestock predation (Yirga et al. 2012). By contrast, in Kenya, human refuse discarded in the vicinity of households was thought to increase livestock predation (Kolowski & Holekamp 2006).

As scavenging carnivores alter their foraging behaviour to utilize human waste (Hopkins et al. 2014, Newsome et al. 2015, Ćirović et al. 2016), we hypothesized that livestock waste attracts carnivores to households within 30 km of the boundary of Ruaha National Park (RNP) in central Tanzania, thereby increasing livestock predation, once other parameters affecting livestock predation are controlled for. We predicted that more wild scavenging carnivores would be attracted to households that produce larger than smaller amounts of livestock waste.

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As scavenging carnivores can turn to livestock predation when livestock waste is not available (Yirga et al. 2012), households producing large amounts of livestock waste are predicted to be particularly vulnerable to predation in periods when they produce little or no livestock waste (Table 1). Additionally, the total amount of anthropogenic food (livestock waste, discarded human refuse and livestock) available to wild carnivores in villages is expected to increase with the number of people living in the village. We predicted that households in villages with larger numbers of inhabitants would be more likely to experience livestock predation than those in villages with fewer inhabitants, provided wild carnivores are not deterred by the expected higher level of human threat and disturbance in larger than smaller villages and that the density of wild carnivores in areas surrounding larger villages is not reduced by the lower abundance of natural prey expected from more intensive bushmeat hunting around larger than smaller villages (Table 1).

In addition to the predicted effect of livestock waste on the likelihood of predation, we also investigated parameters unrelated to livestock waste that are expected to affect a household's likelihood of predation. Of these, the parameters with predicted negative effects (Table 1) on the likelihood of predation included: (1) the number of people in a household; (2) the number of domestic dogs owned; (3) increased distance from the RNP boundary; (4) the suitability of two surveyed areas for large carnivores; and (5) the effect of wet-to-dry season changes in the distribution of natural prey (Table 1). The parameters with predicted positive effects on the likelihood of predation were: (1) an increase in the number of livestock owned; (2) poorly constructed rather than adequately constructed livestock enclosures (*bomas*); and (3) crop production as an important component of household income (Table 1). Ultimately, our study aimed to identify the sources of livestock waste associated with increased livestock predation so that ways to reduce its production and improve its disposal could be found, as these might help reduce human–carnivore conflict fostered by livestock predation.

Methods

Study area

The study was conducted in two areas adjacent to the eastern boundary of RNP in central Tanzania, mostly within the Mbomipa–Idodi–Pawaga (MBOMIPA) and Waga Wildlife Management Areas (WMAs) and adjoining village land. In these WMAs, local communities manage wildlife resources and benefit from the revenues they generate (Lee & Bond 2018). RNP was established in 1964 and was expanded in 2008 to include the Usangu Game Reserve and associated wetlands, making it one of the largest (20.226 km^2) parks in Africa. The main source of surface water for wildlife in RNP during the dry season is the Great Ruaha River, which flows close to the eastern boundary of the park (Mtahiko et al. 2006).

The study area encompassed the transitional vegetation zone between the East African *Acacia–Commiphora* zone and the Southern African *Brachystegia* (*Miombo*) woodland zone. The climate is arid to semi-arid with an annual rainfall of 500–800 mm. Precipitation mostly occurs in the wet season (November–April) and rarely in the dry season (Stommel et al. 2016, Roug et al. 2020). Livestock predators in the area include spotted hyena (*Crocuta crocuta*), lion (*Panthera leo*), leopard (*Panthera pardus*), silver-backed jackal (*Canis mesomelas*), cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) (Dickman et al. 2014). Generally, lion, leopard and spotted hyena densities are higher in *Acacia–Commiphora* than *Brachystegia* habitats, and in *Acacia-Commiphora* habitats these carnivores occur at higher densities within RNP than the MBOMIPA WMA (Searle et al. 2021a). Leopards and spotted hyenas occur throughout the MBOMIPA WMA, whereas lions occur predominantly close to the national park/WMA boundary (Searle et al. 2021a).

The distances of the study villages from the RNP boundary (range 0.5–26.9 km) were supplied by RNP and categorized as 'near' (0–10 km from the park boundary) and 'far' (>10 km from the park boundary). Village council offices supplied the number of inhabitants in study villages (range 299–4763). Villages were categorized as 'small' (<1000 inhabitants), 'medium' (1000–3000 inhabitants) or 'large' (>3000 inhabitants). During daylight hours, livestock were herded to grazing and drinking locations. At night, cattle were kept in each household's main livestock enclosure (*boma*). Sheep and goats were often kept separately in other structures. Occupants of the study villages were ethnically diverse and included people from the Maasai, Barabaig, Sukuma, Hehe and Bena ethnic groups.

Questionnaires

A total of 160 structured questionnaires were conducted (10 randomly selected households in each of the 16 villages). Eight villages were surveyed in Area 1 (80 households in total) between November and December 2016 and eight villages were surveyed in Area 2 (80 households in total) between November and December 2017 (Table S1). Approval for the research was obtained from the leadership of each village. The purpose of the survey was explained to the village leadership and each respondent. Respondents were assured that the information they provided would be anonymous and only used for the purposes of the study, and for this reason raw data from households cannot be provided. Surveys were conducted either in Swahili by MMK or in a local language with the assistance of a local person experienced in translating questionnaire surveys into local languages. Respondents were asked to state the number of cattle, sheep, goats and adult domestic dogs they owned, the number of cattle, sheep and goats they slaughtered, were killed by predators or died from disease, starvation or accidents (which included animals lost while grazing) in the previous 12 months, what they did with diseased livestock carcasses and whether the growth and sale of crops were important for their household income. *Boma* construction was categorized by MMK as 'adequate' if it was likely to hinder easy access of large predators or 'poor' if not. 'Adequate' *bomas* were sturdy constructions of thorn bushes, poles and sometimes wire mesh.

Estimates of livestock financial value

During the study, the exchange rate for one US dollar (US$) was *c.* 2150 Tanzanian shillings (Tsh); hence, the mean purchase prices quoted by respondents for one adult cow (Tsh 598 125 ± 6268), sheep (Tsh 51 050 ± 661) and goat (Tsh 63 742 ± 4851) were approximately equivalent to US$278, US$24 and US$30, respectively. Estimated monetary losses associated with livestock deaths from predation, disease, starvation and accidents (Table S1) were calculated using these prices for adult animals.

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Table 1. The predicted effect of parameters on the likelihood of households within 30 km of the eastern boundary of Ruaha National Park (RNP) in central Tanzania, reporting the occurrence of cattle, sheep or goat predation in the previous 12 months. Included are biologically plausible parameters and those from referenced studies.

Parameter	Predicted effect on predation	References
Amount/reliability of household livestock waste	Positive: larger quantities and breaks in the supply of livestock waste increase predation.	Kolowski and Holekamp (2006), Yirga et al. (2012)
Number of people per household	Negative: livestock protection increases with household size	Ogada et al. (2003)
Adult domestic dogs owned	Negative: livestock protection increases with number of adult domestic dogs owned	Ogada et al. (2003)
Occurrence of livestock predation	Positive: predation on one livestock species increases the likelihood of predation on another livestock species	Ogada et al. (2003)
Number of cattle, sheep or goats	Positive: risk of predation increases with number of livestock owned	Michalski et al. (2006), Woodroffe et al (2007)
Household distance from RNP boundary	Negative (near > far): higher densities of large cats closer to (0–10 km) than further from (>10 km) RNP boundary increase predation	Abade et al. (2018, 2020), Searle et al. (2021a, 2021b),
Crop production	Negative (important > not): crop production curtails livestock protection	
Boma quality	Negative (adequate < poor): predation more likely in poorly than adequately constructed *bomas*	Lichtenfeld et al. (2015), Kissui et al. (2019)
Habitat suitability for carnivores	Negative (Area 1 > Area 2): higher density of predators expected in the area with less crop production and less open habitat	Abade et al. (2018)
Village size category	Positive (large > medium > small): larger villages contain more livestock waste, human food refuse and livestock than smaller villages Negative (large < medium < small): large villages have higher human disturbance and lower levels of natural prey in surrounding areas	Hofer et al. (1996), Rosenblatt et al. (2016)
Season	Negative (wet > dry): dry season aggregation of natural prey by surface water within RNP reduces livestock predation	Stommel et al. (2016), Abade et al. (2018)

Estimating livestock waste

In East Africa, livestock body mass depends on breed, sex, age and forage quality, and body mass declines in the dry season (Cole et al. 1964, Kanuya et al. 2006). As published mean body weights for common local breeds were 22.29 kg for long fat-tailed sheep and 20.50 kg for small East African goats (Shija et al. 2013), we applied a body weight of 20 kg for both sheep and goats. Zebu cattle are common in our study area and cattle herds are composed of more adult females than adult males. In order to be conservative when estimating cattle waste, we applied the relatively low adult body weight of 150 kg, even though adult males may weigh over 350 kg (Lesosky et al. 2013). The weight of discarded body parts from slaughtered livestock depends on carcass size, culinary culture and other uses of body parts. We assumed that the head, tail, skin, bones and gut contents were discarded, which together represent *c.* 25% of live weight (Cole et al. 1964, Shija et al. 2013). To be conservative when estimating livestock waste, we assumed discarded parts were 20% of live weight. Hence, the weight of discarded body parts from sheep and goat carcasses was 4 kg, and this figure was 30 kg for cattle carcasses. In order to avoid substantially overestimating cattle waste by not accounting for the unknown proportion of deaths that were juveniles, we used two-thirds of the weight of discarded body parts from cattle carcasses (i.e., 20 kg). Bones, hooves, tails and heads may be used for culinary and other purposes and then discarded.

The carcasses of cattle, sheep and goats that died of disease and were reported to be entirely discarded were estimated to produce 150, 20 and 20 kg of livestock waste, respectively. Carcasses from animals that died of disease that were reported to be utilized by households and those from animals that died of starvation or accidents (which were all assumed to be utilized) were estimated to produce 20, 4 and 4 kg of cattle, sheep and goat waste, respectively. Livestock waste from animals slaughtered for consumption was mostly discarded in an area designated by households for refuse disposal (<50 m from the dwellings). Discarded livestock carcasses were either buried in shallow pits or 'dumped in the bush' in the vicinity of households, typically within a few hundred metres.

Statistical analyses

We used separate binary logistic regression models for cattle, sheep and goats to examine the parameters likely to affect whether or not households reported the occurrence of predation of each species in the previous 12 months (Table S2). The households included in the model of cattle, sheep or goat predation were those that reported ownership of these livestock species during the previous 12 months. We included 21 parameters in our initial models, including parameters linked to livestock waste production (i.e., the number of cattle, sheep and goats slaughtered and the number of cattle, sheep and goats reported to have died of disease and starvation; Table S2). We expected the likelihood of predation to decline with better protection of livestock (provided by more people, more domestic dogs and adequate-quality *bomas*) and to increase with crop production and sale because this should reduce the time available for livestock protection (Table 1). Daytime guarding was not considered, as most (93.1%, n = 149) households reported the presence of one or more adult male herder.

Livestock predators such as lions, leopards and spotted hyenas (hereafter termed 'hyenas') differ in their adaptability to anthropogenic habitats (Kolowski & Holekamp 2009, Abade et al. 2018, 2020, Mkonyi et al. 2018, Searle et al. 2021a, 2021b). The greater importance of crop production in Area 2 than Area 1 (see the 'Results' section) suggests Area 2 was a more cultivated landscape than Area 1 and thus should be generally less suitable for wild carnivores than Area 1. The potential benefits to foraging carnivores associated with increasing village size category (more livestock, livestock waste and human refuse) may be traded off against increasing costs linked to village size (greater anthropogenic disturbance and declining natural prey abundance in surrounding areas because of bushmeat offtake). The density of lions (Abade et al. 2020, Searle et al. 2021a) and leopards (Abade et al. 2018,

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Searle et al. 2021b) is higher in RNP than in the WMAs flanking its eastern boundary; hence, livestock predation is expected to be higher closer to rather than farther from RNP (Table 1).

Our final models were selected using the Akaike information criterion (AIC). Starting with the full model (Table S2), we selected the model with the smallest number of parameters and the smallest AIC that differed by more than 2 from models with a larger number (or the full set) of parameters (Burnham & Anderson 2002).

We used Mann–Whitney U tests to compare the numbers of cattle, sheep, goats and dogs owned by households between Areas 1 and 2, the number of cattle deaths due to disease, starvation or accident between Areas 1 and 2 and whether *boma* quality was affected by the number of cattle owned. Pearson χ^2 tests were used to compare whether households in Areas 1 and 2 were equally likely to: (1) experience sheep or goat predation; (2) have *bomas* of adequate quality; and (3) state crop production and sale as being important to household income. Mean values, standard errors of the mean (SEM) and 95% upper and lower confidence limits (CL) are presented for quantitative results. Analyses were conducted using *SYSTAT* 13.0 (Systat Software, Inc., Richmond, VA, USA). The significance threshold was set at an α-level of $p \leq 0.05$.

Results

Livestock ownership, losses and protection

There was considerable variation between households in ownership and losses of cattle, sheep and goats (Table S3). Overall, 73.1% of households reported experiencing predation in the previous 12 months; 66.3% of households had an 'adequate' *boma* (Table S4), and these households owned more cattle than those with 'poor' *bomas* (Mann–Whitney U test, $U = 3617.0$, $p = 0.006$; Fig. S1). In addition, 92.5% of households owned domestic dogs (mean 4.6 ± 0.2, CL 4.1–5.0, range 0–13 domestic dogs per household).

Households in Area 1 owned more cattle than those in Area 2 ($U = 3250.0$, $p = 0.03$; Table S1) but not more sheep ($U = 2749.5$, $p = 0.12$) or goats ($U = 3052.0$, $p = 0.61$; Table S1). Cattle-owning households in Area 1 were more likely ($Z = 3.827$, $p = 0.0001$; Table 1) to report cattle predation (Area 1: 47.4%, Area 2: 17.7%; Table S1), and they reported a larger number of cattle killed by predators ($U = 3862.5$, $p = 0.0002$) than those in Area 2; hence, estimated monetary losses from cattle predation were higher for households in Area 1 than Area 2 (Table S1). Households in both areas were equally likely to experience sheep or goat predation (sheep predation, $\chi^2 = 0.254$, $df = 1$, $p > 0.05$; goat predation, $\chi^2 = 1.814$, $df = 1$, $p > 0.05$), and they did not differ in the numbers of sheep ($U = 3278.5$, $p = 0.74$) and goats ($U = 3435.5$, $p = 0.39$) lost to predation (Table S1). *Bomas* were more often scored as adequately constructed in Area 1 (60 adequate, 20 poor) than those in Area 2 (46 adequate, 24 poor; $\chi^2 = 5.45$, $df = 1$, $p = 0.02$). Households in Areas 1 and 2 owned similar numbers of adult domestic dogs ($U = 2805.5$, $p = 0.18$).

Cattle-owning households in Area 1 reported a larger number of cattle deaths from disease than those in Area 2 ($U = 3587.5$, $p = 0.02$). Cattle deaths from starvation ($U = 3345.5$, $p = 0.42$) or accidents ($U = 3293.0$, $p = 0.54$) were similar in both areas. Sheep-owning households in both areas reported similar numbers of sheep deaths from disease ($U = 3239.0$, $p = 0.76$), starvation ($U = 3148.5$, $p = 0.82$) and accidents ($U = 3239.0$, $p = 0.76$; Table S1). Goat-owning households in both areas also reported similar numbers of goat deaths from disease ($U = 2880.0$, $p = 0.14$), starvation ($U = 2951.5.0$, $p = 0.33$) and accidents ($U = 31035.0$, $p = 0.61$; Table S1). Crop production and sale were important to more household incomes in Area 2 than in Area 1 ($\chi^2 = 7.49$, $df = 1$, $p = 0.006$).

Parameters affecting livestock predation

The binary logistic regression model of the occurrence of cattle predation in households within a period of 12 months (likelihood ratio test, $G = -58.538$, $df = 16$, $p < 0.00001$, $AIC = 151.075$; Table 2) revealed that cattle predation was more likely: (1) in households in Area 1 than in Area 2; (2) as the number of cattle that were slaughtered and died from disease per household increased; and (3) as the number of sheep killed by predators increased. Cattle predation was less likely in households: (1) as the number of sheep deaths from starvation increased (whereas the number of cattle and goat deaths from starvation had no effect); 2)) as the number of people in a household increased; (3) at a greater (>10 km) than lesser distance category (0–10 km) to the RNP boundary; and (4) when crop production and sale were not important for household income.

The likelihood of households experiencing sheep predation in a period of 12 months ($G = -79.489$, $df = 9$, $p < 0.0001$, $AIC = 178.978$; Table 3) increased: (1) as the number of cattle killed by predators increased; (2) as the number of sheep deaths from starvation increased; and (3) in *bomas* scored as being in poor rather than adequate condition. Sheep predation was less likely as the number of cattle owned by households increased.

The likelihood of households experiencing goat predation ($G = -76.990$, $df = 5$, $p = 0.030$, $AIC = 165.980$; Table 4) within a period of 12 months ($n = 159$ households) changed with village size. Goat predation was more likely in medium-sized than small or large villages, with there being no significant difference between households in small and large villages.

Estimated livestock biomass taken by wild carnivores

In total, households reported predators killed 95 cattle, 92 sheep and 204 goats in 12 months, which represents an estimated 20 890 kg of livestock (14 250 kg cattle, 1840 kg sheep and 4800 kg goat) or 10.9 kg per household per month.

Estimated livestock waste potentially generated by households

Estimated amounts of livestock waste produced by households in a 12-month period (Table 5) were calculated from the number of 'utilized' carcasses (from livestock slaughtered and those that died from disease, starvation or accident) and diseased carcasses that were discarded whole. The estimated total waste from: (1) animals slaughtered by surveyed households was 8612 kg or 4.5 kg per household per month; (2) diseased carcasses (both utilized and whole) was 16 942 kg or 8.8 kg per household per month; (3) animals reported as dying from starvation was 2272 kg or 1.2 kg per household per month; and (4) animals reported as dying due to accidents was 776 kg or 0.4 kg per household per month. Overall, households produced an estimated 14.9 kg of livestock waste per month.

Discussion

Predation associated with cattle waste

Our estimates indicated that the largest components of livestock waste produced annually by households were from slaughtered

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Table 2. Factors affecting the likelihood of cattle predation within a 12-month period reported by 160 households within 30 km of the eastern boundary of Ruaha National Park, central Tanzania. Shown are logistic regression coefficient estimates and their standard errors (SE), Z-values and associated p-values and 95% confidence limits (CL) in natural log units. Parameters with negative coefficient estimates decreased the likelihood of cattle predation and those with positive coefficient estimates increased the likelihood of cattle predation. For parameters with binary categories, the reference value is in italics. Significant results are in bold.

	Regression coefficients					
	Estimate	SE	Z	P	95% CLs	
Parameter					Lower	Upper
Number of sheep killed by predators	0.907	0.306	2.968	**0.003**	0.308	1.506
Number of people in household	−0.203	0.076	−2.662	**0.008**	−0.352	−0.054
Distance category to park boundary *(far)*	−2.262	0.754	−3.002	**0.003**	−3.739	−0.785
Number of cattle slaughtered	0.305	0.130	2.350	**0.019**	0.051	0.559
Number of cattle deaths from disease	0.342	0.146	2.348	**0.019**	0.056	0.627
Number of cattle deaths from starvation	0.085	0.271	0.314	0.754	−0.446	0.617
Number of sheep slaughtered	−0.270	0.144	−1.441	0.150	−0.488	0.074
Number of goats slaughtered	0.139	0.112	1.242	0.214	−0.080	0.359
Number of sheep deaths from starvation	−0.754	0.287	−2.625	**0.009**	−1.317	−0.191
Number of goats deaths from disease	0.263	0.166	1.585	0.113	−0.062	0.588
Number of goats deaths from starvation	0.071	0.159	0.449	0.654	−0.240	0.382
Boma quality *(adequate)*	−0.743	0.580	−1.281	0.200	−1.880	0.394
Importance of crop sales to income *(0)*	−2.388	0.619	−3.860	**0.0001**	−3.599	−1.175
Area *(1)*	3.878	0.870	4.455	**0.0001**	2.172	5.584
Number of sheep owned	0.028	0.018	1.580	0.114	−0.007	0.064
Number of goats owned	−0.022	0.014	−1.561	0.119	−0.049	0.006
Constant	0.078	0.818	0.095	0.924	−1.525	1.681

Table 3. Factors affecting the likelihood of sheep predation within a 12-month period reported by 160 households within 30 km of the eastern boundary of Ruaha National Park, central Tanzania. Shown are logistic regression coefficient estimates and their standard errors (SE), Z-values and associated P-values and 95% confidence limits (CL) in natural log units. Parameters with negative coefficient estimates decreased the likelihood of sheep predation and those with positive coefficient estimates increased the likelihood of sheep predation. For parameters with binary categories, the reference value is in italics. Significant results are in bold.

	Regression coefficients					
	Estimate	SE	Z	P	95% CLs	
Parameter					Lower	Upper
Number of cattle killed by predators	0.380	0.178	2.133	**0.033**	0.031	0.729
Distance category to park boundary *(low)*	−0.420	0.403	−1.041	0.298	−1.209	0.370
Number of cattle deaths from disease	0.109	0.127	0.856	0.392	−0.140	0.357
Number of cattle deaths from starvation	−0.212	0.226	−0.940	0.347	−0.654	0.230
Number of sheep deaths from starvation	0.421	0.187	2.253	**0.024**	0.055	0.787
Number of goats deaths from starvation	0.236	0.172	1.861	0.063	−0.013	0.485
Boma quality *(adequate)*	1.018	0.467	2.181	**0.029**	0.103	1.932
Number of cattle owned	−0.023	0.008	−2.983	**0.007**	−0.039	−0.006
Number of goats owned	0.013	0.009	1.384	0.166	−0.005	0.031
Constant	−1.757	0.540	−3.255	0.001	−2.814	−0.699

and diseased cattle (Table 5). Consistent with the prediction (Table 1) that larger amounts of livestock waste attract more carnivores than smaller amounts, thereby increasing the chance of predation, we found that households were more likely to report cattle predation as the number of cattle that they slaughtered and that died from disease increased (Table 2). Households that produced larger annual amounts of cattle waste may represent relatively predictable feeding locations for scavenging carnivores, without the need for predation, throughout much of the year. However, during periods when little or no cattle waste is produced, regular scavengers may turn to cattle predation, as has been reported in Ethiopia, when scavenging hyenas turned to livestock predation during periods of religious fasting when the production of livestock waste declined (Yirga et al. 2012).

Predation associated with sheep and goat waste

Livestock in East Africa often succumb to starvation during the dry season when the availability and nutritional content of forage is low (Cole et al. 1964, Kanuya et al. 2006). We found that the likelihood of cattle predation declined as the number of sheep deaths from starvation increased (Table 2). As the far larger estimated amount of waste from starved cattle did not affect the likelihood of cattle predation, it is debatable whether the far smaller estimated amount of waste from starved sheep (Table 5) would do so. Instead, we suggest that increased sheep starvation probably occurs in the dry season, when natural prey aggregate near surface water (Stommel et al. 2016, Roug et al. 2020). This dry season change in the distribution of prey probably increases the foraging success of large carnivores inside RNP (Abade et al. 2020), leading to fewer foraging excursions outside the park and hence reduced cattle predation. Seasonal increases in natural prey elsewhere are also associated with decreased livestock predation (Woodroffe et al. 2005, Kolowski & Holekamp 2006).

Our results also revealed a positive association between the likelihood of households reporting sheep predation and sheep deaths from starvation (Table 3). As the amount of livestock waste produced by starving sheep was small compared to that from diseased and slaughtered sheep (Table 5), which did not affect sheep

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Table 4. Factors affecting the likelihood of goat predation within a 12-month period reported by 160 households within 30 km of the eastern boundary of Ruaha National Park, central Tanzania. Shown are logistic regression coefficient estimates and their standard errors (SE), Z-values and associated p-values and 95% confidence limits (CL) in natural log units. Parameters with negative coefficient estimates decreased the likelihood of goat predation and those with positive coefficient estimates increased the likelihood of goat predation. For the three categories of village size, the reference value was 'small' villages. For parameters with binary categories, the reference value is in italics. Significant results are in bold.

	Regression coefficients					
	Estimate	SE	Z	P	95% CLs	
Parameter					Lower	Upper
Cattle slaughtered	0.141	0.092	1.536	0.125	−0.039	0.321
People in household	−0.072	0.048	−1.499	0.134	−0.166	0.022
Importance of crop sales to income *(0)*	−0.473	0.399	−1.187	0.235	−1.255	0.308
Size category of village (*large*)	0.766	0.564	1.358	0.175	−0.340	1.872
Size category of village (*medium*)	1.316	0.505	2.603	**0.009**	0.325	2.306
Constant	−0.268	0.600	−0.406	0.685	−1.561	1.025

Table 5. The number of cattle, sheep and goats reported by households that were slaughtered and that died of disease (including diseased carcasses utilized in part or discarded whole), starvation or accident over a period of 12 months, the estimated amount of livestock waste (kg) produced per household per month (kg/HH/m) over a period of 12 months for animals that were slaughtered, starved or died in accidents and the combined value for waste from diseased animals, which includes estimated waste from both utilized carcasses and carcasses discarded whole, and the total estimated amount produced by surveyed households over a period of 12 months (total livestock waste).

Potential source of livestock waste	Cattle			Sheep			Goats			Total livestock waste (kg)
	Animals	Waste (kg)	kg/HH/m	Animals	Waste (kg)	kg/HH/m	Animals	Waste (kg)	kg/HH/m	
Slaughtered	292	5840	3.04	337	1348	0.70	356	1424	0.74	8612
Disease utilized	93	1860	7.30	68	272	0.90	60	240	0.69	2372
Disease discarded	81	12 150		67	1340		54	1080		14 570
Starvation	60	1200	0.63	99	396	0.21	169	676	0.35	2272
Accident	22	440	0.23	19	76	0.04	65	260	0.14	776

predation (Table S2), we doubt that waste from starving sheep directly affected sheep predation. Rather, this result possibly reflects an increased likelihood of sheep predation in the dry season. Sheep are less able to digest poor-quality forage than goats, and sheep lack the bipedal stance of goats that provides access to foliage and woody vegetation (Reshma Nair et al. 2021). As a result, sheep may be more nutritionally compromised during the dry season and hence more vulnerable to predation than goats.

Village size (Table S4) did not affect the likelihood of either cattle or sheep predation (Table S2) and was the only parameter affecting goat predation, with predation being more likely in medium-sized than larger or smaller villages (Table 4). This result may indicate a trade-off between the benefits and costs to predators of foraging within villages in different size categories. Foraging opportunities in terms of livestock predation and scavenging of livestock waste and human food in household refuse should increase with village size. However, foraging costs may also increase with village size in terms of reduced natural prey associated with increased bushmeat hunting and habitat change in addition to higher anthropogenic disturbance and threats. The carnivore species that regularly forage close to villages in different size categories may also differ. Lions generally avoid areas with high human disturbance, but this is not necessarily the case for hyenas, silver-backed jackals or leopards (Kolowski & Holekamp 2009, Abade et al. 2018, 2020, Mkonyi et al. 2018, Searle et al. 2021a, 2021b).

Estimates of livestock waste

Our estimates of livestock waste are probably inflated as we did not correct for the consumption of livestock waste by free-roaming domestic dogs, scavenging birds and other species and we assumed all livestock deaths involved adults, whereas an unknown number were probably juveniles. Hyenas probably obtain more food from the estimated 25.8 kg of livestock per households per month (10.9 kg from predation and 14.9 kg from livestock waste) than other scavenging carnivore species because their dentition allows for the ingestion of practically all parts of a carcass and their digestive system extracts nutrients from bone (Kruuk 1972, Houston 1988), which is not the case for other scavenging carnivores. Our estimates suggest that the amounts of food available to carnivores from livestock waste and predation were roughly similar.

Livestock predation not associated with livestock waste

We found that households closer to RNP were more likely to report cattle predation than those farther from the park (Table 1). This is in line with the findings of camera-trap studies indicating higher lion densities within RNP than in the MBOMIPA WMA and that lions rarely occur in the WMA away from the RNP/WMA boundary (Abade et al. 2020, Searle et al. 2021a). People living close to RNP view lions as a major threat to cattle (Dickman et al. 2014), which are an important financial asset and a component of social prestige (Loibooki et al. 2000). The killing of wild carnivores outside protected areas can be highly skewed towards lions (Dickman et al. 2014, Kissui et al. 2019) or more generally large cats (Holmern et al. 2007). Lion populations outside parks are considered particularly vulnerable to reductions in natural prey, habitat degradation and human disturbance (Ripple et al. 2014, Rosenblatt et al. 2016).

In line with the findings of Holmern et al. (2007) from an area within 30 km of the Serengeti National Park, we found no evidence

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that the likelihood of sheep (Table 2) or goat predation was affected by a household's distance from the RNP boundary. However, even though the likelihood of small stock predation was similar within a 30km zone of the RNP boundary, the carnivore species responsible for this predation probably changed with increasing distances from RNP, natural prey in the diet of wild carnivores may have declined and livestock waste, discarded human refuse and livestock probably increased.

Many studies have investigated how *boma* construction affects livestock predation (Kolowski & Holekamp 2006, Lichtenfeld et al. 2015, Sutton et al. 2017, Weise et al. 2018). Contrary to our predictions (Table 1), the likelihood of cattle predation was unaffected by our score of *boma* quality or the number of cattle owned per household (Table 2). Even so, households with larger numbers of cattle more often had adequate-quality than poor-quality *bomas*, suggesting a greater investment of time and resources in *boma* construction (Fig. S1). Our results indicate an association between cattle and sheep predation but not between cattle and goat or sheep and goat predation. Households experiencing cattle predation lost more sheep to predators than those that did not (Table 2), and households experiencing sheep predation lost more cattle to predators than those that did not (Table 3). Research on husbandry practices is required in order to interpret these results, which suggest that cattle and sheep are more closely associated (during daylight and/or at night) than either of these species are with goats.

Households in Area 1 owned more cattle (Table S1) and were more likely to experience cattle predation than households in Area 2 (Table 2). The difference in predation between our study areas may be explained by a lower suitability of the habitat in Area 2 for large carnivores due to it having more crop production and open habitat than in Area 1. As the surveys in both areas were conducted in the same months but in different years, differences in the likelihood of households reporting cattle predation between areas may also represent a year effect. However, as sheep (Table 3) and goat (Table 4) predation were not affected by area (Table S2), a year effect restricted to cattle seems doubtful.

In line with our prediction (Table 1) and the findings of Ogada et al. (2003), we found that the likelihood of cattle predation declined as the number of people in a household increased and that crop production was associated with an increased likelihood of cattle predation (Table 2). Neither household size nor crop production affected sheep or goat predation (Tables 3 & 4), perhaps because households devoted less time to preventing small stock predation.

Specific breeds of domestic dogs can reduce livestock predation (Gehring et al. 2010), but we found no evidence that the number of local adult domestic dogs owned per household reduced cattle (Table 2), sheep or goat predation (Table S3). Other studies either reported similar results (Kolowski & Holekamp 2006) or suggested that domestic dogs may reduce cattle predation but not sheep and goat predation (Ogada et al. 2003). This may in part be because small livestock are usually preyed upon by leopards and hyenas, which also prey upon domestic dogs (Kolowski & Holekamp 2006).

Financial losses

In line with previous studies (Soto-Schoender & Giuliano 2011, East et al. 2012, Dickman et al. 2014), our estimated mean monetary losses per household in both study areas from cattle deaths due to disease were higher than those due to predation, starvation or accidents (Table S1). Our estimated monetary losses may be inflated because the sale price for adult animals was applied even though these losses probably included juveniles. Ideally, the causes of livestock deaths should be verified and monetary losses determined from the age and condition of carcasses.

Livestock waste and African wild carnivores

Relatively little is known about the consumption of livestock waste by wild carnivores in Africa or its effects on either livestock predation or carnivore populations. If, as expected, natural prey populations continue to decline and livestock populations continue to increase, wild carnivores will probably include more livestock in their diet through predation and scavenging. The disposal of livestock waste by wild carnivores can have beneficial outcomes for both humans and scavenging carnivores (O'Bryan et al. 2018), but the presence of livestock waste may increase predation and fuel conflict between predators and people. Our results suggest that the disposal of livestock waste from slaughtered and diseased cattle at large distances from night *bomas* and grazing areas and assistance with measures to reduce cattle deaths from disease might reduce cattle predation and may reduce lethal responses to lions. Disposal of livestock waste and human food refuse well outside of villages may help to reduce goat predation. Whether or not these interventions have these desired outcomes can be experimentally tested (Eklund et al. 2017), and their effects on livestock and carnivore populations could be quantified.

Supplementary material. For supplementary material accompanying this paper visit https://doi.org/10.1017/S037689292200008X.

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