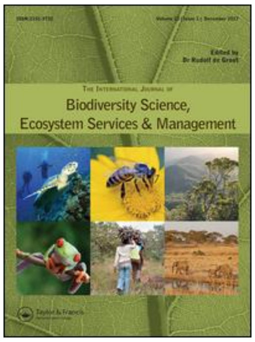

International Journal of Biodiversity Science, Ecosystem Services & Management

ISSN: 2151-3732 (Print) 2151-3740 (Online) Journal homepage: http://www.tandfonline.com/loi/tbsm21

Socio-economic correlates and management implications of livestock depredation by large carnivores in the Tarangire ecosystem, northern Tanzania

Felix J. Mkonyi, Anna B. Estes, Maurus J. Msuha, Laly L. Lichtenfeld & Sarah M. Durant

INTERNATIONAL JOURNAL OF BIODIVERSITY SCIENCE, ECOSYSTEM SERVICES & MANAGEMENT, 2017
VOL. 13, NO. 1, 248–263
https://doi.org/10.1080/21513732.2017.1339734

Taylor & Francis
Taylor & Francis Group

OPEN ACCESS Check for updates

Socio-economic correlates and management implications of livestock depredation by large carnivores in the Tarangire ecosystem, northern Tanzania

Felix J. Mkonyi[a,b], Anna B. Estes[a,c], Maurus J. Msuha[d], Laly L. Lichtenfeld[e] and Sarah M. Durant[f]

[a]School of Life Sciences and Bioengineering, The Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania; [b]Department of Biological Sciences, Dar es Salaam University College of Education, Dar es Salaam, Tanzania; [c]The Huck Institutes of the Life Sciences, Pennsylvania State University, University Park, PA, USA; [d]Tanzania Wildlife Research Institute, Arusha, Tanzania; [e]Tanzania People & Wildlife Fund, Arusha, Tanzania; [f]Institute of Zoology, Zoological Society of London, London, UK

ABSTRACT
Livestock depredation by large carnivores is the key source of human–carnivore conflict worldwide and entails financial losses to livestock keepers. We examined the extent and patterns of livestock depredation, the financial impacts of livestock losses and determinants of livestock depredation by large carnivores in the Tarangire ecosystem of northern Tanzania. Of 300 households surveyed, 74.7% reported losses of 1906 livestock to wild predators over 1.5 years, which represents an annual loss rate of 1.4% of their total herd. Spotted hyena (*Crocuta crocuta*) accounted for 70% of the total livestock loss, followed by leopard (*Panthera pardus*) (12%), African wild dog (*Lycaon pictus*) (8%), lion (*Panthera leo*) (7%) and cheetah (*Acinonyx jubatus*) (3%). This loss equated to a total financial loss of US$141,847 amounting to approximately US$633/household/year. Depredation frequency by all carnivore species increased significantly with increasing number of livestock owned, respondent's residency time, distance from the park boundary and declined significantly with increasing education, number of herders and improved fortified boma for cattle. Livestock depredation peaked during the wet season linked to seasonal migration of wild prey. Our study suggests that improving formal and conservation awareness education, boma fortification as well as improving herding practices could help mitigate the human–carnivore conflict.

ARTICLE HISTORY
Received 31 August 2016
Accepted 29 May 2017

EDITED BY
Carsten Smith-Hall

KEYWORDS
Financial losses; human–carnivore conflict; livestock depredation; livestock keepers; Tarangire ecosystem; wild predators

Introduction

Livestock depredation by large carnivores is one of the most important sources of human–carnivore conflicts as well as a major challenge threatening the conservation of large carnivores around the world (Woodroffe 2000; Treves & Karanth 2003). Large carnivores range widely, in such a way that existing protected areas (hereafter PAs) are not large enough to sustain their long-term viable populations (Woodroffe & Ginsberg 1998). Hence, due to their large home ranges and high dietary protein requirements, large carnivores tend to move outside PAs and overlap with human-dominated landscapes (Treves & Karanth 2003; Patterson et al. 2004; Woodroffe et al. 2005). This close proximity to humans often results in conflict due to the damage they cause to livestock (Woodroffe & Ginsberg 1998; Patterson et al. 2004). Outside PAs, large carnivores are killed either deliberatively or accidentally, thus making the borders a 'sink' in which human-caused mortality might limit survival of predators dispersing from the PAs (Woodroffe & Ginsberg 1998; Kolowski & Holekamp 2005; Kiffner et al. 2009). The economic losses associated with livestock depredation on local communities often provoke retaliatory and preventative killing of the large predators (Ogada et al. 2003; Patterson et al. 2004), which have a substantial impact on carnivore populations and thus jeopardize conservation efforts (Woodroffe et al. 2005; Dickman 2008). Consequently, reducing antagonism towards large carnivores following depredation will contribute towards their conservation and promoting coexistence between humans and large carnivores.

Rates of livestock depredation by large carnivores may be influenced by environmental conditions, e.g. abundance and distribution of natural prey (Mizutani 1999), seasonal patterns (Patterson et al. 2004), socio-ecological factors, livestock husbandry practices and characteristics of livestock enclosures (Ogada et al. 2003). In Tanzania, five large predators (lions, *Panthera leo*; leopards, *Panthera pardus*; cheetahs, *Acinonyx jubatus*; spotted hyenas, *Crocuta crocuta* and African wild dogs, *Lycaon pictus*) are chiefly responsible for livestock depredation (Holmern et al. 2007; Dickman 2008; Kissui 2008). Other carnivores (striped hyenas, *Hyaena hyaena* and caracal, *Caracal caracal*) occasionally prey on livestock as well. The Tarangire ecosystem is one of the richest wildlife areas in northern Tanzania. However, habitat

CONTACT Felix J. Mkonyi mkonyif@nm-aist.ac.tz
The supplemental material for this article can be accessed here.

loss and fragmentation associated with increasing human population and the conversion of land for agriculture and livestock grazing (Msoffe et al. 2011) have resulted in frequent encounters of large carnivores with humans and their livestock in this landscape. Livestock depredation by large carnivores entails economic damage to livestock keepers in Tanzania. However, diseases have been reported to contribute to far more livestock losses than depredation in other Tanzanian areas (Holmern et al. 2007; Nyahongo 2007; Kissui 2008; Nyahongo & Røskaft 2012).

Previous studies in the Tarangire ecosystem have focused either on actual livestock depredation events on a small set of carnivore species (Kissui 2008; Mponzi et al. 2014) or single species conflict i.e., human-lion conflict (Lichtenfeld 2005). In addition, patterns of livestock depredation by large carnivores have been well documented in Ruaha landscape (Dickman 2008) and western Serengeti National Park (Holmern et al. 2007). In this study, we build upon these previous studies by looking more broadly at the patterns of livestock depredation as well as ecological (distance to park boundary) and socio-economic factors (household size, education levels, number of livestock owned) influencing reported conflicts with a wide range of large carnivore species in the eastern part of the Tarangire ecosystem. There is currently limited information on these factors in our study area and across landscapes (Dickman et al. 2014; Hampson et al. 2015). Correspondingly, no empirical data are available on perceived costs of livestock depredation by large carnivores and other causes of livestock losses such as disease and theft on people's livelihoods in this ecosystem. The cost of livestock depredation may play a critical role in shaping people's attitudes and behaviour towards carnivores (Hazzah 2006; Kideghesho et al. 2007; Røskaft et al. 2007; Lyamuya, Masenga, Fyumagwa et al. 2014; Lyamuya, Masenga, Mbise et al. 2014, 2016; Bencin et al. 2016). Furthermore, despite the existing studies on the extent of livestock depredation in Tanzania, relatively few studies have investigated the key determinants (ecological and socio-economic factors) of perceived human–carnivore conflict (Holmern et al. 2007; Dickman 2008, 2010; Koziarski et al. 2016). A better understanding of the extent and patterns of livestock depredation and its drivers is important to developing the most effective conflict mitigation and conservation management strategies (Dickman 2008; Dickman et al. 2014).

Our specific objectives were to (1) determine the reported extent of conflict and patterns of livestock depredation by large carnivores in relationship to other causes of livestock losses, (2) estimate the financial livestock losses caused by large carnivores and other factors and (3) identify factors influencing livestock depredation by large carnivores. Based on our results, we suggest appropriate measures that might be taken to reduce human–carnivore conflict and contribute to improved conservation of large carnivores in the region. We hypothesized that (1) livestock depredation by large carnivores should be higher in households located closest to the PA than further away, (2) livestock depredation is influenced by socio-ecological (distance to park boundary, household size, education levels) and economic factors (number of livestock owned) and that (3) livestock husbandry practices will affect depredation rates. In this paper, we predicted that (1) livestock depredation would decline significantly with increasing distance from the park boundary (Patterson et al. 2004; Holmern et al. 2007), (2) livestock depredation would be negatively associated with social factors (household size, education levels), positively associated with economic factors (number of livestock owned) (Woodroffe et al. 2005; Holmern et al. 2007) and respondent's residency time (Newmark et al. 1993; Arjunan et al. 2006) and (3) livestock depredation would increase significantly during the wet season for non-resident lions, spotted hyenas, cheetahs and wild dogs in response to seasonal migration of wild prey (Kahurananga & Silkiluwasha 1997; Mponzi et al. 2014; Koziarski et al. 2016) – and vary independently with season by resident species such as leopard (Kissui 2008) and (4) improved livestock husbandry practices would be negatively associated with depredation because fortified bomas and increased number of herders should result in decreased depredation (Ogada et al. 2003; Woodroffe et al. 2007; Lichtenfeld et al. 2014).

Methods

Study area

The study was conducted in five villages (Loiborsoit, Terat, Emboret, Sukuro and Loibor Siret) of the Simanjiro Plains in Simanjiro district, northern Tanzania (Figure 1). Simanjiro district is located between 3°52′ and 4°24′S and 36°05′ and 36°39′E and lies within the Tarangire ecosystem of northern Tanzania. The Tarangire ecosystem (20,000 km^2) is defined by the movements of its migratory animals and consists of Tarangire National Park (TNP) (2850 km^2) forming the dry season range for the migratory herds, and its wet season dispersal area and calving grounds in Monduli (including Lake Manyara National Park, Lolkisale Game Controlled Area, Manyara Ranch, Burunge and Randilen Wildlife Management Area) and Simanjiro districts (including Simanjiro plains, Mkungunero Game Reserve) (Borner 1985). The area is characterized by

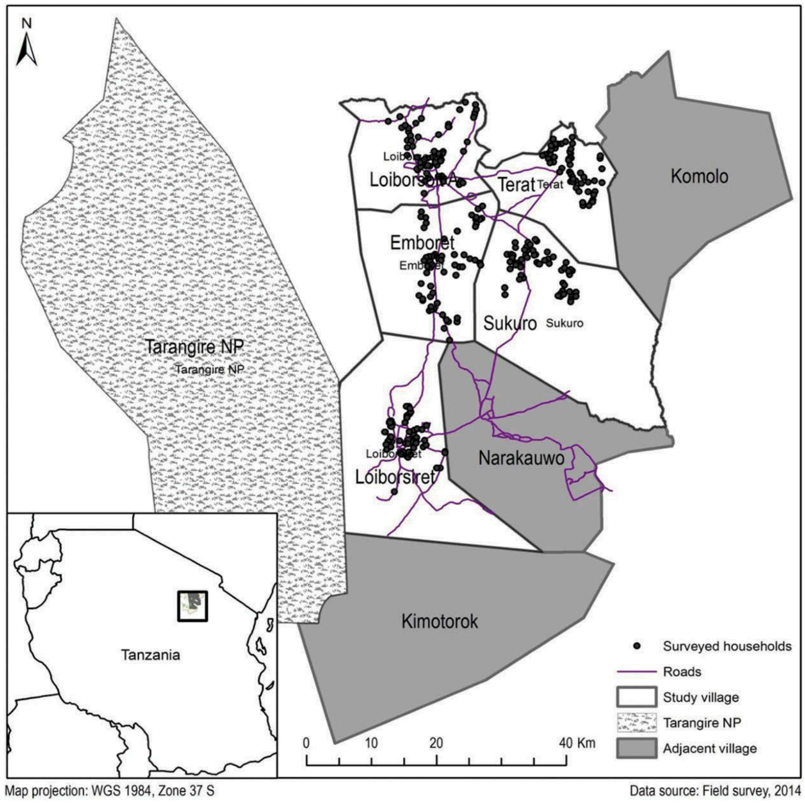

Figure 1. Map showing the location of the studied villages and the households interviewed in the survey.

bimodal rainfall averaging 650 mm per annum, with short rains from November to December and the long rains from March to May. The climate is highly seasonal with the dry season (June–October) and wet season (November–May).

The Simanjiro plains are one of the most important wet season dispersal and calving ranges for wildebeests (*Connochaetes taurinus*) and other ungulates such as zebra (*Equus burchellii*), hartebeest (*Alcelaphus buselaphus*) and fringe eared oryx (*Oryx beisacallotis*). During the wet season (November–May), about 50% of the wildebeest move from the TNP to the northern plains and the other 50% to the Simanjiro plains (Morrison & Bolger 2014). The plains are also important for non-migrant herbivores such as Thomson's gazelle (*Gazella thomsoni*), impala (*Aepyceros strepsiceros*) and an important area for livestock grazing by pastoralists during the dry season (June–October) (Kahurananga & Silkiluwasha 1997). Large mammalian fauna of the area includes lions *P. leo*, cheetahs *A. jubatus*, leopards *P. pardus*, African wild dogs *L. pictus*, striped hyenas *H. hyena* and spotted hyenas *C. crocuta*. African wild dogs are listed as Endangered, lions, cheetahs and leopard are listed as vulnerable, whereas striped hyenas are classified as Near Threatened and spotted hyenas as of Least Concern (IUCN 2016).

The major ethnic groups are the Maasai, Waarusha and Ndorobo. The Maasai are semi-nomadic pastoralists, with a very high dependency on livestock although they have also been practicing subsistence agriculture. Pastoral communities keep a variety of livestock including cattle, goats, sheep and donkeys. Waarusha, Ndorobo and some Maasai are agro-pastoralists who collectively practice subsistence agriculture and pastoralism.

Interview methods and questionnaire design

We used semi-structured questionnaire design to obtain data on perceived human–carnivore conflict. We consulted the village leaders and generated a numbered list of all eligible bomas included in the survey. Then, we selected 60 bomas from each village at random. The questionnaire survey was conducted between June and July in 2014. In designing the questionnaire, we followed the similar format used by Maddox (2003) in northern Tanzania and by Dickman (2008) in southern Tanzania (see Appendix S1, Supporting information). Pre-testing of the questionnaire was conducted on a sample of 15 respondents and revisions were made on the questionnaire to ensure clarity of the questions before the actual data collection started. The questionnaire contained both closed-ended as well as open-ended questions in order to gain more information on participant's attitudes and reasoning. We preserved the confidentiality of the respondent during the interviews. A questionnaire was administered in person by the principal investigator with the help of a local assistant and translator to 300 respondents. Within each boma, we counted the total number of households and utilized a random number generator to select a single household.

Where possible, respondents were selected from any of the three subjects (i.e. the head of the family [usually a man], the head's wife or elder son according to seniority). Women deferred to men in seniority, so respondents were predominantly male, but interviews were conducted with women where they were comfortable to do so. During the interviews, we tested the respondents' knowledge of focal carnivores using the cards of coloured photographs.

The final questionnaire contained six main sections; however, only two are applicable in this part of the study (Appendix S1). The first section focused on information relating to respondents' sociodemographics such as respondent's gender, age, ethnicity, religious beliefs, household size, education level, occupation, residency time, livestock holding, income sources and details on livestock number and type lost to wild predators compared with other causes in the month preceding the survey. The average market values of livestock species by age category (preferably adults) were obtained from livestock traders and the prices were translated to US$ at the exchange rate of the time of the survey (1US$ = 1659 TZS, June 2014). We estimated the direct economic or financial losses of livestock to wild predators and other causes of livestock loss per household based on the prevailing market price of livestock at the time of conducting this survey. The average market value for cattle, calf, small stock and donkey was US$372, US$120, US$48 and US$90, respectively (Table 2). The second section focused on questions about the characteristics of livestock depredation. Respondents were asked to estimate the number and type of livestock they had lost in the previous one and a half years (2013 to July 2014) to wild predators, including place of attack, time and season of attack.

The focus of this study was the reported livestock loss to the wild predators; therefore, we assume that the losses attributed to wild predators were often exaggerated, either deliberately or due to the unintentional attribution of livestock deaths to wild predators. We assumed a 1.5-year period conservative enough for respondents to recall the depredation incidents, and the financial costs are estimates based on these incidents. All respondents were adults (≥18 years of age) who could freely express themselves. The household was chosen as the sampling unit, adapting Maddox (2003) and Dickman (2008), and interviews were restricted to one respondent per household. The questionnaire was conducted in a local language (i.e. Swahili language – with the aid of a translator speaking Maasai where needed) and took approximately 1 h to complete. The research was cleared by the Tanzanian authorities. The Tanzania Commission for Science and Technology reviewed and approved the research protocol (ref. no. 2014-370-NA-97-20). Verbal Informed Consent was obtained from all the subjects prior to participation and data were kept anonymously.

Data analysis

Continuous variables were analysed using standard descriptive statistics (means, standard deviations [SD], ranges, percentages and frequencies of counts, tables and charts). Categorical variables including gender, occupation and education level were converted into a set of dichotomous, dummy-coded variables. The intensity of livestock depredation expressed as the total number of livestock reportedly killed by all predators and by each predator species separately at bomas and in the grazing area was used as a response or dependent variable within generalized linear mixed models (GLMMs) with a Poisson error distribution and a log-link function.

We included the number of owned livestock expressed in Tropical Livestock Units (TLU), respondent gender (male vs. female), respondent age (years), education level (none vs. primary, secondary and tertiary pooled), residency time (number of years since the respondent had arrived in the area), household size expressed in adult equivalent units (AEU), number of herders, distance (km) from the park boundary (measured as the nearest distance between household and the park boundary using *ArcGIS v.10.1* [ESRI, Redlands, USA]) and boma type (fortified or unfortified) as predictor variables in our models. Since households from one village were not statistically independent of each other, we included the village ID as a random effect. Therefore, we used GLMMs to determine the nature of the potential relationship between response variables and all the potential predictor variables. Further descriptive statistics of explanatory variables used in the GLMMs are presented in Table S1, Supporting information. To control for variation in household size, the household size was measured in terms of AEU. The adult-equivalent conversion factors for the number of people in the household by Latham 1965, cited by Collier et al. (1990), were used to determine the AEU as presented in Table S2, Supporting information. First, in order to calculate AEU, the sex and age of surveyed household members were compiled (Cavendish 2002). Second, the AEU by age and sex were summed up for all people in the household to compute the total AEU for the particular household.

For better comparison of herd sizes across households and to account for differences in size and value of different livestock species, we converted number of reported livestock to standard units (i.e. TLUs; see also Table 1). The following conversion factors were used for each species of livestock: one head of

Table 1. Livestock holdings expressed in Tropical Livestock Units (TLU) per adult equivalent unit (AEU) in the study villages in Simanjiro district, Tanzania (2014).

		Livestock type			
Village	*N*	Cattle	Small stock	Donkey	Mean[a]
Loibor Siret	60	20.90	5.05	0.52	26.46
Sukuro	60	20.76	4.58	0.46	25.80
Terat	60	10.55	2.98	0.63	14.16
Emboret	60	16.68	3.83	0.58	21.09
Loiborsoit	60	12.07	2.56	0.61	15.24
Mean ± SD		16.19 ± 4.29	5.87 ± 1.26	3.55 ± 1.22	25.61 ± 5.53
% of the total herd		37.15	61.05	1.80	100
Livestock per AEU		16.19	5.87	3.55	25.61

N: Number of households sampled in the study villages.
[a]Mean TLU per AEU.
TLU conversion factor: 1 head of cattle = 0.7 TLU, 1 sheep or goat (small stock) = 0.1 TLU, 1 donkey = 0.5 (source: Jahnke 1982; LEAD 1999).
The Tropical Livestock Unit (TLU) is commonly taken to be an animal of 250 kg live weight.

Table 2. Financial valuation (in US$) of reported livestock kills (*n*) by large carnivores in the study villages in Simanjiro district, Tanzania, over a period 2013–July 2014.

	Unit value (US$)	Lion	Cheetah	Leopard	Spotted hyena	African wild dog	Overall
Cattle	$371.91	$37,191 (100)	$0	$0	$18,595.5 (50)	$0	$55,786.5 (150)
Calf	$120.00	$0	$0	$0	$1320 (11)	$480 (4)	$1800 (15)
Small stock	$47.84	$1243.84 (26)	$2583.36 (54)	$11,098.88 (232)	$60,278.4 (1260)	$6984.64 (146)	$82,189.12 (1718)
Donkey	$90.04	$270.12 (3)	$90.04 (1)	$0	$1710.76 (19)	$0	$2070.92 (23)
	Total loss	$38,704.96 (129)	$2673.4 (55)	$11,098.88 (232)	$81,904.66 (1340)	$7464.64 (150)	$141,846.5 (1906)
	Mean loss – per AEU[a]	129.02 (0.43)	8.91 (0.18)	37.00 (0.77)	273.02 (4.47)	24.88 (0.50)	472.8 (6.35)
	Mean loss – per AEU[b]	172.79 (0.58)	11.93 (0.25)	49.55 (1.04)	365.65 (5.98)	33.32 (0.67)	633.2 (8.51)
Loss as % of total herd		6.77	2.89	12.17	70.30	7.87	100
	Annual cost	$25,803	$1782	$7399	$54,603	$4976	$94,563

Numbers in parentheses represent the numbers of individuals killed (*n*).
AEU: Adult equivalent unit.
The conversion rate in accordance with prevailing market rates at the time of the survey 1US$ = 1659 Tanzanian shillings.
[a]Considering all the respondents (n = 300).
[b]Considering only the respondents who reported loss (n = 224).

cattle = 0.7, one goat or sheep = 0.1 and one donkey = 0.5 (Jahnke 1982; LEAD/FAO 1999). Total TLU = Livestock Nr × TLU factor. The overall TLU per respondent was then adjusted to 1 TLU being equivalent to an animal with a body weight of 250 kg (Jahnke 1982; LEAD/FAO 1999). Because the factors influencing depredation in the grazing area were distinct from those that influence depredation at bomas, we performed analyses separately for the two distinct contexts. Therefore, we analysed explanatory variables separately for each predator species and for all predators combined and eventually running six separate model sets with all possible variable combinations within GLMMs (Tables S4–S6, Supporting information).

We checked for multicollinearity of the predictor variables using Spearman's correlation coefficients (r_s) for all possible variable pairs. We chose a cut-off of $r_s \geq 0.6$ to indicate high collinearity between predictor variables (Zuur et al. 2010). Using this approach resulted in the exclusion of one of the highly correlated variables from the analysis (see Table S1, Supporting information).

Age was correlated with education, respondent's residency time and number of herders. Moreover, gender was correlated with education, respondent's residency time, household size (adult equivalents) and number of owned livestock (livestock units). In addition, the number of owned livestock (livestock units) was correlated with household size (adult equivalents) and respondent's residency time (Table S3, Supporting information). However, there was no strong collinearity detected among these predictor variables (all $r_s < 0.6$), suggesting that any collinearity among variables was unlikely to affect statistical inference (Zuur et al. 2010). In contrast, boma type small stock was highly correlated ($r_s = 0.76$) with boma type cattle (Table S3, Supporting information) and we therefore excluded boma type small stock from subsequent analyses. Eventually, a total of nine variables were included in the models [age, gender, education level, respondent's residency time, household size (adult equivalents), livestock units, number of herders, distance to park boundary and boma type cattle] (Table S1, Supporting information). We ranked candidate models in order of parsimony based on the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc) and model weights (ω_i) (Burnham & Anderson 2002). We computed model-averaged coefficients of predictor variables based on top-ranked models. We considered all models with ΔAICc < 2 to be equally plausible (Burnham & Anderson 2002).

We chose GLMMs with a Poisson error, the most appropriate distribution for count data because they take into account both fixed and random effects in a single model and deal with non-normal response variables (Zuur et al. 2010). We had six Poisson distributed target/response variables (i.e. number of livestock killed by all predators and number killed by lion, leopard, cheetah, spotted hyena and wild dog). We used the Pearson's chi-squared analyses to test the observed frequency of predation on various types of livestock, contexts of livestock attack events by the five carnivores and the nature of the relationships among independent variables. All statistical analyses were performed using *SPSS v. 22.0* (SPSS Inc., Chicago, IL, USA) and the significance level was measured at $p < 0.05$.

Results

Respondents' demographic, livestock holdings and socio-economic characteristics

Overall, the majority of respondents were the Maasai (96%, n = 288) and the rest were the Waarusha (4%, n = 12). The age group of the respondents ranged from 18 to 92 years old, with an overall mean age of 35.86 ± 14.19 (SD) years. Overall, more males (88.3%, n = 265) than females (11.7%, n = 35) participated in this survey, probably because the Maasai women do not speak in the presence of men or because women deferred to men in seniority. The mean household size (in AEU) was 6.88± (SD 2.11) persons per household ranging from 2 to 12 persons.

Almost all respondents (99%) reported owning cattle, 99% reported owning goats and sheep (hereafter referred to as 'small stock') and 89.3% reported owning donkeys. Total stock holdings were estimated at 93,382 head of livestock (i.e. total TLUs = 7938) in all surveyed households. Mean TLU values ranged between 14.16 and 26.46 per household. The overall mean TLU per household was 25.61± (SD 5.53) (Table 1). Livestock number varied across households but consistently cattle were the dominant livestock species (Table 1, Figure 2). There was a slightly higher mean TLU per household in Loibor Siret and Sukuro due to a relatively high number of cattle and small stock in these villages (Figure 2). On average, respondents from Terat had less livestock (14.16 TLU) compared to other villages.

The majority of respondents were agro-pastoralists 95% (n = 285), while 5% (n = 15) were pastoralists. Of the 300 respondents, 51.3% (n = 154) had no formal education, while the rest had formal education: i.e. 36% (n = 108) primary education, 11.3% (n = 34) secondary education and 1.3% (n = 4) tertiary education. The main source of cash income for respondents was the sale of livestock (91%, n = 272), selling crops (27.3%, n = 82), off-farm activities (35%, n = 105, i.e. business, salaried or casual employment) and fewer people relied on other income generating activities (1.3%, n = 4, i.e. operating a restaurant business and sewing beads, construction works and bee keeping).

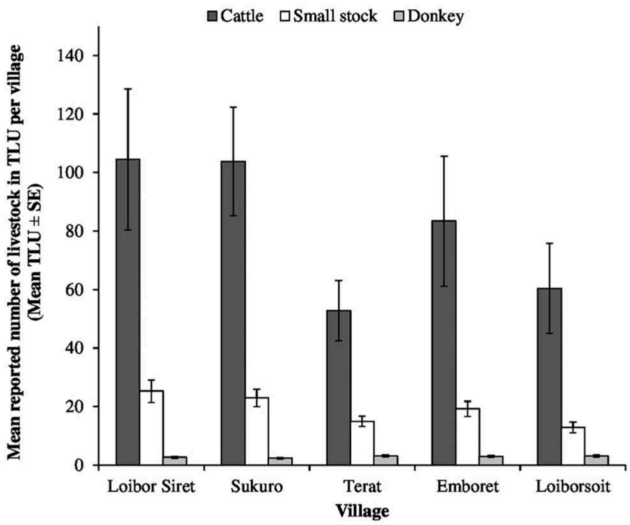

Figure 2. Mean livestock holdings recorded according to location surveyed in Simanjiro district, Tanzania, in 2014, expressed in Tropical Livestock Units (mean TLU ± SE).

Livestock losses due to depredation in relationship to other causes

Seventy-five per cent (n = 224) of respondents reported the loss of 1906 livestock to predators over a 19-month study period (Table 2). Spotted hyenas were reported to be responsible for most of the attacks on livestock (70.3%), followed by leopards (12.2%), African wild dogs (7.9%), lions (6.8%) and cheetahs (2.9%). In addition, cattle 23.5% (n = 56), small stock 75.6% (n = 180) and donkeys 0.8% (n = 2) were occasionally injured in these attacks. Cheetahs, spotted hyenas, leopards and African wild dogs were the main predators of small stock (98.5%) while lions depredated mostly on cattle (59.2%) (Figure 3). Depredation on donkeys was reported to be caused mainly by spotted hyenas (83.3%). Wild dogs (2.4%) were occasionally reported to prey on calves. Depredation frequency varied between livestock species (χ^2 = 846.49, df = 8, $p < 0.001$; Figure 3). Non-predator livestock losses were reported to be associated with diseases particularly Heart water (77.3%), Contagious Bovine Pleuropneumonia (18.2%), East Coast Fever (2.5%), Contagious Caprine Pleuropneumonia (1.4%), diarrhoea (0.5%) and anthrax (0.2%).

Reported causes of livestock losses during a 1-month preceding the survey showed that disease was the main cause of livestock loss, followed by depredation, theft and other causes (snake bites, accidents and buffalo assaults). Overall, disease accounted for 90.8% of all stock losses initially reported, depredation 7.1%, theft 1.3% and all other losses 0.8%. On average, a significantly higher proportion of livestock were reportedly lost to diseases compared to other causes of livestock loss (χ^2 = 4205.70, df = 3, $p < 0.001$). The percentage of stock reportedly lost to depredation over a 1-month period showed that Sukuro (11.8%) had the highest

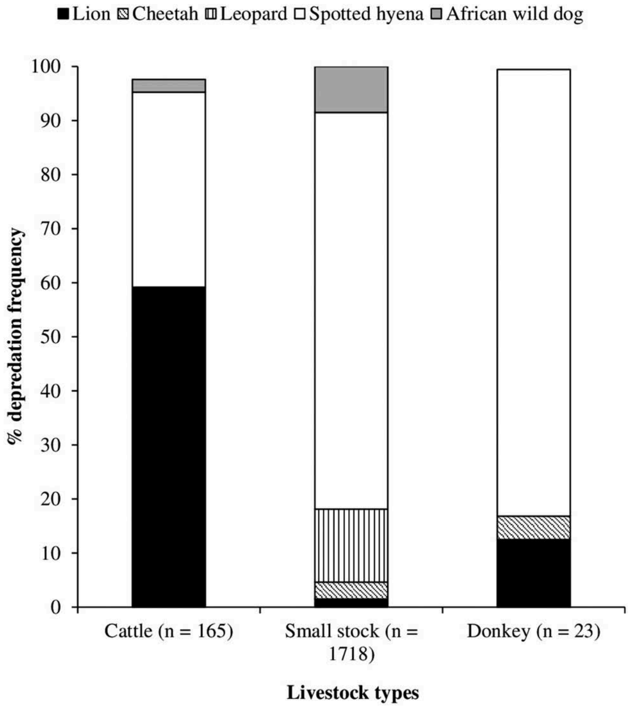

Figure 3. Percentage frequencies of reported attacks of predators on different livestock types in Simanjiro district, Tanzania, over a period of 2013–July 2014. Total numbers of attacks of each type are shown in parentheses.

rates of reported depredation, followed by Loibor Siret (6.5%) and Loiborsoit (5.8%), while the remaining villages constituted 4.4% in total. The average annual loss of the total herd to predators was 1.4% when considering the stocking rate in 2014 (ca. 93,382 total stock) and a total of 1906 depredated livestock.

Contexts of livestock depredation

The contexts of attacks on livestock varied among predators. Spotted hyenas were reported to attack livestock at bomas more often than when grazing at pasture (χ^2 = 1016.34, df = 1, $p < 0.001$), whereas the attacks by cheetahs (n = 55) and wild dogs (n = 150) were reported to occur during the day (in the grazing areas). In contrast, lions and leopards were reported to attack livestock held in boma enclosures during the night as well as the grazing livestock during the day. However, attacks by lions (χ^2 = 0.12, df = 1, p = 0.724) and leopards (χ^2 = 0.52, df = 1, p = 0.469) did not vary significantly between the two contexts. Overall, 75.7% of predator attacks on livestock were reported to occur during the night at bomas, while 24.3% occurred during the day at pasture.

Spatial patterns of livestock depredation

We found that the spatial patterns of livestock depredation were unevenly distributed across the studied villages. The frequency of livestock reportedly lost to different predators differed significantly between villages (χ^2 = 657.51, df = 16, $p < 0.001$). During the 19-month study period, the highest depredation levels were reported in Sukuro (23.2%), Emboret (22.9%) and Loiborsoit (21.9%), with slightly lower levels reported in Terat (17.0%) and Loibor Siret (14.9%). The mean annual livestock loss as reported for all predators was 8.51 head of stock per household (of those that reported loss) (Table 2). Wild dogs and leopards were reported to cause more attacks in Loibor Siret (67.3%, n = 101 and 39.2%, n = 91, respectively). Spotted hyenas were more often reported to have killed livestock than any other predator in all villages, but less frequent in Loibor Siret (3.5%, n = 47). In contrast, lions were reported to have killed more cattle in Loiborsoit (35.7%, n = 46).

Seasonal patterns of livestock depredation

More than three-quarters (76%) of reported attacks by all carnivore species occurred during the rainy season, while 24% were reported to have occurred in the dry season. Spotted hyenas, lions, cheetahs and leopards were reported to attack livestock significantly more often in the wet season than dry season (spotted hyenas: χ^2 = 448.23, df = 1, $p < 0.001$; lions: χ^2 = 12.40, df = 1, p = 0.0004; cheetahs: χ^2 = 21.02, df = 1, $p < 0.001$; leopards: χ^2 = 40.56, df = 1, $p < 0.001$; African wild dogs: χ^2 = 6.41, df = 1, p = 0.01; Figure 4(a)). Overall livestock depredation peaks were greatest in April and May during the wet season (Figure 4(b)).

Financial valuation of livestock losses

The total estimated financial loss for those people interviewed corresponding to 1906 depredated livestock was US$141,847 (equivalent to 235,324,173 Tanzanian shillings) (Table 2). Spotted hyenas accounted for 70.3% (US$81,905) of the total herd and 57.7% financial loss, while lions accounted for 6.8% (US$38,705) of the total herd and 27.3% of financial loss (Table 2). The financial loss due to other predators was comparatively low (Table 2). On average, the annual financial loss per household was estimated to be US$633 (of those that reported loss) and US$473 (considering all the respondents). On average, the financial loss per household (of those that reported stock losses) was estimated to be US $464 during the wet season and US$168 during the dry season. The greatest proportion of stock and financial losses were reported on small stock in proportion to their relative abundance (US$82,189, n = 1718) (Tables 1 and 2). There was a significant difference in terms of financial valuation of livestock species losses (χ^2 = 951, df = 12, $p < 0.001$, n = 1906) and in terms of financial impact among the predators

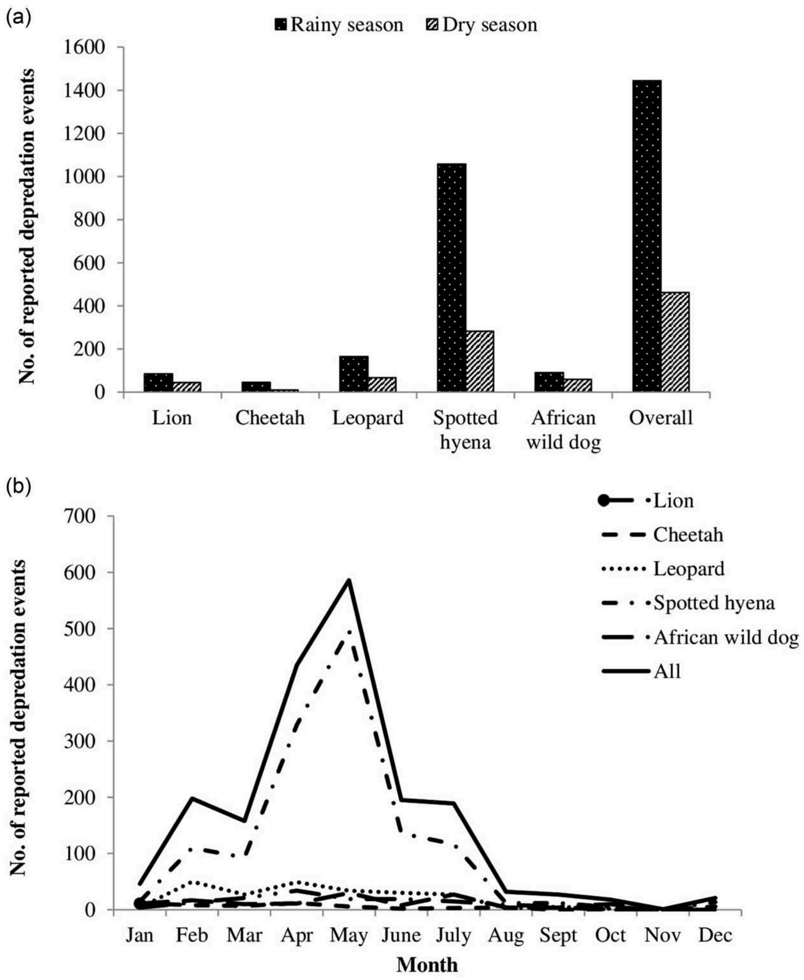

Figure 4. Reported frequencies of livestock depredation by predator species according to (a) season and (b) month in the Tarangire ecosystem during 2013–July 2014.

(χ^2 = 78,020, df = 12, p < 0.001). On average, the financial loss due to various livestock diseases for the month preceding the survey ranked highest US $147,235 (US$491 per household), followed by depredation US$7968 (US$27 per household) and theft US $1695 (US$6 per household) (Table 3). The total financial loss of livestock to large carnivores was relatively higher in Sukuro (US$339,559.30) and lowest in Loiborsoit (US$103,522.60) (Table 3).

Ecological and socio-economic factors associated with livestock depredation

For all predators combined, model selection using AICc identified two models (ΔAICc < 2; Table S4). In the top model, the reported frequency of livestock depredation (all predators combined) was positively associated with distance to park boundary, respondent's residency time and livestock units, but negatively associated with education level, boma type cattle and number of herders in the grazing area (Table 4). Nevertheless, the reported frequency of livestock depredation by lions at bomas was best explained by the global model containing age, gender, education level, respondent's residency time, household size (AEU), distance to park boundary, boma type cattle and livestock units as significant factors (Table S5, Supporting information). The reported frequency of livestock depredation by lions declined significantly with increasing level of education, distance from the park boundary and household size (AEU) (Table 5). Moreover, reported depredation frequency was lower among female interviewees compared to males. In addition, reported depredation frequency declined significantly with age and improved boma for cattle but declined (non-significantly) with number of herders in the grazing area (Table 5). Conversely, reported depredation frequency increased significantly with increasing livestock units and respondent's residency time at their households. On the other hand, the top model for spotted hyenas contained education level, respondent's residency time, livestock units, distance to park boundary and boma type cattle at bomas, while in the grazing area, contained livestock units and number of herders as significant factors (Table S5, Supporting information). The reported frequency of livestock depredation by spotted hyenas increased significantly with increasing distance from the park boundary, respondent's residency time,

Table 3. Livestock reportedly lost to depredation, diseases, theft and other causes in the study villages in Simanjiro district, Tanzania.

	Loibor Siret		Sukuro		Terat		Emboret		Loborsoit		Overall mean values (US$)	
	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock	Cattle	Small stock
Mean value of livestock	348.6	36.9	431.9	57.1	369.2	57.1	331.5	42.6	378.2	45.5	371.9	47.8
Livestock loss (US$)												
*Overall depredation	6274.8 (18)	9557 (259)	9069.9 (21)	24,096.2 (422)	7753.2 (21)	17,244.2 (302)	11,934 (36)	17,082.6 (401)	20,422.8 (54)	16,243.5 (357)	11,090.94	16,844.72
**Depredation	6274.8 (18)	885.6 (24)	4319 (10)	14,446.3 (253)	2953.6 (8)	5767.1 (101)	331.5 (1)	894.6 (21)	2647.4 (7)	1319.5 (29)	3305.26	4662.62
**Disease	101,791 (292)	30,516.3 (827)	218,973 (507)	87,077.5 (1525)	58,703 (159)	70,575.6 (1236)	70,941 (214)	33,313 (782)	44,627 (118)	19,656 (432)	99,006.96	48,227.68
**Theft	3834.6 (11)	1512.9 (41)	0	342.6 (6)	0	0	0	213 (5)	1891 (5)	682.5 (15)	1145.12	550.2
**Others	0	1217.7 (33)	0	0	0	57.06 (1)	331.52 (1)	0	0	0	66.30	254.95
Total financial loss (US$)	**111,900 (321)**	**42,804 (1160)**	**228,043 (528)**	**111,516.3 (1953)**	**66,456 (180)**	**87,876.8 (1539)**	**83,206.5 (251)**	**50,608 (1188)**	**66,940.6 (177)**	**36,582 (804)**	**111,309.34**	**65,877.55**

Only financial losses for adult cattle and small stock are calculated here.
**Based on numbers of livestock reported lost to depredation, diseases, theft and other causes for the month preceding the survey (number of livestock lost are shown in parentheses).
*Based on overall livestock reported lost to depredation over a period 2013–July 2014.
Mean value of livestock: Calculated using the exchange rate at the time of conducting this survey 1US$ = 1659 Tanzanian shillings.
Bold values signify the overall or total economic/financial loss and number (in parentheses) of each livestock type due to depredation, disease, theft and other causes for the month preceding the survey across villages.

Table 4. Summary statistics of model-averaged estimates of coefficients (β) derived from the top model, standard error (SE), *t*-statistic and its 95% confidence interval (CI) from generalized linear mixed models (GLMMs) explaining the reported frequency of livestock depredation by all predators and by leopard in the Tarangire ecosystem, Tanzania 2014.

Parameter	*Estimate (β)*	*SE*	*t-Statistic*	*p-Value*	*Lower 95% CI*	*Upper 95% CI*
a. *At bomas*						
All predators						
Intercept	1.380	0.208	6.646	<0.001	0.971	1.788
Education	−0.450	0.233	−1.933	0.044	−0.908	0.008
PA distance	0.008	0.006	2.202	0.030	0.005	0.020
Residence time	0.055	0.016	3.363	0.001	0.023	0.087
TLU	0.001	0.001	2.405	0.017	0.000	0.002
Boma type cattle	−1.675	0.217	−7.712	<0.001	−2.102	−1.247
Leopard						
Intercept	−0.404	1.305	−0.310	0.757	−2.972	2.163
Residence time	0.026	0.025	1.048	0.296	−0.023	−0.075
Household size (AEU)	−0.344	0.038	−9.060	<0.001	−0.419	−0.269
PA distance	−0.016	0.041	−0.391	0.696	−0.096	0.064
b. In the grazing area						
All predators						
Intercept	1.758	0.456	3.854	<0.001	0.855	2.661
Number of herders	−0.999	0.244	−4.090	<0.001	−1.482	−0.515
Leopard						
Intercept	−0.075	0.482	−0.155	0.877	−1.029	.880
TLU	0.001	0.001	2.223	0.028	0.000	0.002
Number of herders	−0.982	0.290	−3.382	0.001	−1.556	−0.407

PA distance: distance from the park boundary; TLU: total number of livestock owned expressed in Tropical Livestock Unit; AEU: adult equivalent unit. Species-specific models were computed separately for (a) depredation at bomas and (b) depredation in the grazing area. All models consisted of village ID as a random effect. The significance level was set at $p < 0.05$.

Table 5. Summary statistics of model-averaged estimates of coefficients (β) derived from the top model, standard error (SE), *t*-statistic and its 95% confidence interval (CI) from generalized linear mixed models (GLMMs) explaining the reported frequency of livestock depredation by lions and spotted hyenas in the Tarangire ecosystem, Tanzania 2014.

Parameter	*Estimate (β)*	*SE*	*t-Statistic*	*p-Value*	*Lower 95% CI*	*Upper 95% CI*
a. *At bomas*						
Lion						
Intercept	0.255	0.192	1.327	0.186	−0.123	0.633
Age	−0.045	0.002	−17.720	<0.001	−0.050	−0.040
Gender	−1.593	0.056	−28.318	<0.001	−1.704	−1.482
Education	−0.496	0.056	−8.800	<0.001	−0.607	−0.385
PA distance	−0.014	0.002	−6.964	<0.001	−0.018	−0.010
Residence time	0.012	0.002	4.919	<0.001	0.007	0.017
TLU	0.002	7.5074E-05	20.735	<0.001	0.001	0.002
Household size (AEU)	−0.156	0.016	−9.858	<0.001	−0.187	−0.125
Boma type cattle	−1.607	0.045	−35.945	<0.001	−1.695	−1.519
Spotted hyena						
Intercept	1.149	0.589	1.948	0.052	−0.012	2.310
Education	−0.426	0.267	−1.598	0.111	−0.951	0.099
PA distance	0.016	0.001	11.333	<0.001	0.013	0.019
Residence time	0.059	0.020	2.919	0.004	0.019	0.098
TLU	0.001	0.001	2.259	0.025	0.000	0.002
Boma type cattle	−1.981	0.233	−8.490	<0.001	−2.440	−1.522
b. In the grazing area						
Lion						
Intercept	−1.428	0.498	−2.865	0.005	−2.415	−0.441
Number of herders	−0.083	0.281	−0.296	0.768	−0.640	0.474
Spotted hyena						
Intercept	1.863	1.246	1.495	0.138	−0.605	4.331
TLU	−0.004	0.001	−5.144	<0.001	−0.006	−0.003
Number of herders	−2.207	0.692	−3.189	0.002	−3.577	−0.836

PA distance: distance from the park boundary; TLU: total number of livestock owned expressed in Tropical Livestock Unit; AEU: adult equivalent unit. Species-specific models were computed separately for (a) depredation at bomas and (b) depredation in the grazing area. All models consisted of village ID as a random effect. The significance level was set at $p < 0.05$.

livestock units and declined significantly with improved boma for cattle. However, reported depredation frequency decreased (non-significantly) with increasing level of education and declined significantly with increasing livestock units and number of herders in the grazing area (Table 5).

At bomas, the reported frequency of livestock depredation by leopard was best explained by household size (AEU) (statistically significant) (trend: reported depredation frequency declined with increasing household size), respondent's residency time [trend: reported depredation frequency increased (non-significantly) with residency time] and distance to park boundary [trend: reported depredation frequency declined (non-significantly) with increasing distance from the park boundary]

(Table 4). The best-fitting model for wild dog contained two variables; livestock units and number of herders, all showing a negative trend (Table 6, Table S6 Supporting information). However, only livestock unit reached a statistical significance. In the case of cheetahs, the reported frequency of livestock depredation decreased (non-significantly) with increasing livestock units and increased (non-significantly) with number of herders (Table 6).

Discussion

Livestock losses due to depredation in relationship to other causes

Our results showed that 75% of people reported carnivore attacks in their households, which is equivalent to an average of 1.4% of the total herd loss per annum. This figure is within the range of 0.02–2.6% worldwide losses to large carnivores reported by Graham et al. (2004) and is far more than 0.26% of the total herd reported in Ruaha National Park (Dickman 2008), and much less compared to 12% of the total herd reported in Loliondo and Ngorongoro buffer zones (Maddox 2003).

Interestingly, we found that carnivore species preyed selectively upon different livestock species corresponding to the size of the predator and in accordance with the size of their prey, prey preference and abundance. Cheetah, spotted hyena, leopard and African wild dog were the predominant predators of smaller prey species (small stock), while lions preyed mostly on larger prey species (cattle and donkey) and rarely on small-sized prey (small stock). This result confirms the preference of lions for larger prey species as reported in various studies (Hayward & Kerley 2005) and the preference of cheetah, spotted hyena, leopard and African wild dog for smaller prey species (Hayward 2006; Hayward, Henschel et al. 2006; Hayward, O'Brien et al. 2006). Our results are consistent with previous findings that livestock species selection corresponds to the size of the predator (Patterson et al. 2004) and in accordance with the size of their prey (Hayward 2006). However, small stock were the most preferred prey by cheetah, spotted hyena, leopard and wild dog, probably related to their relative abundance in comparison to other livestock. In addition, spotted hyenas also preyed upon larger livestock such as cattle and donkey that are larger than their own body mass probably due to the fact that spotted hyenas do not have distinct prey species preference (Hayward 2006). On the other hand, wild dogs occasionally preyed upon calves, i.e. prey sizes which are significantly larger than their own body mass due to their group hunting strategy (Hayward, O'Brien et al. 2006).

Overall, spotted hyenas and leopards accounted for more small stock attacks compared to other carnivore species. The high plasticity of spotted hyenas (Kruuk 1972; Boydston et al. 2003) and leopards (Nowell & Jackson 1996) in habitat use and diets may explain their predominance as small stock predators compared to other carnivore species. Similar studies have also reported spotted hyenas and leopards being responsible for most of the small stock depredation, e.g. around the Serengeti National Park in Tanzania (Holmern et al. 2007) and in the Maasai Steppe of northern Tanzania (Kissui 2008; Mponzi et al. 2014). However, unlike Tarangire ecosystem, wild dogs and spotted hyenas were considered the most problematic species in the eastern part of the Serengeti ecosystem (Lyamuya, Masenga, Fyumagwa et al. 2014; Hampson et al. 2015) and lions in the Ruaha landscape (Dickman et al. 2014).

The total financial loss of livestock depredation by spotted hyenas, lions and leopards reported in this study was much higher compared with other studies (Holmern et al. 2007). In this case, the financial costs of reported losses might be perceived as significant by households experiencing such losses. In Maasai culture, livestock act as a social capital, a sign of status and wealth (Hampson et al. 2015) such that a single depredation event may be devastating for households owning very few animals, hence posing a significant economic impact on rural communities (Hazzah 2006). Perception of costs may also be higher than actual

Table 6. Summary statistics of model averaged coefficient estimates (β) associated with their standard errors (SE), *t*-statistic and 95% confidence interval from generalized linear mixed models (GLMMs) explaining the reported frequency of livestock depredation by wild dogs and cheetah in the grazing area in the Tarangire ecosystem, Tanzania 2014.

					95% Confidence interval	
Parameter	Estimate (β)	SE	*t*-Statistic	*p*-Value	Lower	Upper
Wild dog						
Intercept	0.272	0.974	0.279	0.781	−1.658	2.201
TLU	−0.003	0.001	−3.038	0.003	−0.005	−0.001
Herders	−1.151	0.594	−1.937	0.055	−2.327	0.026
Cheetah						
Intercept	−1.916	0.598	−3.205	0.002	−3.100	−0.732
TLU	−0.003	0.001	−2.015	0.046	−0.006	−4.888E − 05
Herders	0.312	0.458	0.682	0.497	−0.594	1.218

TLU: Total number of livestock owned expressed in Tropical Livestock Unit; Herders: number of herders.
All models consisted of village ID as a random effect.

costs because, for example, predators are blamed for livestock loss when the cause of livestock death may be due to other factors, such as disease, and a scavenger is blamed for killing livestock when in reality, it is scavenging an animal already dead (Rasmussen 1999). We observed that the total reported livestock loss due to leopard and wild dogs was slightly higher than that by lion, but lion killed cattle contributing to higher financial loss than leopard and wild dogs. Cattle have economic and cultural values placed on them by the Maasai; therefore, loss of cattle is likely to have serious economic and social consequences (Spear & Waller 1993). Our results suggest that diseases were responsible for higher livestock losses than any other cause within and among villages. Our findings concur with other studies conducted in Tanzania, in which disease was found to be the leading cause of livestock loss (Holmern et al. 2007; Dickman 2008; Kissui 2008; Nyahongo & Røskaft 2012). Diseases are particularly known to be responsible for high loss in livestock production (3–6 times higher other than livestock depredation) in sub-Saharan Africa (Gifford-Gonzalez 2000; Frank et al. 2005). Generally, the impact of theft was very low compared to the impacts of livestock depredation and disease contrary to Nyahongo and Røskaft (2012) and Ogada et al. (2003).

Spatio-temporal patterns of livestock depredation

We observed variation in the timing and contexts of depredation by different carnivore species similar to other reported findings. Cheetahs and wild dogs are diurnal and typically attack grazing herds by day (Ogada et al. 2003). Leopards, spotted hyenas and lions attack livestock at any time of the day, either in the grazing area or at bomas (Patterson et al. 2004), although other studies found that spotted hyena and leopard attacks prevail at night at bomas (Woodroffe et al. 2007; Kissui 2008). Surprisingly, we found that the mean annual livestock loss due to depredation was relatively lower for households in Loibor Siret (1.29 per household) and Terat (1.45 per household) than expected compared to other villages. We expected that the reported frequency of livestock depredation would be relatively higher for households in Loibor Siret due to the proximity of this village to the TNP. A possible explanation for the lower depredation rates in Loibor Siret could be due to the presence of fortified bomas which reduced incidences of carnivore attacks on livestock. Between 37% and 40% of respondents reported using fortified bomas in Loibor Siret to keep cattle and small stock, respectively, which might have influenced our results in various ways (Mkonyi *et al.* submitted). In addition, boma type was a good predictor of livestock depredation levels (e.g. boma type for cattle associated negatively with livestock depredation by all predators, lions and spotted hyenas in our boma depredation model). The impact of fortified bomas on large carnivores has also been tested in Loibor Siret where overall depredation rates by lions, leopards and spotted hyenas declined by 90% (Lichtenfeld et al. 2014). Similarly, there were fewer reported incidences of depredation in Terat households. The reason for the lower depredation in this village is uncertain; however, it could possibly reflect the low density of carnivore species around this village. Nevertheless, the highest depredation rates reported in Sukuro, Emboret and Loiborsoit may be related to many factors, including low density of wild prey species, continued human encroachment onto carnivore habitat and poorly constructed night-time enclosures (bomas). Studies show that livestock depredation is more common in areas with low prey abundance (Bagchi & Mishra 2006), high human population, increased encroachment and poor livestock husbandry practices (Treves & Karanth 2003).

Seasonal patterns of livestock depredation

Our study revealed that there was a seasonal variation in livestock depredation by lions, cheetahs, leopards, spotted hyenas and wild dogs, with clear peaks of depredation during the wet season. The depredation peak during the wet season has also been reported by Mponzi et al. (2014) and Koziarski et al. (2016) for the western part of this ecosystem. But in other areas of Africa, depredation mainly occurs during the dry season (e.g. Hemson et al. 2009). Our findings somewhat contradict the 'reduced natural prey hypothesis' which emphasizes that depletion in natural prey abundance promotes attacks on livestock (Khorozyan, Ghoddousi et al. 2015). Our results could reflect the seasonal shifts in wild prey distributions from TNP into the communal village lands (Kahurananga & Silkiluwasha 1977), with more predators (lions, cheetahs, wild dogs and spotted hyenas) following natural prey and hence coming into conflict with humans and livestock. This seasonal variability in depredation patterns has also been reported for hyenas and lions in the Maasai Steppe of northern Tanzania (Kissui 2008; Mponzi et al. 2014) and for lions in Tsavo National Park in Kenya (Patterson et al. 2004). Patterson et al. (2004) found that livestock depredation by lions peaks during the wet season when natural prey are in better condition and more widely dispersed, hence difficult for predators to acquire. Interestingly, we found no support for the prediction that livestock depredation by leopards is independent of season. Hence, it is possible that even leopards could be moving in the same manner with ungulate migrations following the increase in livestock predation by leopards in the wet season.

However, additional research with verified data would be appropriate in explaining this seasonal variation.

Ecological and socio-economic factors associated with livestock depredation

Our hypothesis that socio-ecological (distance to park boundary, education level) and economic factors (number of livestock owned) would influence the reported frequency of livestock depredation by all predator species was supported. Surprisingly, distance to park boundary was positively associated with reported frequency of livestock depredation, which was contrary to our prediction. This is a clear indication that the reported frequency of livestock depredation by all predator species was relatively lower in households located closer to PA than further away. Clearly, there is a high variation in this variable because the households ranged from 7 to 52 km from the park boundary. Our findings contradict with findings reported elsewhere that livestock depredation declines significantly with increasing distance from the park boundary (Patterson et al. 2004; Holmern et al. 2007). This unexpected pattern may be explained by improved fortified bomas in households closest to the park (i.e. around 42% of the traditional bomas were fortified), while distant households had few or no fortified bomas. However, this trend varied significantly by species. For instance, reported lion attacks declined with increasing distance from the park boundary, although the reverse was true for spotted hyenas. This discrepancy can be partly explained by the fact that spotted hyenas killed the largest number of small stock in households located further away from the park where fortified bomas were mostly absent. Moreover, our findings suggest that lions were more likely to attack livestock in households that were closer to the PAs due to the fact that lions usually stay close to their natural habitat (Holmern et al. 2007). However, spotted hyenas often move far from PAs and are able to survive well in human-dominated landscapes due to their opportunistic feeding patterns and adaptive ranging behaviour (Hofer & East 1993; Kolowski & Holekamp 2011). Our findings showed that respondents with formal education experienced lower depredation rates than those without any formal education, consistent with our prediction and previous studies (Woodroffe et al. 2005; Holmern et al. 2007).

Consistent with other studies (Zimmermann et al. 2005; Hemson et al. 2009), our results indicate that people who owned large numbers of livestock experienced more livestock losses to large carnivores. This finding contradicts Koziarski et al. (2016) who found that education, psychological and demographic attributes were more influential in wildlife conflict perceptions than economic considerations (livestock ownership). Moreover, consistent with our prediction, the incidences of attacks on livestock by predators declined with increasing number of herders and fortified bomas as it has been demonstrated in other studies (Ogada et al. 2003; Woodroffe et al. 2007; Lichtenfeld et al. 2014). Our prediction that increased exposure to wildlife-related risks (i.e. long-term residency) would be positively associated with livestock depredation was supported, and this may be because long-term residency has been found to be associated with negative attitudes towards large carnivores (see Newmark et al. 1993; Arjunan et al. 2006). Furthermore, we found that men reported more depredation frequency with lions than women in the study area. This may be because men claim ownership of livestock and they come more frequently into contact with lions during livestock herding (Hampson et al. 2015; Koziarski et al. 2016). We also found that reported depredation frequency with lions at bomas was negatively associated with interviewee age, suggesting that as interviewees get older, they perceive lower levels of depredation. It could be that older interviewees are more likely to have reinforced bomas and this corroborates our previous findings (Mkonyi et al. 2017), showing that the longer people are in a place, the more tolerant they are likely to become. In addition, we assume that retaliatory killing and also culturally motivated killing of lions by humans in response to damages caused by lions is negatively affecting lion populations in this ecosystem (Kissui 2008; Lichtenfeld L. Pers. Comm. 2014). Based on this evidence, we can assume that it is also likely for other species.

Conclusion and management implications

Human–carnivore conflict is a complex issue for management, especially where humans live adjacent to or within PAs (Dickman 2010). Our study suggests that conflict due to livestock depredation could be significantly reduced by improving formal and conservation awareness education at all levels (i.e. during primary, secondary and tertiary school education), fortifying boma enclosures, improving herding practices such as increasing the number of herders (particularly adults) per herd. We also suggest the need for finding out high and low-risk areas where livestock is more or less susceptible while grazing and eventually educating herders to avoid grazing their livestock in high-risk areas (predator hotspots) or always be vigilant while grazing in such areas. Conservation efforts for mitigating conflicts should concentrate more on households that are situated further away from national park by improving boma enclosures for livestock. In addition, local people should receive tangible benefits (through benefit-sharing programmes) from large carnivore presence on village land that could offset costs of livestock losses and increase local people's tolerance for these predators. While increased carnivore attacks on livestock in the study area can engender significant socio-economic costs to local households, conservation efforts would benefit from combined carnivore conservation initiatives and livestock depredation reduction.

Conservation education and awareness programmes focusing on large carnivore behavioural ecology may also reduce the human–carnivore conflict and increase local people's tolerance for large carnivores (Sillero-Zubiri et al. 2007). In order to control and prevent livestock depredation by large carnivores, there is a need to understand predator-specific protection measures which can then be integrated into conflict mitigation programmes. As disease was perceived to be a greater cause of livestock losses than depredation in the surveyed villages, interventions would be to control and manage livestock diseases through preventive vaccinations and increase access to veterinary services (Khorozyan, Soofi et al. 2015).

Our study has provided new insights into the complexities of human–carnivore conflicts among the five large African carnivores and determinants of reported conflict with these species in the Tarangire ecosystem of northern Tanzania. We recommend further research along these lines to evaluate the actual frequency of conflict in the study area (using field verification methods) and continued monitoring of conflict situations over time or other causes of mortality. This might help in understanding the 'conflict hotspots' or sites predisposed to livestock depredation across the village land, allowing herders and wildlife managers to concentrate livestock protection and conservation education programs in such areas.

Acknowledgements

We thank Tanzania Commission of Science and Technology (COSTECH), Tanzania National Parks authority (TANAPA) and Simanjiro District Council authority for granting us the research permits to conduct this study. Special thanks to Sokoine Leposo for his invaluable assistance in administering the questionnaires and local people for invaluable information. We also thank two anonymous reviewers and the journal editor for their constructive comments and suggestions that greatly improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the St. Louis Zoo's Wildcare Institute, the Wildlife Conservation Society and Zoological Society of London. Felix Mkonyi received a postgraduate scholarship from COSTECH through Nelson Mandela African Institution of Science and Technology (NM-AIST).

References

Arjunan M, Holmes C, Puyravaud JP, Davidar P. 2006. Do developmental initiatives influence local attitudes towards conservation? A case study from the Kalakad–Mundanthurai Tiger Reserve, India. J Environ Manage. 79:188–197.

Bagchi S, Mishra C. 2006. Living with large carnivores: predation on livestock by the snow leopard (*Uncia uncia*). J Zool. 268:217–224.

Bencin H, Kioko J, Kiffner C. 2016. Local people's perception of wildlife species in two distinct landscapes of Northern Tanzania. J Nat Conserv. 34:82–92.

Borner M. 1985. The increasing isolation of Tarangire National Park. Oryx. 19:91–96.

Boydston EE, Kapheim KM, Watts HE, Szykman M, Holekamp KE. 2003. Altered behaviour in spotted hyenas associated with increased human activity. Animal Conserv. 6:207–219.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference. A practical information-theoretic approach. 2nd ed. New York: Springer.

Cavendish W. 2002. Quantitative methods for estimating the economic value of resource use to rural households. In: Campbell BM, Mk L, editors. Uncovering the hidden harvest: valuation methods for woodland and forest resources). London: Earthscan Publications Ltd; p. 17–63.

Collier P, Radwan S, Wangwe S, Wagner A. 1990. Labour and poverty in Tanzania: ujamaa and rural development in the United Republic of Tanzania. Oxford: Clarendon Press.

Dickman AJ. 2008. Key determinants of conflict between people and wildlife, particularly large carnivores, around Ruaha National Park, Tanzania [Ph.D. Thesis]. London: University College London.

Dickman AJ. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human-wildlife conflict. Animal Conser. 13:458–466.

Dickman AJ, Hazzah L, Carbone C, Durant SM. 2014. Carnivores, culture and 'contagious conflict': multiple factors influence perceived problems with carnivores in Tanzania's Ruaha -landscape. Biol Conserv. 178:19–27.

Frank LG, Woodroffe R, Ogada MO. 2005. People and predators in Laikipia District, Kenya. In: Woodroffe R, Thirgood S, Rabinowitz A, editors. People and wildlife: conflict or coexistence? Cambridge: Cambridge University Press; p. 286–304.

Gifford-Gonzalez D. 2000. Animal disease challenges to the emergency of pastoralism in Sub-Saharan Africa. Archaeological Rev. 17:95–139.

Graham K, Beckerman AP, Thirgood S. 2004. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. Biol Conserv. 122:159–171.

Hampson K, McCabe JT, Estes AB, Ogutu JO, Rentsch D, Craft ME, Hemed CB, Ernest E, Hoare R, Kissui B, et al. 2015. Living in the greater Serengeti ecosystem: human-wildlife conflict and coexistence. In: Sinclair ARE, Metzger KL, Mduma SAR, Fryxell JM, ediotrs. Serengeti IV: sustaining biodiversity in a coupled

human-natural system. Chicago, IL: The University of Chicago Press ; p. 607–648.
Hayward MW. 2006. Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). J Zool (London). 270:606–614.
Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley GIH. 2006. Prey preferences of the leopard (*Panthera pardus*). J Zool. 270:298–313.
Hayward MW, Kerley GIH. 2005. Prey preferences of the lion (*Panthera leo*). J Zool (London). 267:309–322.
Hayward MW, O'Brien J, Hofmeyr M, Kerley GIH. 2006. Prey preferences of the African wild dog *Lycaon pictus*: ecological requirements for their conservation. J Mammal. 87:1122–1131.
Hazzah L. 2006. Living among lions (*Panthera leo*): coexistence or killing? Community attitudes towards conservation initiatives and the motivations behind lion killing in Kenyan Maasailand [Msc. Thesis]. Madison, WI: University of Wisconsin-Madison.
Hemson G, Maclennan S, Mills G, Johnson P, Macdonald D. 2009. Community, lions, livestock and money: a spatial and social analysis of attitudes to wildlife and the conservation value of tourism in a human – carnivore conflict in Botswana. Biol Conserv. 142:2718–2725.
Hofer H, East ML. 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. III. Attendance and maternal care. Anim Behav. 46:575–589.
Holmern T, Nyahongo J, Røskaft E. 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. Biol Conserv. 135:534–542.
IUCN. 2016. IUCN red list of threatened species: a global assessment. Gland (Switzerland). cited 2016 Dec. Available from: http://www.iucnredlist.org/.
Jahnke HE. 1982. Livestock production systems and livestock development in Tropical Africa. Germany: Kieler Wissenschaftsverlag Vauk; p. 10, 59,157.
Kahurananga J, Silkiluwasha F. 1997. The migration of zebra and wildebeest between Tarangire National Park and Simanjiro Plains, northern Tanzania, in 1972 and recent trends. Afr J Ecol. 35:179–185.
Khorozyan I, Ghoddousi A, Soofi M, Waltert M. 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. Biol Conserv. 192:268–275.
Khorozyan I, Soofi M, Hamidi AK, Ghoddousi A, Waltert M. 2015. Dissatisfaction with veterinary services is associated with leopard (*Panthera pardus*) predation on domestic animals. PLoS One. 10:e0129221.
Kideghesho JR, Røskaft E, Kaltenborn BP. 2007. Factors influencing conservation attitudes of local people in Western Serengeti, Tanzania. Biodivers Conserv. 16:2213–2230.
Kiffner C, Meyer B, Mühlenberg M, Waltert M. 2009. Plenty of prey, few predators: what limits lions in Katavi National Park, western Tanzania? Oryx. 43:52–59.
Kissui BM. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Animal Conserv. 11:1–11.
Kolowski JM, Holekamp KE. 2005. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along the Kenya reserve border. Biol Conserv. 128:529–541.
Kolowski JM, Holekamp KE. 2011. Ecological and anthropogenic influences on space use by spotted hyenas. J Zool. 277:23–36.
Koziarski A, Kissui B, Kiffner C. 2016. Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. Biol Conserv. 199:41–50.
Kruuk H. 1972. The spotted hyena; a study of predation and social behavior. Chicago: University of Chicago Press; 335 pp.
[LEAD] Livestock, Environment and Development Initiative. 1999. Tropical livestock units (TLU). In: Livestock & environment toolbox. Rome (Italy): LEAD/FAO. [cited 2016 Dec 17]. Available from: www.fao.org/ag/againfo/programmes/en/lead/toolbox/Mixed1/TLU.htm
Lichtenfeld LL. 2005. Our shared kingdom at risk : human – lion relationships in the 21 st century [Ph.D.Thesis]. New Haven, CT: Yale University.
Lichtenfeld LL, Trout C, Kisimir EL. 2014. Evidence-based conservation: predator-proof bomas protect livestock and lions. Biodivers Conserv. 24:483–491.
Lyamuya RD, Masenga EH, Fyumagwa RD, Mwita MN, Røskaft E. 2016. Pastoralist herding efficiency in dealing with carnivore-livestock conflicts in the eastern Serengeti, Tanzania. Int J Biodivers Sci Ecosystem Serv Manag. 12:202–211.
Lyamuya RD, Masenga EH, Fyumagwa RD, Røskaft E. 2014. Human-carnivore conflict over livestock in the eastern part of the Serengeti ecosystem, with a particular focus on the African wild dog *Lycaon pictus*. Oryx. 48:378–384.
Lyamuya RD, Masenga EH, Mbise F, Fyumagwa RD, Mwita M, Røskaft E. 2014. Attitudes of Maasai pastoralists toward the conservation of large carnivores in the Loliondo Game Controlled Area of northern Tanzania. Int J Biodivers Conserv. 6:797–805.
Maddox TM. 2003. The ecology of cheetahs and other large carnivores in a pastoralist-dominated buffer zone [Ph.D. Thesis]. London: University College London.
Mizutani F. 1999. Impact of leopards on a working ranch in Laikipia, Kenya. Afr J Ecol. 37:211–225.
Mkonyi FJ, Estes AB, Msuha MJ, Lichtenfeld LL, Durant SM. 2017. Local attitudes and perceptions towards large carnivores in a human-dominated landscape of Northern Tanzania. Hum Dimensions Wildl. Available from: http://dx.doi.org/10.1080/10871209.2017.1323356.
Morrison TA, Bolger DT. 2014. Connectivity and bottlenecks in a migratory wildebeest *Connochaetes taurinus* population. Oryx. 48:613–621.
Mponzi BB, Lepczyk CA, Kissui BM. 2014. Characteristics and distribution of livestock losses caused by wild carnivores in Maasai steppe of Northern Tanzania. Human-Wildlife Interact. 8:218–227.
Msoffe FU, Said MY, Ogutu JO, Kifugo SC, De J, Gardingen PV, Reid RS. 2011. Spatial correlates of land-use changes in the Maasai-Steppe of Tanzania: implications for conservation and environmental planning. Int J Biodiversity Conservation. 3:280–290.
Newmark WD, Leonard NL, Sariko HI, Gamassa DGM. 1993. Conservation attitudes of local people living adjacent to five protected areas in Tanzania. Biol Conserv. 63:177–183.
Nowell K, Jackson P. 1996. Wild cats: status survey and conservation action plan. Gland (Switzerland): IUCN/SSC Cat Specialist Group. IUCN; p. 382 pp.

Nyahongo JW. 2007. Depredation of livestock by wild carnivores and illegal utilization of natural resources by humans in the Western Serengeti [Ph.D. Thesis]. Trondheim: Department of Biology, Norwegian University of Science and Technology.

Nyahongo JW, Røskaft E. 2012. Assessment of livestock loss factors in the Western Serengeti, Tanzania, Abiud Kaswamila (Ed.). Sustainable Natural Resources Management. Available from: http://www.intechopen.com/books/sustainable-natural-resources-management/assessment-of-livestock-loss-factors-in-the-western-serengeti-Tanzania

Ogada MO, Woodroffe R, Oguge NO, Frank LG. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biol. 17:1521–1530.

Patterson BD, Kasiki SM, Selempo E, Kays RW. 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biol Conserv. 119:507–516.

Rasmussen GSA. 1999. Livestock predation by the painted hunting dog *Lycaon pictus* in a cattle ranching region of Zimbabwe: a case study. Biol Conserv. 88:133–139.

Røskaft E, Hãndel B, Bjerke T, Kaltenborn BP. 2007. Attitudes of humans towards large carnivores in Norway. Wildl Biol. 13:172–185.

Sillero-Zubiri C, Sukumar R, Treves A. 2007. Living with wildlife: the roots of conflict and the solutions. In MacDonald DW and Service K, editor. Key Topics in Conservation Biology. Oxford: Oxford University Press; p. 266-272.

Spear T, Waller R. 1993. Being Maasai: ethnicity and identity in East Africa. London (UK): James Currey Publisher; p. 322pp.

Treves A, Karanth KU. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biol. 17:1491–1499.

Woodroffe R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conserv. 3:165–173.

Woodroffe R, Frank LG, Lindsey PA, Ole Ranah SMK, Romañach S. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case–control study. Biodivers Conserv. 16:1245–1260.

Woodroffe R, Ginsberg JR. 1998. Edge effects and the extinction of populations inside protected areas. Science. 280:2126–2128.

Woodroffe R, Thirgood S, Rabinowitz A. 2005. People and wildlife, conflict or co-existence? Cambridge: Cambridge University Press.

Zimmermann A, Walpole MJ, Leader-Williams N. 2005. Cattle ranchers'attitudes to conflicts with jaguar *Panthera onca* in the Pantanal of Brazil. Oryx. 39:406–412.

Zuur AF, Leno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol. 1:3–14.