Biological Conservation 199 (2016) 41–50

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania

A. Koziarski [a], B. Kissui [b], C. Kiffner [b,*]

[a] University of Maryland, College of Agriculture and Natural Resources, Department of Environmental Science and Policy, Symons Hall, College Park, MD, USA
[b] School For Field Studies, Center for Wildlife Management Studies, P.O. Box 304, Karatu, Tanzania

ARTICLE INFO

Article history:
Received 10 July 2015
Received in revised form 8 March 2016
Accepted 26 April 2016
Available online xxxx

Keywords:
Conservation psychology
Human-wildlife conflict
Socioeconomics
Spatial patterns
Tanzania

ABSTRACT

Despite their cultural, economic, and ecological importance, large carnivores are experiencing a global decline, largely due to conflict with humans. In this study we assessed the spatial and temporal patterns and socioeconomic correlates of perceived conflict with lions, leopards, hyenas, cheetahs, and wild dogs in the Ngorongoro Highlands and Tarangire Manyara Ecosystem of Northern Tanzania using structured interviews ($n = 356$). Conflict with large carnivores was mainly prevalent during the wet season, and was spatially highly heterogeneous. Hyenas were the predominant conflict species, followed by leopards. Employing species-specific generalized linear mixed effects models, we assessed spatial, psychological, socio-economic and demographic correlates of perceived conflict. Interestingly, we found few consistencies among correlates for reported conflict frequency. Ethnicity, gender, age, education, fear of large carnivore species, and education had mixed effects on perceived conflict frequency while livestock ownership and relative wealth were negligible in explaining reported conflict frequency. These results suggest that education, psychological and demographic attributes were more influential (though dependent on species and landscape) in wildlife conflict perceptions than economic considerations. Although effective mitigation methods were generally available, they were rarely employed. We suggest that mitigation strategies that address local needs be made more accessible, and that conservation education programs particularly target conflict hotspot areas.

1. Introduction

Worldwide, large predator species are experiencing reduced ranges, declining populations, and local extinctions (Ogada et al., 2003; Kolowski and Holekamp, 2005; Woodroffe et al., 2005; Ripple et al., 2014). Environmental exploitation by humans in areas historically dominated by ecological processes has fostered human-wildlife conflicts (Treves and Karanth, 2003; Galvin et al., 2006; Dickman, 2010). Protected areas serve as refuge for large carnivores; however, carnivores, which often have large home ranges, do not recognize artificial boundaries and thus come into contact with humans and livestock (Ogada et al., 2003; Patterson et al., 2004; Woodroffe et al., 2005). Livestock species often fall into preferred prey weight ranges of large carnivores (Meriggi and Lovari, 1996; Polisar et al., 2003; Hayward and Kerley, 2005; Tschanz et al., 2007; Sundararaj et al., 2012; Soh et al., 2014), making them an attractive choice when natural prey is scarce and livestock keeping practices do not effectively deter predators (Patterson et al., 2004; Woodroffe et al., 2005; De Azevedo, 2008; Kissui, 2008; Valeix et al., 2012). Humans themselves may be vulnerable to wild carnivore attacks, especially in areas where human populations are high and wild prey densities are low (Löe and Röskaft, 2004; Packer et al., 2005). However, documented cases of carnivore attacks on humans are few and often occur during illegal activities (such as poaching or culturally motivated killing of wildlife) leaving it unclear whether these attacks are underreported, or are actually rare (Löe and Röskaft, 2004; Dickman et al., 2014; Hampson et al., 2015).

In East Africa, large carnivores receive a severely negative perception by many local people (Okello, 2005; Romañach et al., 2011), largely because they are considered a key antagonist of livestock and livestock represent a vital part of Maasai culture as people depend on them for sustenance, status, and a form of currency (Hampson et al., 2015). The loss of livestock can represent a substantial detriment to a family's yearly income (Loibooki et al., 2002) and frequently, large carnivores are being killed in response to these losses (Ikanda and Packer, 2008). Even species that are not directly involved in conflict may suffer from retaliation. For example, cheetahs (*Acinonyx jubatus*) rarely attack livestock, but are often killed because they are mistaken for leopards (*Panthera pardus*) which do prey upon livestock, particularly sheep and goats (Dickman et al., 2014). These conflicts result in carnivore population sinks outside and along edges of protected areas (Woodroffe and Ginsberg, 1998; Kolowski and Holekamp, 2005; Kiffner et al., 2009), and in conjunction with substantial habitat loss (Riggio et al.,

* Corresponding author.
E-mail addresses: anna.koziarski@live.com (A. Koziarski), bkissui@fieldstudies.org (B. Kissui), ckiffne@gwdg.de (C. Kiffner).

http://dx.doi.org/10.1016/j.biocon.2016.04.029

2013) have probably contributed to the decline of large African carnivores in recent decades (Ogada et al., 2003; Ripple et al., 2014).

Ecological patterns and socio-economic impacts of large carnivore conflict have been well described in some ecosystems (e.g. Stoddart et al., 2001; Polisar et al., 2003; Tschanz et al., 2007), particularly in the Serengeti ecosystem (Hofer et al., 2000; Holmern et al., 2007; East et al., 2012; Hampson et al., 2015). However, less research on this topic has been conducted in our study area, the Tarangire–Manyara ecosystem and the highlands adjacent to the Ngorongoro Conservation Area.

While the influence of socioeconomic factors in wildlife conservation is acknowledged (e.g. Kolowski and Holekamp, 2005), there is currently limited discussion on how these factors (including education level, ethnic identity, cultural beliefs, vulnerability to conflict, and means to recover from attacks) influence perceived conflicts with different large carnivore species across landscapes (Dickman et al., 2014; Hampson et al., 2015). If these factors are affecting not only locals' vulnerability to conflict, but the way they perceive conflict, those factors are vital to consider when forming and implementing large carnivore management plans and conflict mitigation approaches. Here, we seek to fill this gap by identifying temporal, spatial, and socio-economic factors affecting perceived human-carnivore conflicts in a diverse conservation landscape of Northern Tanzania. We hypothesized that perceived conflict will be greatest during the wet season as compared to dry season (since several wildlife species leave protected areas during this season, possibly triggering similar shifts in large carnivore distributions; Kahurananga and Silkiluwasha, 1997), in closer proximity to protected areas, and for people of a lower socio-economic status.

2. Materials and methods

2.1. Study area

The study was conducted in the Tarangire–Manyara ecosystem ('the valley') and Ngorongoro Highlands ('the highland') of Northern Tanzania (Fig. 1). The Tarangire–Manyara ecosystem is located east of the escarpment of the Great Rift Valley at an altitude of 950–1200 m (Galanti et al., 2006). The Ngorongoro highlands are situated above the escarpment at an approximate altitude of 1600 m (Oates and Rees, 2013). The valley and the highland are characterized by a semi-arid climate with an average annual rainfall of 400–800 mm in the valley and 800–1000 mm in the highland (Prins and Loth, 1988). Dominant vegetation forms vary between rain fed agriculture, grassland, closed bushland, and woodland (Prins and Loth, 1988). Tarangire National Park (TNP), Lake Manyara National Park (LMNP), and Manyara Ranch (MR) are protected areas located in the valley, while the Ngorongoro Conservation Area (NCA) lies in the highland. Protected areas are unfenced but settlements and land-use changes increasingly impair seasonal wildlife dispersal and migration outside the parks (Lamprey, 1964; Borner, 1985; Newmark, 1993, 2008; Morrison and Bolger, 2014; Kiffner et al., 2015). In the valley, pastoralism is the predominant land use outside protected areas. In the highland, small-scale agriculture and some larger commercial farms represents the main land uses in non-protected areas.

2.2. Interviews

We divided the study area into 49 5×5 km cells (21 in the highland and 28 in the valley). Two of the cells in the valley had one household and these data points were omitted from modeling conflict correlates; however the reported conflict frequencies were plotted spatially (Fig. 1) to obtain a thorough overview on the spatial conflict patterns. Within the remaining 47 cells (21 in the highland and 26 in the valley), we interviewed between 3 and 10 households (mean households interviewed per cell = 8). We selected households along a diagonal transect through the cell; if there were not enough households along transects, we searched systematically (looking and asking for locations of households) for additional households within each cell. Overall, we conducted 356 structured interviews with local residents in the study area: 192 in the highland and 164 in the valley. Candidate interviewees were approached and asked for voluntary participation. Generally the head of household answered questions; if the head of the household was not available, another household member answered the questions. Interviews were conducted in Swahili with the help of local translators. Interviewees were guaranteed anonymity and had the right to discontinue the interview at any time. Questions were pre-defined and aimed at obtaining background information for each interviewee (ethnicity, age, gender, education, socio-economic background) and at generating information on different aspects of conflict with the five major large carnivores: lions (*Panthera leo*), leopards, spotted/striped hyenas (*Crocuta crocuta* and *Hyaena hyaena* combined because local people usually do not differentiate between them), cheetahs, and wild dogs (*Lycaon pictus*). For each carnivore species, we asked (1) the type of conflict, (2) the frequency and seasonal patterns of conflict, (3) applied mitigation measures and (4) whether interviewees were afraid of the species. For the frequency and seasonal patterns of conflict, interviewees were asked to recall during which calendar months (1–12) they either saw or conflicted with a large carnivore, and how many times during that month did conflict occur. The interview protocol (Appendix 1) was reviewed and approved to meet the conditions for exemption from Institutional Review Board (IRB) review, under Type B, Category 2 of the U.S. federal code 45 Part 46 on human subjects protections in research (IRB: TZ-02-13-14).

2.3. Data analysis

Because the highland differed considerably from the valley in terms of major ethnicities and main land use we conducted data analyses separately for the two distinct landscapes. We first assessed temporal and spatial patterns of conflict using descriptive statistics. To test if reported mean monthly conflict occurrence differed between dry (June–October) and wet season (November–May) months we used a Mann–Whitney-U test.

In order to examine how socioeconomic and spatial variables affected reported patterns of conflict, we fitted generalized linear mixed models with binomial error distribution to the data using R 3.1.2 (R Core Team, 2014). The target variable was defined as the reported frequency of large carnivore conflict in a year (successes), over the maximum possible number of trials (365 days a year). The hypothesized explanatory variables were defined as distance (km) to the nearest protected area (measured as the nearest distance between household and a protected area using ArcGIS9.1, ESRI, Redlands, USA), gender (male vs. female), age (interviews were restricted to persons >18 years of age), education (primary, secondary and higher, or none), ethnicity (Maasai, Iraqw, or other), tropical livestock units (TLU, linear predictor), wealth index (linear predictor), and fear of the species (yes or no). In the highland, the reference level for ethnicity was Iraqw, and in the valley the reference variable was Maasai; due to low relative abundance of other tribes we combined other ethnicities. In line with other socio-economic research conducted in East Africa, we assessed household wealth with an index (e.g. Mgawe et al., 2012; Hedges et al., 2016). This index was generated by converting the possession of specific household assets (bicycle, car/motorbike, sofa set, TV, and radio) into a numerical score using a principal component analysis (Mgawe et al., 2012). The wealth index score was on an inverse scale where 0 represented wealthiest households, and 5.5 represented the poorest households. To account for differences in size and value of different livestock species, we converted number of reported livestock into tropical livestock units (TLUs) using the following conversion factors: one cow = 0.71, one goat or sheep = 0.17, and one pig = 0.2 (Pica-Ciamarra et al., 2007). Since households within the same block were possibly not independent of each other, we assigned the block ID

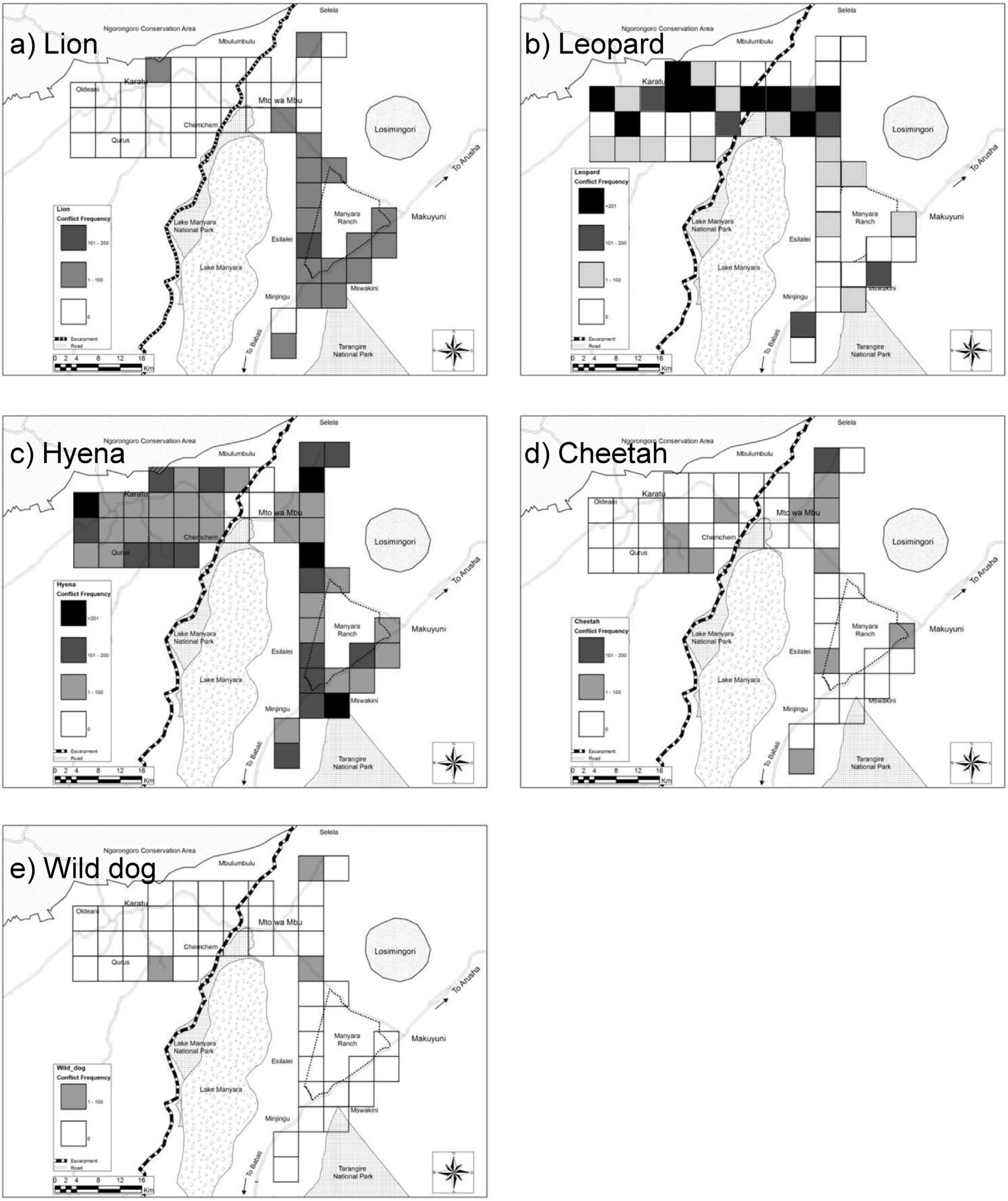

Fig. 1. Spatial distribution of average reported conflict frequency (days per year) with large carnivore species in Northern Tanzania.

as a random effect in the logistic model and allowed the explanatory variables to have random slopes (Schielzeth and Forstmeier, 2009). We tested for collinearity of variables that were hypothesized to be closely related (valley: fear and livestock units and fear and education; highland: fear and wealth index and fear and education) using logistic regression models. In the valley, the wealth index was not included as an explanatory variable, because the population is dominated by Maasai people who mainly define their wealth by the number of owned livestock (assessed with TLUs). In the five datasets, none of the measures of wealth (wealth index, livestock units) were significantly related to fear (all $p > 0.28$). Interviewees with primary education were significantly ($p < 0.01$) more afraid of lions and leopards in the valley than people without any formal education; interviewees with secondary education were not more afraid than the reference group ($p > 0.05$). In the highland, there was no significant relationship between fear and education level ($p > 0.05$). Since the level of collinearity was moderate, we retained all hypothesized variables.

After fitting full models, we standardized the regression coefficients using the *arm* package in R (Gelman and Su, 2014) and used the *dredge* function of the *MUMIN* package (Bartón, 2013) to generate model sets with all possible variable combinations (Appendix 2 and 3). In all cases we generated model-averaged coefficients based on models within 2 AICc scores (Grueber et al., 2011).

To predict the relationships between explanatory variables and the reported frequency of conflict, logistic regression coefficients were converted into odds ratios by taking the exponent of the averaged regression estimates. The resulting odds ratios indicate how much the likelihood of reported occurrence of conflict changed when the explanatory variable changed by one unit (or in the case of categorical variables, how much the outcome changed compared to the reference level) (Crawley, 2005). We restricted analyses to species/landscape combinations with at least 30 cases of reported conflicts. This threshold allowed us to retain two species in both landscapes while still having substantial variation in the response variable, yet excluded models on conflict with cheetahs (valley and highland), wild dogs (valley and highland), and lions (highland).

3. Results

3.1. Socio-economic characteristics of interviewees

In the highland, females and males represented 60% and 40% of the sample respectively, with an age range of 18–100 (mean: 43). The majority of interviewees had primary education (68%), followed by no formal education (17%), and secondary education (15%). The main source of income was combined farming and pastoralism (75%), while few solely grew crops (17%), or solely depended on livestock (2%), or had other occupations (6%). Most people belonged to Iraqw ethnicity (92%) and only 8% belonged to 26 other ethnicities. Household size ranged from 1 to 13 persons (average: 6).

In the valley, the sex ratio of interviewees was nearly balanced (51% females, 49% males). Ages of interviewees ranged from 18 to 100 (mean: 39 years). The highest education level was primary education for 50% of interviewees, followed by no formal education (40%), and secondary (10%). Similar to the highland, agriculture and pastoralism were practiced by the majority of participants (69%), although a much larger percentage of people solely practiced pastoralism (23%), and fewer people relying solely on agriculture (7%) or other occupations (1%). In the valley, livestock ownership was much higher (mean: 90.98 TLU, range: 0–1430) than in the highland (mean: 3.75 TLU, range: 0–60).

The valley was dominated by Maasai (69%), with a variety of other ethnicities representing the remainder (31%). The mean household size in the valley was 13 (range 1–100) and thus larger than in the highland. The wealth index ranged from 0 to 5.553; the average wealth index (4.27) indicated a poorer population compared to interviewees in the highland (mean: 3.788, range 0–5.553).

3.2. Spatial patterns of conflict and mitigation

In both the highland and the valley, the majority of interviewees (68% highland; 79% valley) reported some conflict with large carnivores (Fig. 1). The most commonly reported conflict species in both the highland and the valley were hyenas (67% highland; 73% valley). Overall, large carnivore conflict was more frequently reported in the valley (49% lion; 37% leopard; 73% hyena; 10% cheetah; 7% wild dog) than the highland (0.5% lion; 15% leopard; 67% hyena; 5% cheetah; 0.5% wild dog), with a strong clustering of reported lion conflict around MR (Figs. 1, 2a). Leopard conflict in the highland was reported in closer proximity to NCA and the escarpment above LMNP. Hyena conflict was reported throughout the study area. Conflicts with cheetah and wild dogs were rarely reported. In the highland, most households reported conflict with only one species (52%), and less 16% of households reported conflict with 2 or more large carnivore species. However, valley households often dealt with multiple carnivore species (59%) (Fig. 2b). The most prevalent type of conflict across the landscape was livestock predation, especially by hyenas (Fig. 3). Hyenas were also the only species that reportedly caused substantial conflict other than livestock predation such as causing damage to property (16% highland; 4% valley). In the valley, attacks on people were reported for all species except cheetahs but these reports were rare (Fig. 3).

In the highland, guarding of livestock by people was the most common type of mitigation, followed by keeping guard dogs, and fencing (Fig. 4a). In the valley, guarding was also the mitigation method most used for large carnivore conflict (Fig. 4b), except in the case of lions. Retaliatory killing (destroying a carnivore that is believed to have caused conflict) and preventative killing (proactively destroying a carnivore before it has a chance to cause conflict) was most commonly used to mitigate lion conflict (17%). Lethal mitigation for all species was more commonly reported in the valley (17% lion; 6% leopard; 9% hyena; 2% cheetah; 2% wild dog) than the highland (0% for all species except 0.5% for hyena).

3.3. Temporal patterns of conflict

In the valley, reported conflicts with lions ($W = 4$, $p = 0.034$), leopards ($W = 0$; $p = 0.005$), hyena ($W = 5$, $p = 0.046$), cheetah

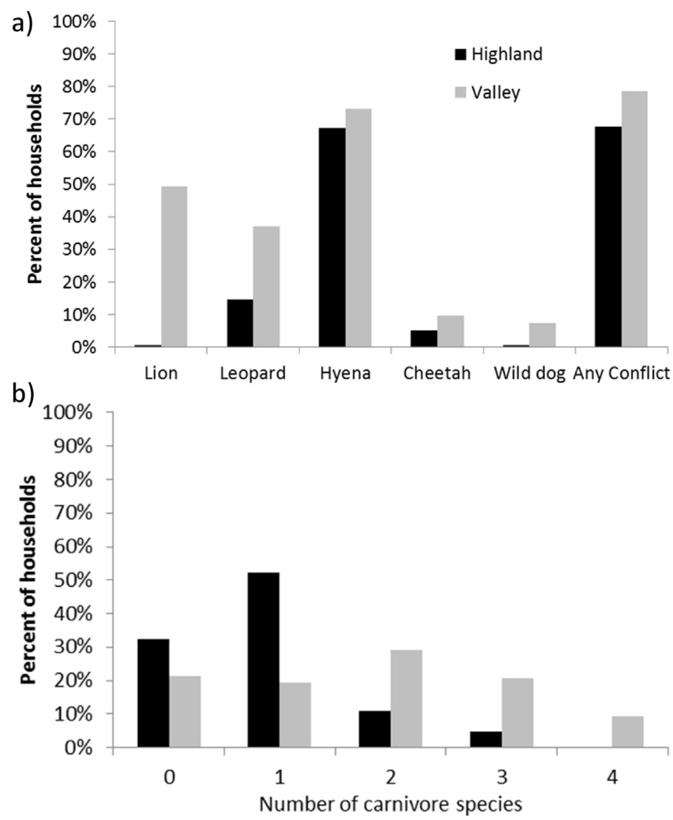

Fig. 2. a) Percent of households that reported conflict with different large carnivore species ('Hyena' entails spotted and striped hyena because local people rarely differentiate these species) in the Ngorongoro highlands ('Highland') and the Tarangire–Manyara Ecosystem ('Valley') of Northern Tanzania. b) Relative frequency of households reporting conflict with number of unique large carnivore species in the Ngorongoro highlands ('Highland') and the rift valley ('Valley') of Northern Tanzania.

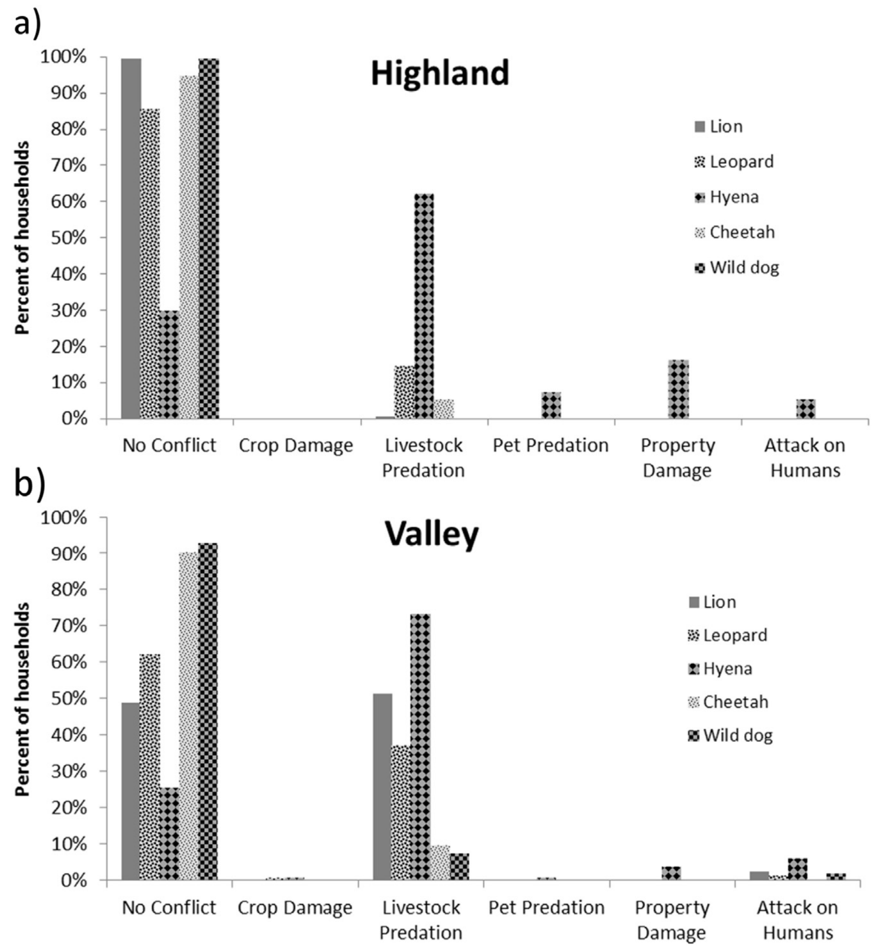

Fig. 3. Reported carnivore-species specific percentage of different conflict types in a) the Ngorongoro highlands ('Highland') and b) the rift valley ('Valley') of Northern Tanzania.

($W = 1, p = 0.072$) and wild dog ($W = 1, p = 0.007$) were significantly higher during the wet season than the dry season (Fig. 5). Reported conflict frequency in the highland was significantly higher during the wet season for leopards ($W = 3, p = 0.021$) and wild dogs ($W = 6, p = 0.0075$); for the other three species conflict did not vary significantly between seasons in the highland (all p-values > 0.10).

3.4. Lion conflict correlates

The top models explaining variation in reported conflict with lions in the valley, contained fear, gender, education, age and distance to nearest protected area (Table 1a). Reported conflict frequency declined significantly with increasing distance to nearest protected area and male interviewees reported 14 times more frequent conflict than female interviewees (Table 1a). Age (trend: conflict frequency declined with age), fear (trend: fearful interviewees reporting more frequent conflict) and education (trend: reported conflict frequency declined with increasing education) were non-significantly associated with reported conflict frequency. For all explanatory variables, the standard deviations of the random slopes were relatively large, suggesting substantial variation in the strength of the variables across survey blocks.

3.5. Leopard conflict correlates

In the valley, reported conflict with leopards was best explained by the distance to the nearest protected area only and even this relationship differed substantially from block to block (large standard deviation of intercept and slope) and was non-significant (Table 1a).

In the highland, reported conflict frequencies with leopards were best explained by education, age and distance to protected area (Table 1b). Reported conflict frequency increased (non-significantly) with increasing level of education; compared to interviewees with no formal education. With each year of age, the reported conflict frequency increased (non-significantly) and reported conflict frequency declined significantly with increasing distance from protected areas (Table 1b).

3.6. Hyena conflict correlates

In the valley, variation in reported conflict frequency with hyenas was best explained by ethnicity and education (both statistically significant), and fear, gender, age and distance to protected area (all non-significant) (Table 1a). Subjects from other ethnicities reported 5.3 times more conflict than Maasai people. Compared to subjects with no formal education, interviewees with primary education reported 40% more conflict (non-significant) whereas those with secondary education reported 93% less frequent conflict (significant). Distance to protected areas (negative trend), gender (trend: males reporting more conflict), age (positive trend), and fear (trend: fearful interviewees reporting 25% more conflict) were also among the top models, but these relationships did not reach statistical significance (Table 1a).

In the highland, fear (trend: fearful interviewees reporting 7.2 times more conflict), gender (trend: males reporting 46 times more conflict), age (positive trend), wealth index (negative trend), education (trend: interviewees with primary education reporting more frequent conflict, and those with secondary education reporting less frequent conflict), ethnicity (members of Iraqw tribe reporting more frequent conflict)

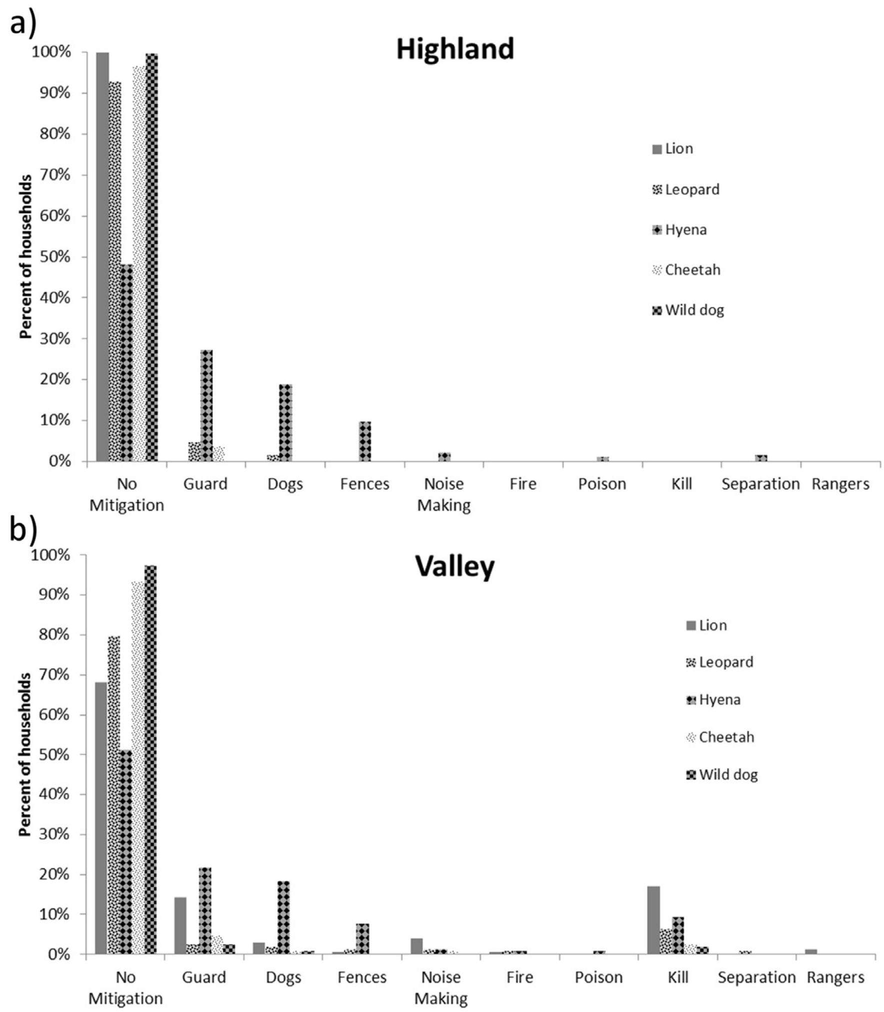

Fig. 4. Reported relative frequency of mitigation methods in response to large carnivore conflict in a) the Ngorongoro highlands ('Highland') and b) the rift valley ('Valley') of Northern Tanzania.

and distance to protected area (positive trend) were among the top models but did not reach statistical significance.

4. Discussion

Our landscape-scale study suggests that conflicts with large carnivore species are widespread but heterogeneously distributed across the landscape and occur mainly during the wet season. Hyena depredation on livestock was the most frequent type of conflict and proximity to protected areas was only partially related to perceived conflict frequency with large carnivores. Interestingly, we found no generalities in socio-economic correlates of reported conflict frequency. Even within species-specific models, a high variability in the strength of correlations was observed (indicated by substantial standard deviations of random intercepts and slopes).

4.1. Patterns of large carnivore conflict

In line with strong seasonal fluctuations in precipitation and associated shifts in large herbivore distributions from protected areas to communal areas (Lamprey, 1964; Kahurananga and Silkiluwasha, 1997), large carnivore conflicts mainly peak during the wet season in the valley. Studies based on actual conflict frequency also reported this seasonal variability in predation patterns by both hyena and lions in the valley (Kissui, 2008; Mponzi et al., 2014). Thus, lions, and other large carnivores in this ecosystem appear to follow natural prey and then come into contact with humans and livestock (Packer et al., 2005). Yet, it remains to be explicitly tested to what degree lions and other carnivores shift their home ranges in response to the distribution of wildlife, livestock, and humans in this ecosystem (cf. Valeix et al., 2012) and to what degree depletion of natural prey species contributes to livestock depredation (Khorozyan et al., 2015a, 2015b). In the highland, conflict appears more homogenous across seasons; this might be because seasonal range shifts of large mammals may occur to lesser extents than in the valley.

The distribution of perceived large-carnivore conflict was patchy across the landscape and proximity to protected areas predicted conflict frequency in some, but not all cases. We suggest that these mixed effects can be explained by several, mutually non-exclusive explanations. First, all of the studied species are wide-ranging and have large home ranges (Carbone and Gittleman, 2002; Woodroffe and Ginsberg, 1998). Second, conservation planning in the studied ecosystem has only partly been based on ecological considerations and wildlife populations are frequently found outside formally protected areas (Kiffner et al., 2015). Third, some of the studied species, in particular spotted hyenas and leopards, have been shown to thrive relatively well in human-dominated landscapes, given their flexible feeding patterns and adaptive ranging behavior (Hayward et al., 2006; Kolowski and Holekamp, 2008, 2011). Fourth, cheetahs and wild dogs were very rare in the studied ecosystem, and thus were rarely encountered or considered as problem species (Estes, 1991; IUCN, 2014). Overall, however, large-scale, spatial features (highland vs. valley and distance to protected area)

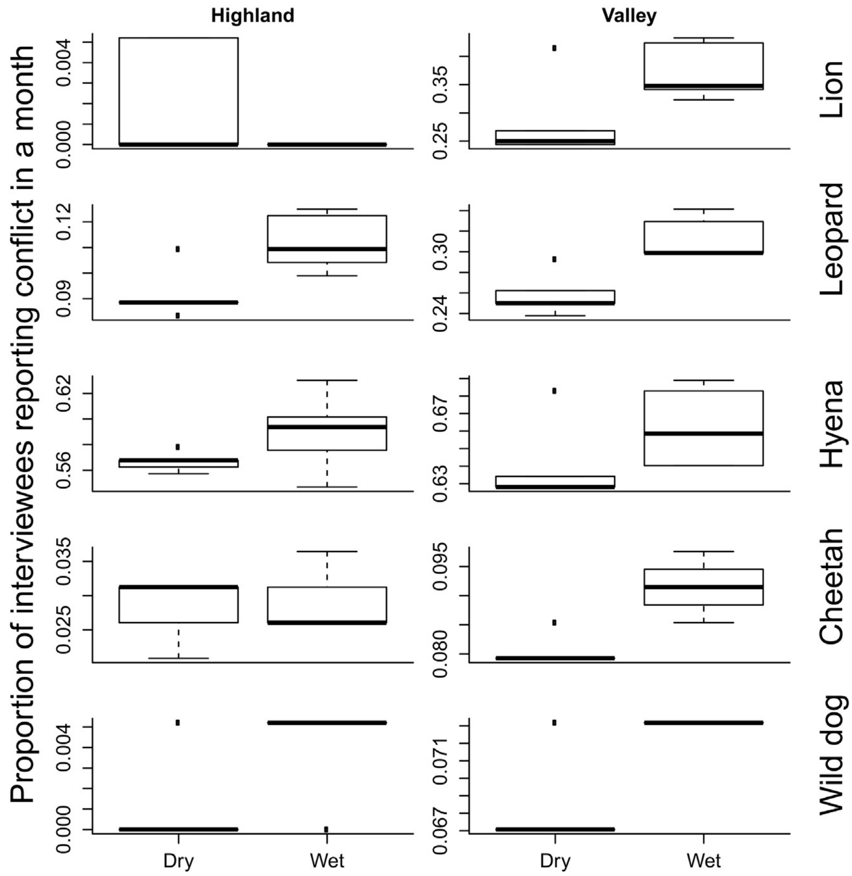

Fig. 5. Proportion of interviewees reporting large carnivore conflicts during wet and dry season months in the Ngorongoro highlands ('Highland') and the rift valley ('Valley') of Northern Tanzania.

and temporal patterns apparently affected large carnivore conflict, stressing the importance of landscape and local context on human-wildlife conflict (Michalski et al., 2006; Inskip and Zimmerman, 2009).

Hyenas were considered the most problematic species, consistent with previous studies in the Tarangire–Manyara ecosystem (Kissui, 2008; Mponzi et al., 2014). This is in contrast to other areas of Tanzania. For example, in the eastern part of the Serengeti ecosystem, wild dogs and spotted hyenas were considered main conflict species (Lyamuya et al., 2014; Hampson et al., 2015) and in the Ruaha landscape, lions were perceived as most problematic (Dickman et al., 2014). We assume that the proximity of our study area to the Ngorongoro Conservation Area and its presumed high density of spotted hyenas coupled with the tendency of this species to forage outside of its core territory (Hofer and East, 1993; Höner et al., 2005), contributes to a high conflict frequency of this species in the highland. In addition, there is no active rabies vaccination program in place (in contrast to areas bordering the Serengeti; Lembo et al., 2008), and thus certain instances of conflict may be attributed to rabid carnivores.

Specifically, attacks on humans were a minor (in terms of frequency) perceived conflict type, yet, almost all interviewees expressed the most impassioned response to this type of conflict, indicating that most people were highly concerned about these incidences. Because of their traumatic nature, these attacks remain memorable to the community and foster animosity towards wildlife (Knight, 2000; Dickman et al., 2014). The design of this study did not investigate if or to what degree reported conflicts differed from actual conflict events but we assume that the perceived conflict frequencies for the species were often exaggerated, based mainly on ecological probability (Chardonnet et al., 2010). Future investigations ought to examine real vs. perceived conflict in the study area by recording and investigating instances of conflict over a certain period (Kissui, 2008), or by employing indirect methods that assess actual conflict with and direct killing of conflict species (St. John et al., 2010).

4.2. Psychological, demographic and socio-economic correlates

In the valley, several interviewees that reportedly did not fear hyenas said that this was because hyenas were not as dangerous when compared to lions. In contrast, fear of hyenas as a somewhat important determinant in the highland may have resulted from past attacks of hyenas on humans. For example, in 2012, at least two incidents of hyena attacks in the highland occurred and caused several injuries and at least one fatality in the immediate neighborhood of the senior author. Clearly, fear resulting from direct or indirect experiences could aggravate the perceived severity of actual conflict (Kaltenborn et al., 2006). Moreover, these findings suggest that conflict perceptions are context-dependent and often based on previous experiences (Carter et al., 2012).

Men were more likely (yet not always significantly so) to report conflict with hyenas and lions in the studied landscape. We assume that this is because men usually claim ownership of livestock and are responsible for protecting their families and property; possibly they also come more frequently into contact with lions and hyenas (Hampson et al., 2015). Furthermore, men (as well as women) may further exaggerate reports of conflicts as they might report conflict that occurred in the community even if they were not personally affected ("contagious conflict"; Dickman et al., 2014). Livestock depredation is often interpreted as conflict against the community as a whole. These considerations of local people may be substantial drivers of exaggerated levels of large carnivore conflict. Yet, gender-related perceptions of human-large carnivore conflict seem to differ among cultures. For example, in India, no gender related differences in human wildlife conflicts were found (Ogra, 2008),

Table 1
Summary statistics of model averaged coefficient estimates explaining the likelihood of perceived large carnivore conflict in relation to hypothesized spatial (Distance to protected areas) and interviewee related (gender; age; education; livestock: tropical livestock units TLU; wealth: index calculated based on assets, inversely scaled) variables and associated odds ratios. Significant relationships ($p < 0.05$) are highlighted in bold. The standard deviations (Std. Dev.) for the random intercepts and slopes of the regression coefficients are given as well. Species-specific models were computed separately for a) the Tarangire–Manyara ecosystem ('valley') and b) the Ngorongoro highlands ('highland') of Northern Tanzania.

	Estimate	SE	z-value	P-value	Odds ratio	Std. dev. intercept	Std. dev. slope
a) Valley							
Lion							
Intercept	**−9.342**	**1.645**	**5.630**	<**0.001**		0.009	
Age	−1.236	1.084	1.130	0.258	0.29049	3.062	4.276
Distance to PA	**−9.685**	**3.331**	**2.882**	**0.004**	**0.00006**	0.013	16.301
Fear (vs. no fear)	1.641	1.472	1.105	0.269	5.15878	6.693	4.048
Gender (male vs. female)	**2.655**	**1.019**	**2.583**	**0.010**	**14.23068**	4.279	4.319
Education primary (vs. non)	−0.636	0.408	1.547	0.122	0.52925	0.140	0.231
Education secondary (vs. non)	−1.497	0.999	1.485	0.138	0.22373	0.140	2.557
Leopard							
Intercept	**−17.780**	**2.673**	**6.595**	<**0.001**		2.133	
Distance to PA	−4.384	6.460	0.673	0.501	0.01248	9.687	31.203
Hyena							
Intercept	−2.552	2.210	1.151	0.250		0.002	
Gender (male vs. female)	0.564	0.679	0.822	0.411	1.75681	3.554	2.859
Education primary (vs. non)	0.338	2.235	0.150	0.881	1.40186	0.005	10.898
Education secondary (vs. non)	**−2.591**	**0.720**	**3.567**	<**0.001**	**0.07492**	0.005	8.330
Ethnicity (Other vs. Maasai)	−3.017	2.508	1.192	0.233	0.04894	5.291	3.433
Age	1.853	1.239	1.482	0.138	6.37638	5.019	4.973
Distance to PA	−5.546	4.130	1.330	0.183	0.00390	0.005	19.307
Fear (vs. no fear)	0.230	1.501	0.152	0.879	1.25885	2.910	5.026
b) Highland							
Leopard							
Intercept	−38.199	9.933	3.820	<**0.001**		0.688	
Education primary (vs. non)	7.065	7.091	0.989	0.323	1170.28197	0.332	6.461
Education secondary (vs. non)	10.583	6.509	1.614	0.107	39,458.31195	0.332	3.591
Distance to PA	**−33.119**	**11.148**	**2.949**	**0.003**	<**0.00001**	21.584	28.755
Age	5.741	3.998	1.425	0.154	311.37563	4.165	5.033
Hyena							
Intercept	−5.218	4.556	1.138	0.255		0.003	
Fear (vs. no fear)	1.970	1.193	1.640	0.101	7.16996	7.214	3.815
Gender (male vs. female)	3.845	2.618	1.458	0.145	46.73531	0.009	10.524
Education primary (vs. non)	4.263	4.303	0.984	0.325	70.98723	11.679	13.997
Education secondary (vs. non)	−0.584	5.014	0.116	0.908	0.55761	11.679	15.432
Wealth index	−2.174	3.549	0.608	0.543	0.11373	4.578	15.781
Ethnicity (Other vs. Iraqw)	−2.062	9.385	0.218	0.827	0.12721	3.730	16.753
Age	3.809	4.428	0.854	0.393	45.10982	0.001	19.706
Distance to PA	0.341	4.525	0.075	0.940	1.40635	0.004	19.535

while women in China perceived carnivore conflict as more severe than men did (Alexander et al., 2015).

For some species/locations (valley: hyena; highland: leopard and hyena), interviewee age and conflict were positively correlated. This may be because repeated encounters with wildlife over compounding years may have created a more consistent idea of the severity of conflict. In contrast, conflict with lions in the valley was negatively correlated with interviewee age. This contrasting finding may be caused by potentially declining population sizes of lions. Yet, given the mixed and non-significant effects and the paucity of literature addressing the relationship between age and perceived human wildlife conflict, these relationships are rather speculative.

While education is often presented as the obvious solution to reduce human wildlife conflict, our study found rather mixed effects of education on perceived conflict frequency. In some cases, we found linear decreases (conflict with lions in the valley), linear increases (leopard conflict in the highlands) and non-linear relationships: reported conflict frequency with hyenas (both in the highlands and the valley) increased among interviewees with primary education and decreased among subjects with secondary education. These mixed effects are well documented in the literature as education has been shown to decrease animosity felt towards wildlife species in some studies (Madden, 2004; Chardonnet et al., 2010; Dickman, 2010), while other studies showed that education programs are not necessarily effective at teaching skills to avoid wildlife conflict (Baruch-Mordo et al., 2011) or that education actually increases fear of large carnivores (Kaltenborn et al., 2006 and see relationships between fear and education in our study). While our correlation analyses do not allow providing causal explanations for these mixed effects of education, they suggest that directed conservation education aiming at fostering positive attitudes towards large carnivores could be very effective in primary schools.

Wealth (present in one of five) and livestock ownership (not present in any model) did not affect conflict perceptions substantially. These findings suggest that conflict perception is not primarily dependent on economic considerations, actual risk, or impact of livestock losses, but rather dependent on psychological and cultural circumstances (Dickman, 2010; Dickman et al., 2014).

4.3. Mitigating large carnivore conflict

Surprisingly, the use of mitigation methods was very limited in our study area. Many households reported not being able to afford sturdy fencing materials for their livestock and several livestock enclosures are poorly constructed (usually thorn bush enclosures), highlighting the important, yet apparently insufficient (in terms of scale) attempts of NGOs to support construction of sturdy livestock enclosures in the ecosystem (Kissui, 2008; Lichtenfeld et al., 2015). In the valley, lion hunts are an integral part of Maasai culture, making lethal 'mitigation' a relatively common occurrence; this culturally sensitive aspect further stresses the need to reduce large carnivore conflict by reducing contact rates between livestock and large carnivores (Kissui, 2008).

5. Conclusion and management recommendations

Because protected areas in Tanzania are unfenced, management schemes need to be implemented that foster coexistence, rather than force mere tolerance. Substantial efforts have been made to develop effective large carnivore conflict mitigation methods in these ecosystems (Kissui, 2008; Lichtenfeld et al., 2015) but are rarely in place. These mitigation strategies (construction of predator proof bomas, lion guardians) are geared towards the needs of individual communities, and ensure that both local knowledge and opinion is incorporated into management (Hazzah et al., 2014). Based on our study, we suggest improving conservation awareness education during primary school education. In addition, we suggest that programs aimed at shifting attitudes would be most effective if they were addressed to people who frequently come into contact with large carnivores. Benefits sharing from wildlife via institutional development at the village level could empower local communities and would give a greater sense of control and security about their own futures (Hemson et al., 2009; Carter et al., 2012,). Additionally, the implementation of programs aimed at improved livestock husbandry, including veterinary support may improve perceptions conservation of large carnivores (Dar et al., 2009; Khorozyan et al., 2015b). The results of this study may help identify particular areas (Fig. 1) in strong need of conflict mitigation projects. Overall, tolerance for large carnivores appeared very high, with very few individuals admitting lethal control of large carnivores. Thus, conservation efforts need to particularly address people residing in conflict hotspots and need to consider compensation payments in cases where conflict mitigation is not feasible.

While these short-term measures are crucial, effective human-wildlife conflict reduction (as well as biodiversity conservation) depends to a great extent on limiting human population growth (e.g. via safe, efficient and inexpensive means of family planning) in the long-term.

Acknowledgements

This research was carried out with permission from TAWIRI/Costech: 2014-324-ER-2013-191. We sincerely thank our local guides for their extraordinary help navigating the study area and translating; all interviewees for their time and openness and the School for Field Studies Center for Wildlife Management Studies for funding and logistical support. Constructive comments from three anonymous reviewers greatly improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.04.029.

References

Alexander, J., Pengju, C., Damerell, P., Youkui, W., Hughes, J., Shi, K., Riordan, P., 2015. Human wildlife conflict involving large carnivores in Qilianshan. China and the minimal paw-print of snow leopards. Biol. Conserv. 187, 1–9.

Bartón, K., 2013. Model selection and model averaging based on information criteria (AICc and alike). Available at: http://cran.r-project.org/web/packages/MuMIn/index.html.

Baruch-Mordo, S., Breck, S.W., Wilson, K.R., Broderick, J., 2011. The carrot or the stick? Evaluation of education and enforcement as management tools for human-wildlife conflicts. PLoS One 6, 1–8.

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

Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. Science 295, 2273–2276.

Carter, N.H., Riley, S.J., Liu, J., 2012. Utility of a psychological framework for carnivore conservation. Oryx 46, 525–535.

Chardonnet, P., Soto, B., Fritz, H., Cosmary, W., Drouet-Hoguet, N., Mesochina, P., Pellerin, M., Mallon, D., Bakker, L., Boulet, H., Lamarque, F., 2010. Managing the conflicts between people and lion: review and insights from the literature and field experience. Wildlife Management Working Paper 13. Food and Agriculture Organization of the United Nations, Rome.

Crawley, M.J., 2005. Statistics. An Introduction Using R. John Wiley & Sons Ltd., Chichester, U.K.

Dar, N.I., Minhas, R.A., Zaman, Q., Linkie, M., 2009. Predicting patterns, perceptions, and causes of human-carnivore conflict in and around Machiara National Park, Pakistan. Biol. Conserv. 14142, 2076–2082.

De Azevedo, F.C.C., 2008. Food habits and livestock depredation of sympatric jaguars and pumas in the Iguaçu National Park Area, South Brazil. Biotropica 40, 494–500.

Dickman, A.J., 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Anim. Conserv. 13, 458–466.

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

East, M.L., Nyahongo, J.W., Goller, K.V., Hofer, H., 2012. Does the vastness of the Serengeti limit human-wildlife conflict? In: Somers, M.J., Hayward, M. (Eds.), Fencing for Conservation: Restrictions of Evolutionary Potential or a Riposte to Threateing Processes? Springer, USA, pp. 125–152

Estes, R.D., 1991. The Behavior Guide to African Mammals. Twentieth Anniversary ed. University of California, California, USA.

Galanti, V., Preatoni, D., Martinoli, A., Wauters, L.A., Tosi, G., 2006. Space and habitat use of the African elephant in the Tarangire–Manyara ecosystem, Tanzania: implication for conservation. Mamm. Biol. 71, 99–114.

Galvin, K.A., Thornton, P.K., Pinho, J.R., Sunderland, J., Boone, R.B., 2006. Integrated modeling and its potential for resolving conflicts between conservation and people in the rangelands of East Africa. Hum. Ecol. 34, 155–183.

Gelman, A., Su, Y.-S., 2014. Arm: data analysis using regression and multilevel/hierarchical models. R package version 1.7–07 http://CRAN.R-project.org/package=arm.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699-71.

Hampson, K., McCabe, J.T., Estes, A.B., Ogutu, J.O., Rentsch, D., Craft, M.E., Hemed, C.B., Ernest, E., Hoare, R., Kissui, B., Malugu, L., Masenga, E., Cleveland, S., 2015. Living in the greater Serengeti ecosystem: human-wildlife conflict and coexistence. In: Sinclair, A.R.E., Metzger, K.L., Mduma, S.A.R., Fryxell, J.M. (Eds.), Serengeti IV: Sustaining Biodiversity in a Coupled Human-Natural System. The University of Chicago Press Press, USA, pp. 607–648.

Hayward, M.W., Kerley, G.I.H., 2005. Prey preferences of the lion (*Panthera leo*). J. Zool. 267, 309–322.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (*Panthera pardus*). J. Zool. 270, 298–313.

Hazzah, L., Dolrenry, S., Naughton, L., Edwards, C.T.T., Mwebi, O., Kearney, F., Frank, F., 2014. Efficacy of two lion conservation programs in Maasailand, Kenya. Conserv. Biol. 28, 851–860.

Hedges, S., Borgerhoff Molder, M., James, S., Lawson, D.W., 2016. Sending children to school: rural livelihoods and parental investment in education in Northern Tanzania. Evol. Hum. Behav. 37, 142–151.

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, M.L., 1993. The commuting system of Serengeti spotted hyenas: how a predator copes with migratory prey. I. Social organization. Anim. Behav. 46, 547–557.

Hofer, H., Campbell, K.L.I., East, M.L., Huish, S.A., 2000. Modelling the spatial distribution of the economic costs and benefits of illegal game meat hunting in the Serengeti. Nat. Resour. Model. 13, 151–177.

Holmern, T., Nyahongo, J., Røskraft, E., 2007. Livestock loss caused by predators outside the Serengeti National Park, Tanzania. Biol. Conserv. 135, 518–526.

Höner, O.P., Wachter, B., East, M.L., Runyoro, V.A., Hofer, H., 2005. The effect of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. Oikos 108, 544–554.

Ikanda, D., Packer, C., 2008. Ritual vs. retaliatory killing of African lions in the Ngorongoro conservation area, Tanzania. Endanger. Species Res. 6, 67–74.

Inskip, C., Zimmerman, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx 43 (1), 18–34.

IUCN, 2014. The IUCN red list of threatened species. Version 2014.3 http://www.iucnredlist.org.

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.

Kaltenborn, B.P., Bjerke, T., Nyahongoa, J., 2006. Living with problem animals—self-reported fear of potentially dangerous species in the Serengeti region, Tanzania. Hum. Dimens. Wildl. 11, 397–409.

Khorozyan, I., Ghoddousi, A., Soofi, M., Waltert, M., 2015a. Big cats kill more livestock when wild prey reaches a minimum threshold. Biol. Conserv. 192, 268–275.

Khorozyan, I., Soofi, M., Hamidi, A.K., Ghoddousi, A., Waltert, M., 2015b. Dissatisfaction with veterinary services is associated with leopard (*Panthera pardus*) predation on domestic animals. PLoS One 10 (6), e0129221.

Kiffner, C., Meyer, B., Mühlenberg, Waltert, M., 2009. Plenty of prey, few predators: what limits lions in Katavi National Park, western Tanzania? Oryx 43, 52–59.

Kiffner, C., Albertini, M., Ede, A., Donnellan, B., Hahn, N., McGinnis, M.A., Nietlisbach, N.A., Tate, J., Kioko, J., 2015. Performance of individual species as indicators for large mammal species richness in Northern Tanzania. Ecol. Indic. 53, 70–77.

Kissui, B.M., 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Anim. Conserv. 11, 422–432.

Knight, J. (Ed.), 2000. Natural Enemies: People-Wildlife Conflicts in Anthropological Perspective. Routledge, London, U.K.

Kolowski, J.M., Holekamp, K.E., 2005. Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along the Kenya reserve border. Biol. Conserv. 128, 529–541.

Kolowski, J.M., Holekamp, K.E., 2008. Effects of an open refuse pit on space use patterns of spotted hyenas. Afr. J. Ecol. 46, 341–349.

Kolowski, J.M., Holekamp, K.E., 2011. Ecological and anthropogenic influences on space use by spotted hyenas. J. Zool. 277, 23–36.

Lamprey, H.F., 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire game reserve and the Masai steppe in Tanganyika. East Afr. Wildl. J. 2, 1–46.

Lembo, T., Hampson, K., Haydon, D.T., Craft, M., Dobson, A.P., Dushoff, J., Eblate, E., Hoare, R., Kaare, M., Mlengeya, T., Mentzel, C., Packer, C., Cleaveland, S., 2008. Exploring reservoir dynamics: a case study of rabies in the Serengeti ecosystem. J. Appl. Ecol. 45, 246–1257.

Lichtenfeld, L., Trout, C., Kisimir, E.L., 2015. Evidence-based conservation: predator-proof bomas protect livestock and lions. Biodivers. Conserv. 24, 483–491.

Löe, J., Röskaft, E., 2004. Large carnivores and human safety: a review. Ambio 33, 283–288.

Loibooki, M., Hofer, H., Campbell, K.L.I., East, M.L., 2002. Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: the importance of livestock ownership and alternative sources of protein and income. Environ. Conserv. 29, 391–398.

Lyamuya, R.D., Masenga, E.H., Fyumagwa, R.D., Roskraft, 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.

Madden, F., 2004. Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. Hum. Dimens. Wildl. 9, 247–257.

Meriggi, A., Lovari, S., 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? J. Appl. Ecol. 33, 1561–1571.

Mgawe, P., Borgerhoff, M., Caro, T., Martin, A., Kiffner, C., 2012. Factors affecting bushmeat consumption in the Katavi-Pukwa ecosystem of Tanzania. Trop. Conserv. Sci. 5, 446–462.

Michalski, F., Boulhosa, R.L.P., Faria, A., Peres, C.A., 2006. Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. Anim. Conserv. 9, 179–188.

Morrison, T.A., Bolger, D.T., 2014. Connectivity and bottlenecks in a migratory wildebeest *Connochaetes taurinus* population. Oryx 48, 613–621.

Mponzi, B.B., Lepczyk, C.A., Kissui, B.M., 2014. Characteristics and distribution of livestock losses caused by wild carnivores in Maasai steppe of Northern Tanzania. Hum. Wildl. Interact. 8, 218–227.

Newmark, W., 1993. The role and Design of Wildlife Corridors with examples from Tanzania. Ambio 22, 500–504.

Newmark, W.D., 2008. Isolation of African protected areas. Front. Ecol. Environ. 6, 321–328.

Oates, L., Rees, P.A., 2013. The historical ecology of the large mammal populations of Ngorongoro crater, Tanzania, East Africa. Mammal Rev. 43, 124–141.

Ogada, M.O., Woodrogge, R., Oguge, N.O., Frank, L.G., 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conserv. Biol. 17, 1–10.

Ogra, M.V., 2008. Human wildlife conflict and gender in protected borderlands: a study of costs, perceptions, and vulnerabilities in Uttarakhand (Uttaranchal), India. Geoforum 39, 1408–1422.

Okello, M., 2005. Land use changes and human-wildlife conflicts in the Amboseli area, Kenya. Hum. Dimens. Wildl. 10, 19–28.

Packer, C., Ikanda, D., Kissui, B., Kushnir, H., 2005. Lion attacks on humans in Tanzania. Nature 436, 927–928.

Patterson, B.D., Kasiki, S.M., Selempo, E., Kays, R.W., 2004. Livestock predation by lions (*Panthera leo*) and other carnivores on ranches neighboring Tsavo National Parks, Kenya. Biol. Conserv. 119, 507–516.

Pica-Ciamarra, U., Otte, J., Chilonda, P., 2007. Livestock policies, land and rural conflicts in sub-Saharan Africa. IWMI/ICRISAT, Land Reform, pp. 19–33.

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., Eisenberg, J.F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biol. Conserv. 109, 297–310.

Prins, H.H.T., Loth, P.E., 1988. Rainfall patterns as background to plant phenology in Northern Tanzania. J. Biogeogr. 15, 451–463.

R Core Team, 2014. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL http://www.R-project.org/).

Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R., Henschel, P., de Iongh, H., Lichtenfeld, L., Pimm, S., 2013. The size of savannah Africa: a lion's (*Panthera leo*) view. Biodivers. Conserv. 22, 17–35.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 124,484.

Romañach, S.S., Lindsey, P.A., Woodroffe, R., 2011. Attitudes toward predators and options for their conservation in the Ewaso ecosystem. In: Georgiadis, N., Moss, J., King, A., Malleret-King, D. (Eds.), Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem. Smithsonian Institution Scholarly Press, USA, pp. 85–93.

Schielzeth, H., Forstmeier, W., 2009. Conclusions beyond support: overconfident esrtimates in mixed models. Behav. Ecol. 20, 416–420.

Soh, Y.H., Carrasco, L.R., Miquelle, D.G., Jiang, J., Yang, J., Stokes, E.J., Tang, J., Kang, A., Liu, P., Rao, M., 2014. Spatial correlates of livestock depredation by Amur tigers in Hunchun China: relevance of prey density and implications for protected area management. Biol. Conserv. 169, 117–127.

St. John, F.A.V., Edwards-Jones, G., Gibbons, J.M., Jones, J.P.G., 2010. Testing novel methods for assessing rule breaking in conservation. Biol. Conserv. 143, 1025–1030.

Stoddart, L.C., Griffiths, R.E., Knowlton, F.F., 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. J. Range Manag. 54, 15–20.

Sundararaj, V., McLaren, B.E., Morris, D.W., Goyal, S.P., 2012. Can rare positive interactions become common when large carnivores come livestock? Ecology 93, 272–280.

Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv. Biol. 17, 1491–1499.

Tschanz, B., Bersier, L., Bacher, S., 2007. Functional responses: a question of alternative prey and predator density. Ecology 88, 1300–1308.

Valeix, M., Hemson, G., Loveridge, A.J., Millis, G., Macdonald, D.W., 2012. Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. J. Appl. Ecol. 49, 73–81.

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

Woodroffe, R., Lindsey, P., Romañach, S., Stein, A., Ranah, S.M.K., 2005. Livestock predation by endangered African wild dogs (*Lycaon pictus*) in northern Kenya. Biol. Conserv. 124, 225–234.