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Article

Creating Landscapes of Coexistence: Do Conservation Interventions Promote Tolerance of Lions in Human-dominated Landscapes?

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Abstract

The range-wide decline of lions has led to their conservation becoming a top priority. Protection of free-ranging lion populations is dependent on securing space for lions but also on the ability and desire of local communities to coexist with lions. Our investigation takes a comparative and case study approach to explore the individual and societal desire to maintain current lion populations alongside communities in, or surrounding, Zimbabwe's Hwange National Park, Tanzania's Ruaha National Park, and Kenya's southern Maasailand. Using data from attitudinal questionnaire surveys, we compare the desire to maintain current lion populations as well as the prevalence and success of conservation interventions aimed at increasing human-lion coexistence. In Maasailand, 88% of the respondents expressed a desire to see current lion populations maintained, while only 42% of the respondents in Ruaha and only 5% of the respondents in Hwange expressed this desire. More respondents reported predation by lions (lion predation) on livestock in Maasailand than in Hwange; personal benefits from conservation were greatest in Maasailand; and exposure to conservation education was highest in Ruaha. The Hwange findings were confounded by Zimbabwe's political and economic climate. In Ruaha and Maasailand, communal and individual conservation benefits influenced desired changes to lion population. Once variation between sites was controlled for, twinning personal benefits and conservation education together was most likely to increase an individual's desire to see current lion populations maintained.

Keywords: human-lion conflict, coexistence, community-based conservation, Maasailand, Hwange, Ruaha, Kenya, Zimbabwe, Tanzania

INTRODUCTION

The African lion (*Panthera leo*), an archetypal charismatic felid, has suffered a dramatic reduction in range and a concurrent population decrease, now occurring only in around 8% of its historic range (Riggio et al. 2013; Bauer et al. 2015a). Countries such as Tanzania, Zimbabwe, and Kenya are vital to maintaining the long-term viability of Africa's free-ranging lion meta-populations, with five of the continent's lion strongholds (contagious areas with over 2000 lions) being fully or partially encompassed within their boundaries (Riggio et al. 2013). Human-lion conflict is ubiquitous across the lion range in Africa and considered to be one of the greatest threats to the remaining lion populations, who mostly live within or surrounded by human-dominated landscapes (Lindsey et al. 2017; Loveridge et al. 2017). For viable lion populations to be maintained, a degree of tolerance for, and coexistence with, lions is necessary. As defined by Bruskotter and Fulton (2012), tolerance can be considered to be the "passive acceptance of a wildlife population". Borrowing from Carter and Linnell (2016), we consider human-lion coexistence to be the sustainable cohabitation of people and lions within a shared landscape.

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Human-wildlife conflicts (HWC) occur when wildlife threatens peoples' livelihoods, property, or safety (Inskip and Zimmermann 2009). Redpath et al. (2013) further identify that a clear distinction is needed between human-wildlife conflicts and human-human conflicts created by conservation. Conservation interventions can often create human-human conflicts between communities, non-governmental organisations, and governments who have differing agendas (West et al. 2006; Redpath et al. 2013). Such is the case surrounding Amboseli National Park in Kenya, where Maasai pastoralists live adjacent to the park where restricted access to grazing in the park leads to a higher stated propensity to kill lions (Hazzah et al. 2013). Understanding the current state of lion conservation and human-lion coexistence requires a broader knowledge of how tolerance is created, and the effects of conservation efforts aimed at promoting coexistence.

Socio-psychological theories such as the theory of planned behavior can advance our understanding of wildlife tolerance (St John et al. 2011). The wildlife tolerance model (WTM) by Kansky et al. (2016) and the human-tiger tolerance model by Inskip et al. (2016) are two examples of how psychological models have been used to develop models of human-carnivore tolerance. We propose that tolerance is best explained by Bruskotter and Wilson's (2014) hazard acceptance model. The hazard acceptance model suggests that tolerance is determined by the interplay between five components: 1) an individual's perceived control over the threat (wildlife damage), 2) societal trust (in the management authorities), 3) affect for the species, 4) perceived benefits, and 5) perceived costs.

Conservation efforts aimed at promoting human-carnivore coexistence and tolerance of carnivores can be grouped into three broad approaches, namely 1) reducing predation by lions (lion predation) on livestock, 2) providing economic incentives for coexistence, and 3) creating tolerance for carnivores through conservation education.

Reduction in lion predation on livestock commonly involves targeted interventions that aim to improve livestock husbandry, reduce depredation, or prevent retaliatory carnivore killing (Hazzah et al. 2014; Lichtenfeld et al. 2015). Improving the quality of livestock enclosures and livestock guarding does reduce the likelihood of lion predation (Ogada et al. 2003; Woodroffe et al. 2007). The use of guard dogs is another way to deter lion predation on livestock both in pastures and around livestock corals, but the effectiveness of this method varies depending on the predator and context (Marker et al. 2005; Eklund et al. 2017). Local participation in lion monitoring has been shown to reduce lion killings, and foster positive perceptions of lions, but its applicability and effectives across a broader range of carnivore species and contexts has not been evaluated (Dolrenry 2013; Hazzah et al. 2014). Despite the prevalence of initiatives aimed at reducing lion predation on livestock through improved livestock husbandry, there is little consensus about the results or about whether reduced rates of lion predation lead to greater tolerance of large carnivores (Miller et al. 2016).

Economic incentives for coexistence can be further classified into 1) compensation payments which offset the cost of predation on livestock, and 2) those that provide economic incentives for coexistence with carnivores (Lindsey et al. 2007; Nelson 2009). Compensation offsets are commonly used to offset losses incurred by predation and are a disincentive for retaliatory killing of carnivores, but have been criticised for encouraging bad husbandry and increasing predation rates (Ravenelle and Nyhus 2017). In India, compensation was shown to be ineffective due to barriers of corruption, wealth, and gender that prevented access (Ogra and Badola 2008). However, donor-funded private compensation schemes in Kenya that incorporated penalties for predation resulting from poor livestock husbandry have been effective at reducing rates of retaliatory killings (Okello et al. 2014; Bauer et al. 2015b). These examples suggest that compensation schemes require strong leadership, institutional infrastructure, and verification based on clear guidelines to be effective (Treves et al. 2009).

In countries like Kenya and Namibia, community-based conservation (CBC) and community-based natural resource management (CBNRM) have been used to provide financial incentives, which may improve coexistence with wildlife (Jones and Weaver 2009; Western et al. 2015). This hypothetical direct connection between economic benefits and perceptions of carnivores is often complicated by existing human-human conflicts and the socio-political context (Dickman et al. 2011; Zimmermann 2014; Inskip et al. 2016). Kleptocracy of leaders or the misappropriation of benefits by elites, and locally perceived wrong-doing by conservation organisations involved in CBC/CBNRM can compound human-wildlife conflict (Nelson et al. 2007; Goldman et al. 2013; Calfucura 2018).

An alternative approach to providing economic incentives for coexistence are performance payments. Performance payment are made to an individual or group for achieving a predefined conservation indicator (Zabel and Engel 2010). In Sweden, for example, performance payments fostered coexistence between livestock owners and wolverines (*Gulo gulo*) and wolves (*Canis lupus*), leading to an increase in populations of both species (Zabel and Holm-Muller 2008; Persson et al. 2015). The question is whether performance payments are appropriate to the African context, given the challenges of equity and transparency that CBC and CBNRM have faced (Nelson 2009; Zabel and Engel 2010; Dickman et al. 2011).

Conservation education aimed at promoting coexistence is commonly used to increase understanding and acceptance of wildlife (Treves et al. 2006; Gore et al. 2008), but its effectiveness is controversial. Schultz (2011) argues that conservation education and increased knowledge do not change an individual's behaviour, which is predominantly driven by individual motivation linked to societal norms and values. For example in the US, education campaigns were shown to have little effect on reducing bear-related impacts (Baruch-Mordo et al. 2011), while in the Philippines, public education campaigns that highlighted the illegality of crocodile killing and emphasised the importance of their protection (van der Ploeg et al. 2011) succeeded in reducing the killing of crocodiles. How information on risks and benefits associated with carnivores are communicated plays a pivotal role in influencing how a species is perceived (Bruskotter and Wilson 2014). In some cases, tolerance of carnivores may actually decrease when information on how to decrease wildlife impact is communicated in isolation (Slagle et al. 2013). Communication of benefits and positive behavioural traits, on the other hand, is likely to lead to positive perceptions of carnivores (Bruskotter and Wilson 2014). This was the case for coyotes, for which positive perceptions among school children in the US were created by sharing positive behavioural traits of, and pictures of, coyotes (Draheim et al. 2011).

Previous studies of human-lion conflict in human-dominated landscapes (Dickman 2009; Hazzah et al. 2009, Mkonyi et al. 2017, and others) have investigated the drivers of conflict and perceptions of lions at specific sites. This paper aims to build on the existing body of knowledge and enhance our understanding of how different conservation interventions influence an individual's desire to see current lion populations *maintained* or *increase* in human-dominated landscapes. By taking a comparative case study-based approach across multiple sites, we provide an indication of the effectiveness of conservation interventions across three different landscapes in which humans and lions coexist. To do this, we use data from attitudinal questionnaire surveys conducted in three study sites across Africa, to compare the societal and individual desire to maintain current lion populations within human-dominated landscapes. Specifically, we test the following hypotheses:

H1: Across all the three case studies, respondents expressed a predominant desire to see lion populations *decrease*.
H2: Recent exposure to lion predation contributes to individual desire to see lion populations *decrease*.
H3: Perceived personal benefit from conservation promotes individual desire to see lion populations *maintained* or *increase*.
H4: Exposure to conservation education influences the desire to see lion populations *maintained* or *increase*.

METHODS

Study Sites

We discuss case studies from three sites: Zimbabwe's Hwange National Park (Hwange), Tanzania's Ruaha National Park (Ruaha), and Kenya's southern Maasailand (Maasailand). Sites were selected based on the presence of lion populations on community lands and the presence of conservation interventions aimed at 1) reducing lion predation on livestock, 2) providing economic incentives for coexistence, and 3) conservation education efforts.

Hwange, Zimbabwe

Hwange National Park (14,500 sq. km) is located in western Zimbabwe. Surveys were conducted in two districts, Tsholotsho and Hwange, which includes 3306 sq. km of land adjacent to the National Park (Loveridge et al. 2017). Ndebele agro-pastoralists are the dominant ethnic group in Tsholotsho, and the district is predominantly covered by Kalahari Sands savannah forest. Hwange District is inhabited predominantly by agro-pastoral Nambya, Tonga, Shona, and Ndebele. It consists of *Miombo* and *Mopane* woodland. Rainfall in the region is between 324–1160 mm (Loveridge et al. 2009). Very little wildlife is resident year-round in either location, but temporary movement of prey populations and lions in and out of Hwange National Park is common. Lion density in Hwange National Park is estimated to be 3.5 lions per 100 sq. km. Lions here are part of the larger Okavango-Hwange meta-population (~2300 individuals; Riggio et al. 2013).

Ruaha, Tanzania

Surveys were conducted on village land associated with the Pawaga-Idodi Wildlife Management Area (PI-WMA), a 750 sq. km area adjoining the south-eastern border of the Ruaha National Park (RNP) in central Tanzania. The study area is part of the Rungwa-Ruaha region, which covers over 45,000 sq. km, and includes the 20,226 sq. km Ruaha National Park and its adjacent Game Reserves as well as the PI-WMA. The PI-WMA is a vital part of the Rungwa-Ruaha ecosystem, as it provides dry season habitat for many species of Ruaha National Park (Dickman 2005; Dickman and Marker 2005). The Ruaha river runs along the border of RNP and is a key resource for wildlife in the area, drawing species towards the park boundary with the PI-WMA. The area is noted for its high biodiversity and species endemism (WCS 2005). It is situated within one of the World Wide Fund for Nature's 'Global 200' ecoregions (Olson and Dinerstein 1998) and encompasses two Important Bird Areas (WCS 2005). The area harbours an intact array of large carnivore fauna, including the continent's third-largest population of African wild dogs (*Lycaon pictus*), and is considered a priority 'hotspot' for African carnivore conservation (Mills et al. 2001; WCS 2005). The Ruaha complex is particularly important for lions, since it supports the second largest lion population in the world, accounting for nearly 10% of the world's lions (Riggio et al. 2013). The area is also of international ecological significance, as it is the only protected area system representing the transition between the East African *Acacia-Commiphora* zone and the Southern African *Brachystegia* or *Miombo* zone (Williams 1999). The climate is semi-arid to arid, with approximately 500 mm of rainfall annually; rainfall seasons fall in December–January and March–April (Walsh 2000). The vegetation is a mix of typical East African semi-arid savannah vegetation and *Zambezian miombo* woodland, with common species including *Acacia, Combretum*, and *Commiphora* (Sosovele and Ngwale 2002).

The area is home to a heterogeneous mix of agriculturalists, agro-pastoralists, and pastoralists, with at least 35 tribes represented (Dickman 2009). It is a particularly important area for pastoralists, as it forms a movement corridor linking this pastoralist rangeland with those to the north-east, north-west, and south-west of the Rungwa-Ruaha system (Williams 1999).

Maasailand, Kenya

Kenya's Maasailand comprises of two southern counties, Kajiado and Narok. Questionnaire surveys took place in adjacent ecosystems within Kajiado County, namely the Greater Amboseli Ecosystem (GAE; 9,000 sq. km) and the South Rift Ecosystem (SRE; 10,000 sq. km). Swamps form the ecological foundations of both systems. In the GAE, Nkongo Narok and Lonkinye swamps are key dry season concentration areas for wildlife, while Amboseli National Park covers 392 sq. km around these swamps (Western 1973). GAE is a semi-arid environment with variable rainfall (ranging from 132 mm to 533 mm annually) and variable pastures (Berger 1993; Altmann et al. 2002). In the SRE, the seasonal concentration and dispersion of ungulates mirrors that of Amboseli, with ungulates concentrating in the Ewaso Nyiro swamps during the dry season. Unlike Amboseli, no national park exists within the South Rift, but two community conservancies (Olkiramatian and Shompole) have been established to promote wildlife and rangeland conservation. Rainfall is low and variable, ranging from 200 mm to 600 mm annually (Tyrrell et al. 2017).

Maasailand has Kenya's largest lion population (~800 individuals) (KsNLCT 2008). Survey locations within each ecosystem reflected the presence of permanent lion populations on communally-owned pastoral lands known as group ranches. Group ranches are governed on behalf of their members by democratically-elected group ranch committees. Mbirikani, Eselenkei, and Olgulului group ranches cover 2,400 sq. km of the GAE, supporting a population density of 1.3 adult lions/100 sq. km (Dolrenry 2013). Shompole and Olkiramatian group ranches span 890 sq. km of the SRE, and sustain a population density of 13.6 adult lions/100 sq. km (Schuette et al. 2013). Across all five group ranches, Maasai are the dominant ethnic group, and they depend on sheep, goats, and cattle as their main source of livelihood.

Survey Design

Our study is based on the Wildlife Stakeholders Acceptance Capacity (WAC) concept, which indicates the "maximum wildlife population level in an area that is acceptable" (Bruskotter et al. 2015). Proposed by Decker and Purdy (1988), the WAC concept has been used across wide range of studies including Inskip et al. (2016) in their model of human-tiger tolerance in the Sundarbans region of Bangladesh. Bruskotter et al. (2015) demonstrated that WAC was a reliable indicator of tolerance for wildlife and may explain the prevalence of a species within an area. WAC concepts have commonly been tested by asking individuals whether they would like to see wildlife populations increase, decrease, or stay the same. In our study, we extracted the question "What would you like to see happen to the numbers of lions in this area, and why" to provide a quantitative measure of tolerance from three independently-designed and -administered questionnaire surveys.

Site-specific questionnaires were designed and administered by AL in Hwange, AD in Ruaha, and GW in Maasailand. The use of independently-designed questionnaires incorporating common questions allowed the complexity and range of human-wildlife interactions within each site to be captured, and ensured that the data being collected in each case study took into account local conservation practices, cultures, and legislation. "Site" was included in fixed effect in cross site comparisons to account for site-specific differences in survey administration and human-lion interactions. Surveys in southern Maasailand were adapted by GW from questions used in Hwange and Ruaha for cross-site comparisons, but focused more specifically on human-lion conflicts. In all sites, questionnaires were piloted on representative members of the community before deployment. Questionnaires at each site included information on 1) desired changes in lion population, 2) lion predation on livestock, 3) benefits accrued from conservation, and 4) exposure to conservation education (Table S1). Complete questionnaires for each site can be found in Appendix S1-4.

In Hwange and Kenya, responses to the question on *desired changes in lion populations* were grouped into four categories, based on whether respondents were *unsure*, wanted to see local lion populations *decrease*, *stay the same* or *increase*. In Ruaha, responses to this question were grouped into five categories, i.e., *disappear completely*, *decrease*, *stay the same*, *increase*, and *not sure*. To simplify comparisons, the '*disappear completely'* and '*decrease*' responses from Ruaha were combined into a single group to standardise categories across all three sites (with the final categories being *unsure*, *decrease*, *stay the same*, *increase*).

Of the 757 respondents, the 31 who stated they were *unsure* were excluded from subsequent models and calculations, as it could not be ascertained whether they understood the question and the strength of their preference for any change in lion numbers was unclear. Three ordered groups (*decrease*, *stay the same*, *increase*) were created for use in site-specific and inter-site cumulative link models. Ordered groups were also converted into a numeric change scale (decrease = -1, stay same = 0, increase = +1) to calculate mean desired change in lion populations. In all three sites, respondents were also asked an open-ended question about their reasons, with answers categorised by GW based on the predominant theme of the response (e.g., lion predation, revenue from tourism, etc.).

Lion predation on livestock

Data on reported lion predation was collected during interviews. In Maasailand and Hwange, respondents were asked to list how many livestock they had lost to lions in the last year. In Ruaha, the time frame for that question was based on months. The number of reported lion predation events was used as an explanatory variable to investigate variation in desired change in lion populations for each case study. For comparisons between case studies, a binary (predation, no predation) was created from reported livestock mortality during the last year in Maasailand and Hwange, and the last month in Ruaha.

Perceived benefits from conservation

Perceived benefits from conservation were not predefined in any of the questionnaires but were left open to interpretation by the respondent. Hwange respondents were asked whether or not they had received any benefits from Hwange National Park or Communal Areas Management Programme for Indigenous Resources (CAMPFIRE), and the binary response to each question was combined to create a benefit score (0 = No Benefit, 1 = CAMPFIRE or Park Benefit, 2 = both CAMPFIRE and Park Benefit). To assess the impact of perceived benefits from conservation in Maasailand and Ruaha, we used identical five-point Likert scales: categories ranged from *no benefit* to *very big benefits*. Respondents in Ruaha were asked what level of personal benefit they received from the presence of carnivores. Interviewees in Kenya were asked about perceived personal benefit from lions specifically. Likert scales were converted to numeric benefit scores (*No benefit* = 0, *small benefit* = 1, *big benefit* = 2, *very big benefit* = 3). In Ruaha and Maasailand, respondents who indicated they were unsure were grouped under the no benefit category. A binary metric of personal benefit from conservation (benefit/no benefit) was created and used in cumulative link models for comparisons between case studies.

Conservation education

Exposure to conservation education included engagement with conservation organisations, national park staff, or community conservation officers, during which information relating to carnivore conservation was discussed. Respondents in Maasailand were asked if they had ever had someone come and talk to them about lion conservation. Subsequent questions were to identify who they had engaged with and the type of engagement. In Hwange, the question was phrased as whether representatives from the national park had ever come to talk to them about lion conservation. To create a scale of exposure to conservation education in both Hwange and Maasailand, respondents who had no engagement with conservation education were scored as 0, respondents who had engagement with conservation education but could not recall the message as 1, and respondents who had engagement with conservation education and were able to recall the conservation message as 2. Interviewees in Ruaha were asked three questions about conservation education: had they experienced a wildlife video night, received a household visit, or been given any other advice by the Ruaha Carnivore Project (RCP). Responses to each question were coded on a binary scale and summed to create a conservation education exposure scale which ranged from 0 = *no exposure* to 3 = *maximum exposure*. Conservation education exposure scales were only used within case studies, while a binary metric of conservation education (*education, no education*) was used to compare differences in exposure across case studies and was included in the combined cumulative link model for data from all sites.

Survey Administration and Sample Selection

In Hwange, village heads were first met with to obtain permission for the survey. We aimed to interview 15% of households in large villages (~30–50 households) and 20% in smaller ones as a rule of thumb (24 in Mabale and Gwaai, and 56 in Tsholotsho).

The interviewers started at one side of the village and sampled every 2nd or 3rd household until the required number of interviews had been obtained. The head of the household or the most senior adult present in each household was interviewed (average age of interviewees was 48 years). We interviewed approximately 15% (n = 353) of ~2300–2400 households in a 30 km buffer from the park boundary within our study areas.

In Ruaha, the household or *olmarei* was chosen as the sampling unit, following Maddox (2002), and interviews were restricted to one respondent per household. In each village, the chairman and/or headman was approached, the research explained, and he was then asked for locations of Maasai, Barabaig, Hehe, and Bena households in that village. Once a list of households and their locations was made, 20% were randomly selected. Upon arrival at the household, the most senior member of the household was asked for permission to conduct the interview and asked to participate. Women deferred to men in seniority, so interviewees were predominantly male, but interviews were conducted with women where they were happy to do so. If nobody of appropriate seniority was available, enumerators moved on to another randomly selected household until the required sample size was reached. As a result, neither the selection of the household nor the individual respondent was influenced in any way by previous interactions with Ruaha Carnivore Project (RCP) staff.

Everyone of appropriate seniority agreed to participate in the survey. All interviewees were adults (> 18 years old). Interviews were conducted in Swahili and took approximately one hour to complete, with results translated into English by trained enumerators. There were ~136 Maasai households, ~56 Barabaig households, ~110 Hehe households, and ~68 Bena households in the study area. Our study sampled 78% of the Maasai households, 100% of the Barabaig households, 74% of the Bena households, 42% of the Hehe households.

Questionnaires *in Maasailand* were translated into and conducted in the local language, Maa, by enumerators selected from each community and trained by GW. Three independent back-translations into English were used to ensure that the translations were accurate. Answers to open-ended questions were recorded in English. Enumerators conducted two trial interviews prior to the commencement of the survey; they were asked to translate respondents' answers from Maa to English to gauge their understanding of the questions and ability to translate. We used homesteads (bomas) as our sampling unit. There are approximately 1000–1100 homesteads in the settlement areas of interest. Quota sampling (Newing et al. 2011) was used to select ~12% of homesteads from each settlement within the lion range. Equal numbers of women, young men (aged 18–45 years), and elderly men (aged 45+ years) were chosen at random from a homestead list. In cases where randomly selected respondents were unavailable, we contacted others within each location who matched our selection criteria identified by local chiefs, who recommended respondents on the basis of our age and gender criteria and availability.

Data Analysis

The Statistical Package R (version 3.3.0) was used to test data trends. Data for each case study and comparisons between sites were analysed separately. For each case and across case studies non-parametric Chi squared and Kruskal Wallis tests were used to determine if desired change in lion population varied among individuals with differing exposure to predation, benefits from conservation, and conservation education. Spearman rank correlations and Pearson product moment correlations were used to assess whether correlations were present ($r > 0.7$) in ordinal and continuous predictors.

The package "*ordinal*" (Christensen 2015) was used to create cumulative link models (clm) to test the strength of the relationship between desired change in lion population and the explanatory variables. All three case studies used the same key explanatory variables, which were treated as numeric variables; these included personal benefit, lion predation, and conservation education.

To assess the overarching relationship between desired change in lion population and exposure to three key variables, data from all three case studies were combined. The variables were converted to a "Yes"/"No" binary code to account for inter-site variation in sampling methodology and scales. Candidate models were created from a global cumulative link model in which predation, benefit, and education were included as explanatory variables. Competing models were compared using package *MuMin* in R (Barton 2016) based on an information theoretic approach "IT", which used Akaike's Information Criterion (AIC) corrected for small sample size (AICc) to identify the best model (Burnham and Anderson 2004).

RESULTS

A total of 757 surveys were collected from the three study sites (Hwange 353, Ruaha 280, Maasailand 124). *In Hwange*, the 353 respondents included Ndebele (267) and Nambya (77), and were predominantly male (male = 53%, female = 47%). The 280 respondents (male = 67.5%, female = 32.5%) *in Ruaha* were 107 Maasai, 59 Barabaig pastoralists, 49 Bena, and 46 Hehe agro-pastoralists. All 124 respondents *in Maasailand* were Maasai (male = 70%, female = 30%).

Desired Change in Lion Populations

In Hwange and Ruaha, respondents expressed a predominant desire to see lion populations decrease, while in Maasailand respondents primarily wanted to see lion populations increase. The variation in desired change in lion population between case studies was significant (X-squared = 254.77, df = 6, $p < 0.001$). *In Maasailand*, 88.0% (n = 109) of interviewees expressed a desire to see lion populations either *stay the same* (12.9%, n = 16) or *increase* (75.0%, n = 93) compared to 42% (n = 119) *in Ruaha* and 5% (n = 16) *in Hwange* (Figure 1a). In Ruaha, 32% (n = 91) of respondents wished to see lions *disappear completely*, but data on desired extirpation was not available for Hwange or Maasailand. The average desire of respondents to see lion populations maintained at current levels or higher was significantly (Kruskal-Wallis = 340.62, df = 2, $p < 0.001$) greater in Maasailand (0.64, SE = 0.06) than in Ruaha (-0.43, SE = 0.04) or Hwange (-0.95, SE = 0.01) (Figure 1a).

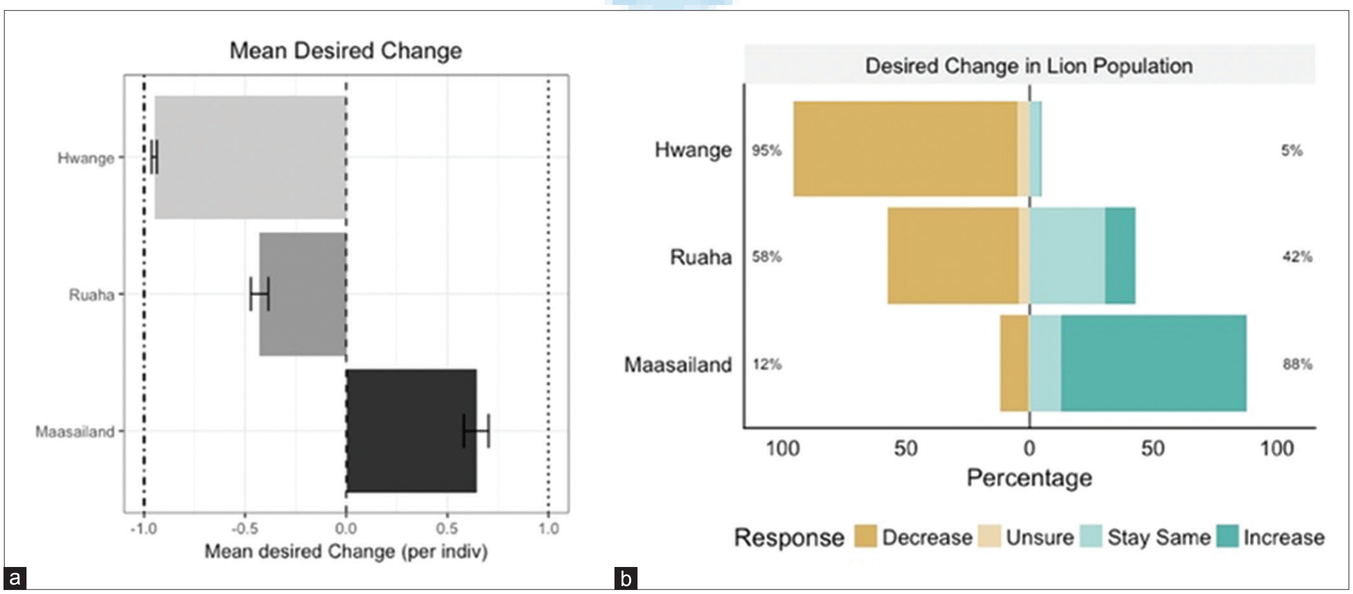

Figure 1
Bar plots depicting variation across sites in (a) reported mean desired change in lion populations (–1=decrease, 0=stay the same, 1= increase), (b) proportion of respondents in each site who wished to see lion populations decrease, stay the same, increase, or were unsure. Percentages on the Y-axis indicate the proportion of respondents who desired lion populations to stay the same or increase compared to those with who wished to see lion populations decrease or were unsure

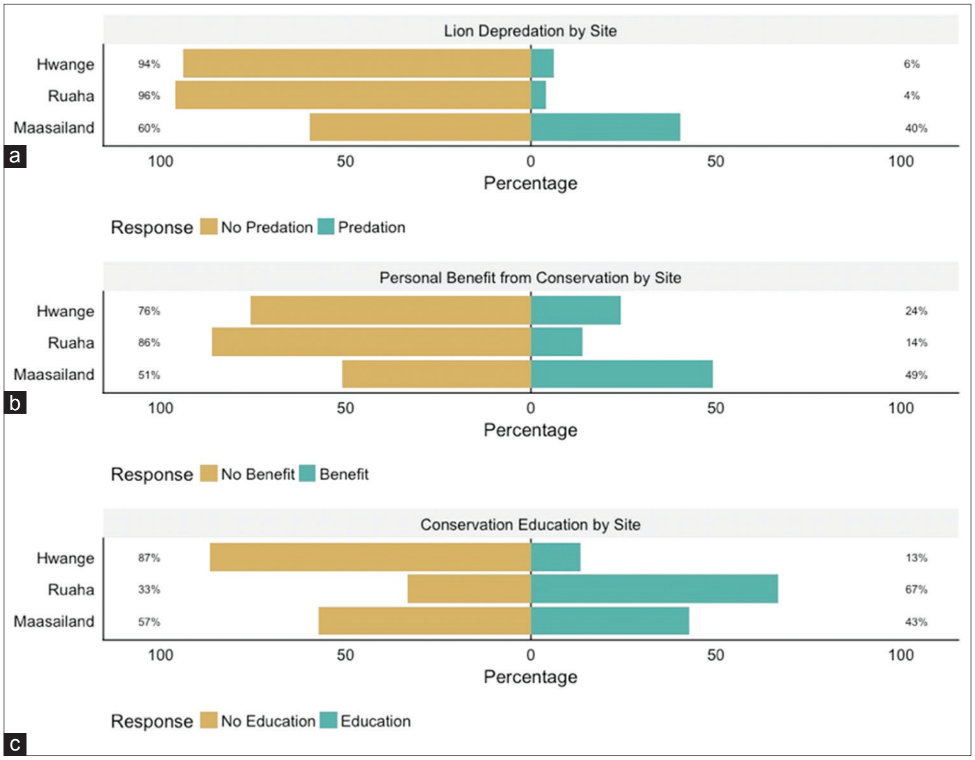

Figure 2
Bar charts depicting the proportion for respondents who (a) reported losing livestock, (b) received personal benefit from conservation, (c) had been exposed to conservation education

Table 1
Site specific cumulative link models showing factors affecting desired change in lion populations by case study

	Desired Change in Lion Populations		
	Maasailand	Ruaha	Hwange
Lion Predation	-0.214 (0.211)	0.274 (0.126)	-10.80 (1308)
	z=-1.013	z=2.176	z= -0.008
	P=0.196	P=0.030*	P=0.993
Personal Benefit	0.413 (0.260)	0.616 (0.120)	-0.022 (0.259)
	z=1.586	z=5.137	z= -0.085
	P=0.113	P<0.01**	P=9.3151
Conservation Education	-0.475 (0.469)	0.262 (0.147)	0.567 (0.675)
	z= -1.013	z=1.782	z=0.840
	P=0.311	P=0.075‘’	P=0.400
Observations	123	178	335
Log Likelihood	-85.842	-169.878	-65.441

Signif. codes: **P<0.1; *P<0.05; ‘’ 0.10

Inter-site variations

There was significant variation across sites in the proportion of respondents reporting lion predation on livestock (X-squared = 131.78, df = 2, p-value < 0.001), benefits received from conservation (X-squared = 174.11, df = 2, p-value < 0.001), and exposure to conservation education (X-squared = 191.13, df = 2, p-value < 0.001) (Figure 2).

Recent exposure to lion predation

Recent exposure to lion predation influenced respondents' desire to see lion populations *decrease*, but the relationship was complex being both timescale- and site-dependent. In Maasailand and Hwange, cumulative link models revealed no significant relationship between desired change in lion population and recent exposure to lion predation (Table 1). Conversely, the Ruaha cumulative link model showed a strong, statically-significant link between the recent number of livestock lost to predation in the last month and desired change in lion population (Table 1). Respondents in Ruaha who had experienced lion predation in the last month where more likely (odd ratio = 1.32) to state a desire to see lion populations decrease.

Across all sites, respondents who had not lost livestock to lion predation in the recent past did not express significantly different views from those who had (Table 2). In Hwange and Ruaha, reported mean livestock mortality was not significantly higher among respondents than those who desired to see lion populations decrease (Table S2). In Maasailand, however, respondents who wanted to see lion populations *increase* or *stay the same* reported marginally lower livestock losses than those who wished to see them *decrease* (Kruskal-Wallis chi-squared = 7.1623, df = 3, p-value = 0.06) (Table S2).

Despite the lack of relationship between lion predation and desired change in lion population in Hwange and Maasailand, qualitative data suggest that lion predation plays a role in influencing respondents' desire to see lion populations *decrease*. In Hwange, among the 90.3% (n = 313) respondents who wished to see lions decrease, 52.3% (n = 167) cited predation on livestock as the main reason. While the 11.2% (n = 14) respondents in Maasailand who indicated that they wanted to see lion populations decrease named predation (85.7%, n = 14) as the primary motivation.

Respondents from all three sites indicated that lions were responsible for substantial levels of lion predation. *In Hwange*, 6.2% (n = 22) of the 353 respondents reported lion predation in the last year. Mean livestock mortality across all Hwange respondents was 0.23 livestock per individual per year. Of the 280 respondents *in Ruaha*, 3.9% (n = 11) reported lion predations in the last month and mean rates of predation were 0.09 head of stock per individual per month. *In Maasailand*, 40.3% (n = 50) of the 124 respondents reported lion predation in the last year, mean livestock mortality across all Maasailand respondents was 0.73 head of livestock per year. Yearly predation rates and the proportion of respondents reporting predation were significantly lower in Hwange than in Maasailand (Wilcox Test = 27666, p-value < 0.001, Chi-square = 49.019, df = 7, p-value = < 0.001).

Perceived benefits from conservation

Perceived personal benefit did influence respondents' desire to see lion populations *maintained* or *increase*, but its ability to do so was strongly site- and context-specific. No relationship between perceived personal benefit and desired change in lion populations existed in Hwange. In Ruaha, a strong relationship existed between perceived personal benefit and desired change in lion population, while in Maasailand a weak, non-significant relationship was present (Table 1).

In Hwange, 24.4% (n = 86) of respondents perceived personal benefits from conservation yet the majority (90.69%, n = 78) still expressed a desire to see lion populations *decrease* (Figures 1 and 2). Perceived personnel benefit from CAMPFIRE and Hwange Park were closely linked, with all respondents who reported personnel benefit from CAMPFIRE

Table 2
Inter- and intra-site variation in the proportion of all respondents desiring to see lion populations decrease, stay the same or increase among groups with differing exposure to livestock predation, perceived personal benefit, and conservation education

		Desired Change in Lion Populations				Sample Size	χ^2	*P*
		Unsure	Decrease	Stay Same	Increase			
Respondents who reported livestock predation								
Maasailand	No Predation	0.81%	4.03%	8.87%	45.97%	124	4.66	0.198
	Predation	0.00%	7.26%	4.03%	29.03%			
Ruaha	No Predation	3.93%	51.43%	29.64%	11.07%	280	2.78	0.427
	Predation	0.00%	1.79%	1.07%	1.07%			
Hwange	No Predation	5.10%	84.14%	4.25%	0.28%	353	2.5	0.475
	Predation	0.00%	6.23%	0.00%	0.00%			
Respondents who perceived personal benefits from lion conservation								
Maasailand	No Benefit	0.00%	6.45%	7.26%	37.10%	124	1.51	0.679
	Benefit	0.81%	4.84%	5.65%	37.90%			
Ruaha	No Benefit	3.93%	50.71%	23.93%	7.50%	280	33.91	0.025**
	Benefit	0.00%	2.50%	6.79%	4.64%			
Hwange	No Benefit	3.97%	68.27%	3.12%	0.28%	353	0.41	0.938
	Benefit	1.13%	22.10%	1.13%	0.00%			
Respondents who received conservation education								
Maasailand	No Education	0.00%	8.06%	8.87%	40.32%	124	3.82	0.282
	Education	0.81%	3.23%	4.03%	34.68%			
Ruaha	No Education	2.14%	21.79%	7.86%	1.43%	280	14.65	0.002**
	Education	2.14%	31.43%	22.50%	10.71%			
Hwange	No Education	3.68%	79.32%	3.40%	0.28%	353	4.32	0.229
	Education	1.42%	11.05%	0.85%	0.00%			

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ''

Table 3
Model comparison showing predictive models of desired changed in lion populations across all three sites

Model	K	logLik	AICc	AICc delta	AICc weight
Change ~ Ben + Edu	6	-342.21	696.54	0	0.501
Change ~ Ben + Dep + Edu	7	-342.13	698.43	1.89	0.195
Change ~ Edu	5	-344.75	699.6	3.06	0.109
Change ~ Ben	5	-344.83	699.75	3.2	0.101
Change ~ Dep + Edu	6	-344.67	701.48	4.94	0.042
Change ~ Ben + Dep	6	-344.69	701.52	4.98	0.042
Change ~ Null Model	4	-348.44	704.94	8.39	0.008
Change ~ Dep	5	-348.29	706.67	10.13	0.003

Ben=Personal and or communal benefit, Edu=Exposure to conservation education, Dep=Exposure to livestock Depredation, Null Model=Change ~ Site

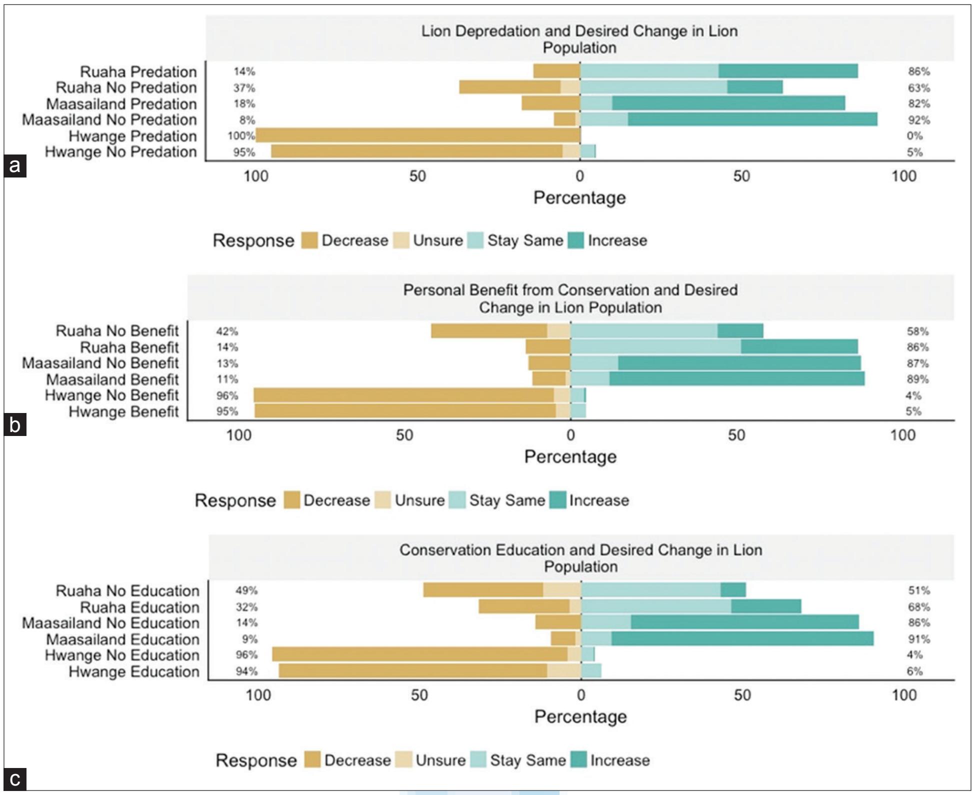

Figure 3

Bar charts depicting cross-site and intra-site variation in desired change in lion populations amongst respondents in relation to their reported exposure to (a) lion depredation, (b) personal benefit from conservation, (c) conservation education

also reporting receiving benefits from Hwange National Park. Of the personal benefits identified in Hwange school improvement was the most common benefit (32%, n = 28), followed by borehole creation (19.8 %, n = 17) and CAMPFIRE revenue (19.8 %, n = 17).

In Ruaha, the cumulative link model (Table 1) revealed a strong positive relationship between desired change in lion population and personal benefits (Personal benefit clm: $z = 5.14$, $p < 0.01$; Table 3). Those who perceived personal benefit (13.9%, n = 39) from conservation were more likely (odds ratio = 1.87) to express a desire to see the lion population *maintained* or *increase*. Chi-square tests further revealed the proportion of respondents in Ruaha who desired to see lion populations *increase* was greater among respondents perceived personal benefits from conservation compared to who did not (Figure 3, Table 2). Perceived benefit from conservation in Ruaha was predominantly attributed to revenue generation from tourism (35. 9 %, n = 14) and the value of being able to see lions (28.2%, n = 11). However, the level of perceived benefit was low. Mean personal benefit scores for respondents in Ruaha were 0.25 per individual (Benefit scale: *No benefit* = 0, *small benefit* = 1, *big benefit* = 2, *very big benefit* = 3).

In Maasailand, 49.2% (n = 61) of respondents perceived personal benefit from conservation. Yet the cumulative link model revealed no relationship between receiving personal benefit and desired change in lion population (Table 1). Respondents did associate an increase in lions with a greater potential to generate tourism revenue. When asked why they would like to see lion populations change, of the 75% (n = 93) of Maasailand respondents who wanted to see lion populations *increase*, 68.8% (n = 64) cited increased personal and communal benefits from wildlife as the predominant reason and 15.1% (n = 14) of respondents felt lions increased tourism. Respondents in Maasailand perceived substantial benefit was accrued from conservation. Mean personal benefit scores reported by all respondents in Maasailand was 1.90 per individual (Benefit scale: *No benefit* = 0, *small benefit* = 1, *big benefit* = 2, *very big benefit* = 3). Perceived personal benefit in Maasailand was primarily from student scholarships (40.3%, n = 23), tourism revenue generation (29.0%, n = 18), and employment (24.1%, n = 15).

Exposure to conservation education

Exposure to conservation education did not create a desire to see lion populations *maintained* or *increase*. Cumulative link models revealed that no statistically significant relationship existed between exposure to conservation education and desired change in lion populations expressed by respondents in Hwange and Maasailand, but a weak relationship existed in Ruaha (Table 1). Mean exposure to conservation education was also marginally higher (Kruskal-Wallis = 7.57, df = 3, p-value = 0.056) among respondents in Ruaha who desired to see lion populations increase (Table S2). Across the sites, the prevalence of conservation education varied substantially. *In*

Hwange, only 13.3% (n = 47) of respondents reported being exposed to conservation education compared to 66.8% (n = 187) *in Ruaha* and 42.7% (n = 53) *in Maasailand* (Figure 2).

Cross-site Predictors of Desired Change in Lion Populations

Analysis of inter-site variation (Table S3) revealed significant variation between predation, benefit, and education across sites, hence "site" was subsequently included in all cross-site candidate models as a fixed effect. Cumulative link models, which included site as fixed effect and combined responses from Hwange, Ruaha, and Maasailand, revealed that desired change in lion population was best predicted by a benefit and education model (Table 3). The full model, which included exposure to predation, personal benefit from conservation, and conservation education as binary variables, could be considered (ΔAICc = 1.89) a top model contender (ΔAICc< 2), but the AICc weight was considerably lower, indicating the model held less explanatory power than the more parsimonious benefit and education model. None of the three variables, treated in isolation, proved to be good predictors of the respondents' desire to see a change in lion populations.

DISCUSSION

Our results show that across all three case studies, respondents did not express a predominant desire to see lions decrease. Contrary to our hypothesis, significant numbers of respondents in Ruaha (42%) and Maasailand (88%) expressed a desire to see population *maintained* or *increase.* Despite lion predation being prevalent across all three cases studies, it proved to be a good predictor of an individual's desired change in lion population in only one of the three case studies. This suggests that livestock loss to lions is not the principal factor influencing the desired change in lion population; decreasing the level of predation on livestock does not necessarily reverse the perceptions of lions.

Perceived benefits from conservation and conservation education played a role in fostering a desire to see populations maintained at current levels or higher, but their ability to do so was also highly site-specific. This suggests that these interventions may improve the tolerance of lion presence, but their effects may be confounded by a variety of factors, including national wildlife and conservation policies, pre-existing cultural beliefs, and economic factors.

Hwange and Zimbabwe

In Hwange, respondents wished to see lion populations decrease. Similar attitudes towards lions were also present among community members living around Zimbabwe's Gonarenzhou National Park (Gandiwa et al. 2013), suggesting that negative perceptions of lions may be widespread across the country. Applying Bruskotter and Wilson (2014) hazard acceptance model of tolerance to Hwange, we suggest that the failure of CAMPFIRE, and Zimbabwe's current political and economic state is likely to play a major part in shaping local perceptions of lions by 1) lowering social trust in wildlife management authorities, 2) reducing the perceived and actual benefits from lions, and 3) increasing the risk/costs associated with lions.

CAMPFIRE emerged in the 1980s to cultivate the sustainable use of wildlife as an economic incentive for conservation (Alexander and McGregor 2000; Taylor 2009). Though it had some initial success, CAMPFIRE has not achieved its intended aim of devolving wildlife management or generating substantial revenue from conservation (Sibanda 2014). Sanctions placed on Zimbabwe since 2000 further stifled CAMPFIRE, decreasing its donor support from USD 35 million between 1989 and 2003 to less than USD 600,000 between 2003 and 2009 (Taylor 2009). Following the 2000 sanctions, the revenue received by CAMPFIRE communities dropped significantly; Gandiwa et al. (2013) report that the revenue from CAMPFIRE received by Chibwedziva community (~11,000 people) adjacent to Gonarezhou National Park dropped from USD 109,000 in 2001 to almost zero in 2010. The failure of CAMPFIRE is likely to have played a major role in lowering the societal trust placed in rural district councils and wildlife management authorities to deliver benefits from conservation and mitigate lion predation.

World Bank statistics indicate that between 1997 and 2008, Zimbabwe's GDP dropped from USD 8.5 billion to USD 4.4 billion. Surveys in Hwange were conducted in 2010. Against this back drop of economic and political hardship, our results show that predation on livestock was considered a major risk to respondents around Hwange, with the majority citing predation as the principal reason for wanting lion numbers to decrease. Actual monetary losses to lion predation among these same communities totalled USD 49,843 per year, leading to an average household cost of lion predation of USD 79 per year (Loveridge et al. 2017). During this period of economic hardship, respondents' perceptions of costs associated with lion predation may have been heightened and contributed to the predominant desire to see lion populations decrease.

Ruaha and Tanzania

In Ruaha, our findings showed that just over half of the respondents 53% (n = 119) wanted to see lion populations decrease, indicating more tolerance of lion presence than in Hwange, but less than in Maasailand. Unlike in Hwange and Maasailand, in Ruaha, the desired change in lion populations was related to lion predation during the last month, suggesting that very recent exposure to predation on livestock influences a respondent's stated tolerance in the short term but may not have a lasting effect. As the cumulative link model for Ruaha demonstrates, perceived personal benefits from conservation was the most important factor influencing the desired change in lion populations stated by respondents. Interpreting these results through the lens of the hazard acceptance model once again provides useful insights (Bruskotter and Wilson 2014).

Tanzania's political and environmental policies appear to have created a situation where respondents in Ruaha perceived very little benefit from conservation and have been disenfranchised by state-centric wildlife management policies.

Tanzania's communities like those surrounding Ruaha have been alienated from their land and their resources by colonial and post-colonial government policies (Nelson et al. 2007). Starting with the creation of National Parks in the 1940s, local communities across Tanzania were repeatedly evicted to make space for protected areas (Igoe and Brockington 1999). During the 1970s, under President Nyere's socialist policy known as "Ujamaa", nearly five million Tanzanians were resettled into consolidated villages, leaving a lasting legacy of failed land-reform, resettlement, and increased conflicts over resources such as grazing (Homewood and Rodgers 2004). The Wildlife Conservation Act of 1974 further vested rights over wildlife utilisation to the central government, and village land continued to be annexed for the expansion of national parks (Nelson 2010). Despite the formation of wildlife management areas (WMAs) under the Wildlife Policy of 1998, ownership and management of wildlife in Tanzania remains focused on the State (new Wildlife Policy of 2008 and Wildlife Conservation Act of 2008). As recently as 2008, local communities were evicted from the nearby Usangu Game Reserve to allow for its inclusion in the newly expanded Ruaha National Park, continuing the legacy of community evictions to create space for conservation (Benjaminsen et al. 2013; Kiwango et al. 2017).

WMAs have been beset by issues such as poor governance and perceived inequalities. Communities like those around Ruaha were not actively engaged in the creation or management of WMAs, and these have not delivered significant economic benefits to the communities, thereby devaluing the importance of conservation as a livelihood and land-use option (Kiwango et al. 2017). Given this long history of elite capture and state-centric management, there is a strong need to increase the perceived benefits from conservation and societal trust placed in government and conservation institutions. The evidence from this study suggests that even communities like those in Ruaha having relatively little ownership of their wildlife or natural resources can still be positive about wildlife presence if benefits are directly linked to wildlife presence. This requires benefits to reach communities directly and equitably allowing for societal trust to be generated.

Maasailand and Kenya

Viewing the Maasailand context through the hazard acceptance model reveals a possible explanation for why Maasailand was the only site where the desire to see lion populations increase was the norm rather than the exception. High-level perceived benefits documented in Maasailand are also complemented by a degree of social trust, affect for lions, formal compensation programs, and informal societal safety nets.

In Maasailand, an individual's desire for lion populations to increase was predominantly attributed to increasing tourism revenue. This strong link between benefits from tourism and lion conservation although not statistically significant is exemplified by an interviewee who stated, *"It was the community that made the decision to stop killing lions, so they could reap the benefits of tourism"*. In other parts of the lion range, the relationship between conservation, tourism benefit, and personal benefit is not as tangible. For example, Hemson et al. (2009) showed that in Botswana, tourism revenue did not accrue at the community level and very few respondents valued tourism.

In Kenya, conservancies and CBC initiatives have grown organically since the creation of the Kimana Conservancy in 1997, which set a precedent for CBC in Kenya and paved the way for over 150 community conservancies that exist in Kenya today (Bedelian and Ogutu 2017). Western (2012) demonstrated that in Maasailand communities perceived ownership of lions with whom they choose to coexist. In combination with our findings, these results suggest that CBC and conservancies in Maasailand have effectively succeeded in building societal trust in conservation by allowing communities to both benefit from, and perceive ownership of, wildlife. In Hwange and Ruaha, respectively, the ability of CAMPFIRE and WMA initiatives to create similar results to those seen in Maasailand may have been constrained by state-centric wildlife management and government policies which undermined societal trust. We propose that more research is needed to investigate whether this interplay between perceived ownership, individual benefit, and societal trust does in fact promote a desire to see lion populations increase.

Affect has been shown to play a large part in determining tolerance for wildlife and is defined by Bruskotter and Wilson (2014) as "one's instinctual and emotive response to a species". In the case of Maasailand, a pre-existing affect for lions may have been shaped by cultural practices and values. Among the Maasai, lions are both both feared and respected, often being referred to as the 'great predator' "*olowaru kitok*" (Spencer 1988). Across Maasailand, lions are an important part of cultural ceremonies, and male lions are actively killed during *Olamayio* hunts to demonstrate the bravery of young warriors (*illmurran)* (Goldman et al. 2013). Positive portrayals of lions are also present in Maasai folk stories in which lions protect and escort women back to their homesteads (Goldman et al. 2010). Maasai affect for lions is, however, difficult to categorise as demonstrated by previous ethnographic studies of Maasai, which offer both positive and negative portrayals of Maasai lion-relationships (Roque de Pinho 2009; Goldman et al. 2010). In contrast to our results from Kenya's Maasailand, in the adjacent Maasai Steppe region of Northern Tanzania, 76% of Maasai respondents wished to see lions decrease or disappear completely (Mkonyi et al. 2017), providing further evidence that Maasai affect for lions cannot be generalised and varies across political and economic landscapes.

The strong desire to see lion populations increase by respondents in Maasailand is surprising, given the prevalence of predation on livestock. However, previous studies have also shown that recent predation on livestock does not necessarily influence perceptions of carnivores. One case comes from the

Sundarbans region of Bangladesh, where tolerance of tigers was not linked to an individual's personal experience with tigers (Inskip et al. 2016).

Formal compensation schemes for loss of livestock operated on two (Mbirikani and Olgulului) of the five group ranches. Compensation schemes on Mbirikani and Olgulului have reduced retaliatory lion killing, but further research is needed to determine whether they have also influenced individuals' desires to see lions increase (Hazzah et al. 2009; Maclennan et al. 2009; Okello et al. 2014). In Maasailand, the impact of livestock losses, including those from lion predation, is still commonly offset by informal and reciprocal insurance schemes known as '*stock associateship*'. Stock associates are members of an individuals family or friends within the broader community who can be called upon to donate livestock to replenish their herd after loss to drought, disease, or predation (Spencer 1988; Galvin 2008).

CONCLUSIONS

Although there is no single solution to resolving human-wildlife conflict, this study suggests that positive attitudes towards lions can be maintained and promoted even amongst those who suffer the direct costs of the presence of lions. Our results show that an individual's desire to see current lion populations maintained was highly site- and context-dependent. In the absence of context-specific constraints, we suggest that multi-pronged efforts that provide tangible personal benefits from conservation and incorporate conservation education are more likely to foster coexistence than targeted initiatives that only utilise a single conservation tool, particularly those initiatives focused merely on reducing predation by carnivores.

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