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# From avengers to hunters: Leveraging collective action for the conservation of endangered lions

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#### ABSTRACT

Fewer than 40,000 lions are left in Africa, perhaps 40% of which reside in Tanzania. Lions in East Africa are commonly killed in situations where they prey on livestock, either to retaliate for loss or avert future attacks. Among the Sukuma, Tanzania's largest cattle-raising ethnic group, tradition allows a lion killer to visit households, perform a special dance, and demand rewards for ridding the area of a potentially dangerous predator. Here we document how this tradition of gift-giving provides sufficient economic incentive that lion killers no longer act as avengers, retaliating for loss or averting future attacks, but as hunters, pursuing non-threatening lions far from residential and grazing areas and often inside protected areas. Our study reveals that Sukuma householders are less likely to reward a lion dancer if they have received frequent visits from dancers (indicative of donor fatigue) and if they perceive change in motivation from avenging to hunting. These findings suggest that it may be possible to reduce illegal killing of lions by working through Sukuma institutions responsible for collective action within the local community, and to remove the economic incentive for killing non-problem lions.

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#### 1. Introduction

African lions *Panthera leo* (Linnaeus) are estimated to number 30–40,000 individuals, a reduction of 60% from the mid-1900s (Chardonnet, 2002; Bauer and Van Der Merwe, 2004; Riggio et al., 2013). All but four of the West African populations are considered extinct (Henschel et al., 2014), leaving substantial lion populations only in Eastern and Southern Africa, the largest populations being in Tanzania (Riggio et al., 2013). Habitat loss due to changing land use (Riggio et al., 2013), disease (Munson et al., 2008), trophy hunting (Packer et al., 2011; Edwards et al., 2014), direct killing by local people for both defensive (Frank et al., 2006) and ceremonial reasons (Ikanda and Packer, 2008) have all contributed to the continent wide population decline.

Killing of lions and other predators that threaten, or are believed to threaten, livestock and humans is characteristic of many pastoral (and agropastoral) communities in East Africa including the Maasai (Spencer, 1988), Samburu (Spencer, 1965),

Barabaig/Datoga (Wilson 1953; Dickman, 2008) and Sukuma (Borgerhoff Mulder et al., 2009) and is usually associated with depredation events (but see Marchini and Macdonald, 2012). For example, Kenyan Maasai who have experienced livestock losses to lions show a higher propensity for killing lions than those who have suffered no loss (Hazzah et al., 2009). Indeed, working with Tanzanian Maasai, Kissui (2008) observed that every case of predation by lions is followed by a retaliatory killing, and there is a positive association at the village level between livestock depredation and retaliatory lion killing. Furthermore across ecological zones lion killing is most common where livestock losses to lions are highest (Ikanda and Packer, 2008). Here we focus on the defensive lion killing among Sukuma agropastoralists living to the south of the Katavi-Rukwa ecosystem in western Tanzania. Across many parts of Tanzania, Sukuma men who have killed lions adorn themselves in the spoils of their prey and become prestigious local figures, visiting households to perform a vigorous dance illustrating their physical prowess, and to demand gifts. Households welcome these men as local heroes, and reward them for the perceived service of ridding the area of dangerous predators. This killing of lions for defensive reasons, which might be in direct retaliation for the loss of life (domestic livestock or human) or merely aimed at







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averting the potential damage of lions in the neighbourhood, we term "avenging", with no implication that the killing is necessarily effective in reducing predation risk although this is the intended purpose.

Additionally, however, in our study area it is widely recognized (by locals and protected area authorities alike, and corroborated by health staff at local dispensaries) that men now venture far from the livestock herding areas (often into protected areas) to kill lions that pose no direct risk to their and their neighbours' stock. They do this despite a low lion population in adjacent protected areas, and a virtual absence of lion predation on livestock and people. We call this new behaviour "hunting", following local terminology. Hunting is incentivized by the common East African pastoralist tradition (outlined above) of rewarding lion killers who are believed to have successfully ridded the area of dangerous predators. We show an emerging trend among some households to deny rewards to suspected hunters which opens an opportunity for a novel conservation intervention scheme to protect the remaining lion population. Our case study is of general significance because it reveals how the study of collective action (Ostrom et al., 1992), specifically the questions of who bears the cost of paying for the services of avengers, and (more recently) who is refusing to reward hunters, is central to solving conservation dilemmas. By focusing on variability among households in the provision of collective action, we introduce new ideas into the discussion of how to design lion (and other) conservation interventions which, to date, are largely restricted to the technicalities of better protecting livestock (e.g., husbandry practices, (Ogada et al., 2003)) on compensation for economic losses (Dickman et al., 2011), or on establishing guardian programs (Hazzah et al., 2014), when clearly governance reforms are also required (Nelson et al. 2013).

Specifically, we conducted our research in the Katavi-Rukwa Ecosystem (KRE), comprising Katavi National Park (KNP) (4471 km<sup>2</sup>) gazetted in 1974 (Fig. 1), and the Rukwa Game Reserve (RGR) (4323 km<sup>2</sup>) to the east and south. Kiffner et al. (2009) estimated the adult lion population in KNP at between 166 and 205 individuals in 2005, 40% lower than expected from prey densities (see also Caro, 1999). Lion presence was far lower outside and within the periphery of the national park than in the park centre (Kiffner et al., 2009), despite no parallel edge effect in herbivore abundances (Kiffner et al., 2012). Yet even in the central part of KNP there has been a probable decline over the last 15 years (Caro, 2008, 2011), likely driven by overly high tourist hunting quotas, Sukuma lion killing, and perhaps a lowered prey base resulting from bushmeat exploitation and water diversion (Caro, 2008; Caro et al., 2013; Packer et al., 2011; Martin and Caro, 2013).

Our study was conducted in Mpimbwe (Borgerhoff Mulder et al., 2007), at the time an administrative division of Mpanda District, Rukwa Region, and area that runs along KNP and RGR's southern border (latitude 6°45′ to 7°05′, longitude 30°45′-31°25′). Along some of this border, the Kavuu river and extensive human land conversion form a "hard" protected area boundary. At the time of study, there were 14 villages in Mpimbwe, with a total population that in 2012 reached 53,298 (URT, 2012). Mpimbwe is the traditional homeland of the Pimbwe (Mgawe et al., 2012) but has since the mid-1970s seen a large influx of Sukuma agropastoralists from northern Tanzania (Madulu et al., 1991). Sukuma live in extended family units (mji [ki-Swahili] household) in close proximity to both their agricultural and common-pool grazing lands, outside the Pimbwe village centres. Households consist of related nuclear families (usually a man with his wives, his sons and their wives) and are headed by the eldest male, although in practice grown sons play an important role in household decisions, as do older wives, particularly as the titular head ages. Sukuma invest their wealth in livestock, principally cattle and goats. Traditionally as avengers (as defined above) young Sukuma men killed lions encountered near their corrals or pastures, either to retaliate or avert stock loss. More recently, however, hunting (as defined above) has emerged, a behaviour that appears incentivized by the traditional reward system. Both avengers and hunters dance for rewards so, following local usage, we refer to men claiming rewards for lion killing as *dancers*, irrespective of provocation or motivation (See inset in Fig. 1).

Specifically, we ask: (1) What is the statistical support for our ethnographic inference that dancing persists despite minimal levels of predation on livestock, and (2) What is the evidence of a change from avenging (defensive killing) to hunting (pursuit of non-problem lions)? We then turn to questions that allow us to identify dynamics that may contribute to the persistence of lion hunting in the absence of livestock depredation, namely (3) What are the characteristics of households whose members perceive this apparent change from avenging to hunting? (4) Which households do dancers target for the collection of rewards? (5) What characteristics of households determine whether or not a dancer is rewarded? The data we collected suggest that it may be possible to reduce the killing of lions by working through the institutions responsible for collective action within the local community, specifically by halting the rewarding of dancers who have hunted rather than avenged, thereby removing the economic incentive for hunting non-problem lions. While our results focus on the Sukuma people, they illustrate principles at the interface of anthropology and conservation that are of relevance across Africa and beyond (Hicks et al., 2012; Orlove and Brush, 1996).

#### 2. Methods

#### 2.1. Sample

Households (n = 214) were interviewed in 7 of the 14 villages in Mpimbwe (Fig. 1). Village Executive Officers provided estimates of the relative distribution of Sukuma across sub-villages enabling us to allocate effort in proportion to the number of Sukuma present. Within each sub-village households were randomly selected, avoiding nearest neighbours who tend to be related.

#### 2.2. Interview and survey

Together with a local Sukuma assistant EF conducted interviews between May 2009 and August 2010, composed in ki-Swahili, using ki-Sukuma translation of certain questions when requested by the interviewee. In each household the team explained the research objectives and obtained verbal consent. The strongly hierarchical structure of Sukuma society dictated that, should he be present and consent, the senior male household head or his eldest son would be interviewed. Since our interest lay with the attitudes and behaviour of the household, this was most appropriate for our purposes. If the senior male was unavailable we sought another senior member of the household (male or female), as is appropriate in the Sukuma cultural context. The survey was comprised of both qualitative and quantitative questions in a semi-structured format, focusing on four themes - evidence that the household had direct experience of human-wildlife conflict, perception of the motives for lion-killing, reported number of visits from and rewards given to dancers, and basic household socioeconomic characteristics. The survey took approximately 1 hour.

#### 2.3. Data analysis

#### 2.3.1. Variables

Basic descriptive statistics for all independent and dependent variables are presented in Table 1. *Dancer visits* were defined as the sum total of dancers reported to have visited the household

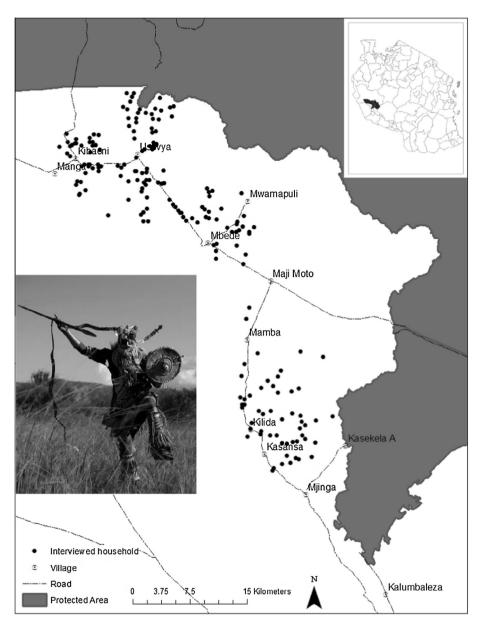


Fig. 1. The villages of Mpimbwe showing the location of sampled households (*n* = 214) across 7 villages. Inserts highlight (1) the location of Katavi-Rukwa Ecosystem in Tanzania, and (2) a contemporary dancer (photo credit: Aditya Swami).

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Descriptive statistics on predictor variables in sample households calculated from the complete data set (n = 198).

Variable	Data component	Mean (SD)	Number (% 'yes')
Distance protected area	Distance to KNP (km)	8.22 (3.7)	
Residency time	Years since arrival in Mpimbwe	17.11 (10.75)	
Wealth	Household size (people)	11.4 (6.27)	
	Area farmed (acres)	16.43 (13.39)	
	Cattle	25.84 (15.0)	
	Sheep/goats	18.17 (21.63)	
Livestock predation	Total livestock predated per household	0.7 (3.14)	
•	Livestock to lions	0.03 (0.29)	
	Livestock to leopards	0.16 (0.92)	
	Livestock to hyenas	0.55 (2.2)	
Dancer visits	Reported having been visited by a dancer between 2000 and 2010	0.65 (1.06)	74 (37%)
Change	Reports hunting as a modern motive for lion killing	. ,	121 (61%)
Family lion dancer	Someone in their family having killed a lion		81 (41%)

between 2000 and 2010 (inclusive) originating from Mpimbwe and reported (or at least suspected) to have killed their lion in the KRE (rather than elsewhere in Tanzania). *Livestock predation* was the sum of the reported number of all livestock owned by that household lost to lions, leopards (*Panthera pardalis*) and spotted hyenas (*Crocuta crocuta*) during the preceding 12 months. *Family lion dan*- *cer* indicated that someone among the household's family (*familia* [ki-Swahili]) had killed a lion and danced; no time restriction was placed on this response. By using the modern Swahili term '*familia*' we exclude members of a wider clan (*ukoo* [ki-Swahili]), restricting the response to relatively close blood relatives. With this question we capture whether a household believed a family member had participated in lion-killing. *Residency time* in Mpimbwe was calculated as the number of years since the respondent's family unit had arrived in Mpimbwe. Finally, the GPS co-ordinates for each interviewed household was used to calculate the shortest straight line distance to the border of a protected area (KNP or RGR) (ArcGIS v.10) which generated the variable *distance protected area* (*distance PA*).

The independent variable *wealth* was a composite of four indicators reported in the survey. The first was an asset score for material goods. Counts of key household possessions were weighted following procedures of Morris et al. (2000) and summed. This method has been shown to provide a fair approximation of household wealth in rural African settings. The second indicator was the sum of the number of cattle, sheep and goats, converted into total livestock units (TLU) following FAO (1999). The third indicator, area farmed, consisted of the total number of hectares farmed across all crops in the previous harvest. The fourth indicator, household size, was the sum of all current household residents, adults and children, predicated on the common perception that in rural Africa, where production is often highly labour-intensive, people (including children) are both a source and an indicator of wealth (Guyer, 1993). These four indicators, asset score, total livestock units, total area farmed and household size, were all strongly positively correlated. To overcome the problem of collinearity this would have caused in subsequent models we reduced these for wealth indicators to a single variable using Principal Components Analysis. Variables where transformed using a natural log and PCA generated only one factor with an Eigenvalue over 1 (Eigenvalue = 2.62) explaining 65.5% of the variation. This factor became our wealth variable.

We considered three response measures – *change*, *targeted* and reward: To determine whether the motivation for lion-killing has changed over time we compared responses across two questions 'what was the traditional motive for lion-killing?' and 'what is the modern motive for killing lions in Mpimbwe?' Responses were classified into 'livestock protection', 'hunting', 'ceremonial purposes', 'opportunistic' and 'don't know'. Households were identified as having perceived a change in the drivers of lion-killing if they included "hunting" in the current but not traditional time period. This generated the categorical variable *change*: '0' = no change, '1' = change, '2' = don't know. To determine whether or not a household was targeted by dancers, we derived a binomial variable (targeted) from the variable dancer visits. The code '1' indicated a household had been visited by a dancer between 2000 and 2010. Finally, using only those households that had been visited by a dancer (targeted = 1), and treating each dancer visit as an independent instance, we used responses to questions on gifts given to each dancer to generate the variable reward, indicating whether the dancer's visit was rewarded ('1') or not ('0').

Of the 214 household interviews conducted during the main study, 16 contained missing data on independent variables. We confirmed these data were missing at random (Field, 2009) and analyzed only households with complete independent variable measures (n = 198).

Several variables (*dancer visits, reward*, and *livestock predation*) rely on interviewee recall over 10, 10 and 2 years respectively. While this might lead to underestimates we strongly suspect this is not so, given the salience of lion dancers in Sukuma culture, and that livestock loss to predators is not easily forgotten. Furthermore no inherent biases with the independent variables seem obvious.

#### 2.3.2. Summary statistics

We derived basic descriptive statistics to summarize each variable (Table 1) and we examined our data on dancer visits over time and on livestock predation by different predators using Spearman's rank correlation coefficients and Kruskal–Wallis tests respectively (SPSS v.20).

#### 2.3.3. Non-metric multidimensional scaling

We used non-metric multi-dimensional scaling (NMDS) to explore clustering in reported traditional and modern motives for lion-killing. NMDS analysis was performed using a Bray-Curtis derived presence-absence similarity matrix (PRIMER v.5). Each NMDS score was classified based on cluster membership and linked back to the original household data. This enabled us to determine which responses were represented in each cluster (a traditional or current response and motive for lion-killing given). To confirm significant clustering in the data around traditional and current responses we performed an Analysis of Similarity (ANOSIM) on the Bray-Curtis similarity matrix (no transformation or standardization).

#### 2.3.4. Generalized linear modeling and Akaike model selection

To explore our three principal questions we fitted three sets of generalized logistic models with binomial error structures and logit link-functions. (1) First we evaluated determinants of household perception of a change in motive for lion-killing (binary response variable change/no change). We excluded households that answered 'don't know' from this analysis, giving n = 180. (2) The second set of models evaluated traits of households targeted by dancers using the binary response variable targeted/not targeted, with village as the random factor on all 198 complete household interviews. (3) Our final model set explored determinants of whether or not each recorded Dancer visit was rewarded by the household. Households could be visited multiple times by different dancers. Using the binary variable rewarded/not rewarded, this model explored the outcome of the 128 dancer visits reported across 71 households to identify factors predicting whether or not the visit was successfully rewarded. In this case household was included as a random factor.

For each model set we identified potential predictors based on information gathered during the preliminary study, ethnography and the literature (as recommended by Burnham and Anderson (2002)), and we present the logic for model selection in Table 2. We tested for multi-collinearity among using non-parametric, point-biserial and binary correlation as appropriate (Field, 2009). The final variable group was used to define the global model. To ensure that slight collinearity present in our independent variables did not inflate the standard errors we calculated Variance Inflation Factors for all variables in our global model; each was well below the worry point of '4' (Zuur et al., 2009). Given that collinearity was not a problem, we used the global model to generate a set of possible candidate models identified as those models within 6  $\Delta$ Akaike's Information Criterion adjusted for sample size (AIC<sub>c</sub>) of the model with the lowest AIC<sub>c</sub> (Burnham and Anderson, 2002; Richards, 2008). Following Richards (2008) we removed all models that were simply more complex versions of a model with a lowest AIC<sub>c</sub> value to reveal our final set. The Akaike model weight was calculated for each model in our final set to determine the relative probability of each model being the most parsimonious. We computed model-averaged parameter estimates (Grueber et al., 2011) and standard errors using the natural average method which calculates the parameter estimate from only those models in which the variable of interest appears. To evaluate the relative importance of each parameter across candidate models we summed model weight of all models containing the parameter of interest (Burnham and Anderson, 2002). All generalized logistic

Table	2
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Justification for variable inclusion in each generalized linear model.

Analysis	Predictor variable	Rationale for inclusion
Perceived change	Dancer visits Family lion dancer	Increased exposure to dancers is expected to raise the probability of a household perceiving change Households closely related to a dancer are expected to be more aware of the changing tradition
	Wealth Residency time Distance	Wealthy households, who are more socially connected, are expected to be more aware of change Households settled in the area for a long time are expected to be more aware of change Remoter households are expected to be less likely to acknowledge change
	Protected Area Livestock to predators	Households most exposed to livestock predation are expected to be less likely to perceive or acknowledge change
Household targeting	Wealth Residency time	Wealthy households are expected to be targeted by dancers looking for profits Longer established households are likely to be better known to a larger number of people in Mpimbwe, and therefore preferable targets for the purpose of signalling status
	Family lion dancer Distance PA	Ethnographic evidence states that a lion dancer (traditionally at least) only visited and received rewards from clan ( <i>ukoo</i> , [ki-Swahili]) members Households situated closer to a protected area are expected to feel more vulnerable to wildlife in general, and therefore more likely to reward
Rewarding behaviour	Wealth Family lion dancer	Wealthy households are expected to be more likely to offer rewards on account of the reduced relative cost Relatedness to a lion dancer might plausibly enhance sympathy for the custom
	Distance PA	Those living close to the park are expected to perceive more threat from wildlife, and are accordingly more likely to feel gratitude to those claiming to have killed a lion
	Livestock predation	Livestock predation is expected to sensitise household to the dangers of lions, and therefore dispose them favourably towards rewarding lion dancers
	Dancer visits Change	Households receiving frequent dancer visits are expected to make fewer rewards on account of donor fatigue Households sensing the demise of traditional defensive lion killing, and a switch from avenging to hunting, might be less keen to reward a dancer

mixed modeling was performed in R (2012). Model averaging and calculation of model weights were done using the MuMIn [R] library. We use Odds Ratios (ORs) to present effect sizes. These give the predicted ratio of the odds for a positive response comparing observations differing by an increment of 1.0 in a continuous or ordinal predictor, or between classes for a categoric predictor. For example if a predictor increases the probability of a response from 0.5 (odds = p/(1 - p) = 1) to 0.75 (odds = 3), the odds ratio = 3.0. We use an increment of 10 years for residency time to allow this effect to be visualized on the same scale as other predictors.

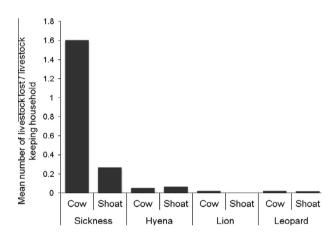
#### 3. Results

#### 3.1. Dancer visits and evidence of human-lion conflict

The proportion of households visited by a dancer has been rising steadily (Spearman's rho = 0.818, p = 0.002), although failing memory may in part account for this trend, insofar as more recent visits are more salient. Traditionally, Sukuma killed lions after cases of livestock depredation, but livestock depredation by lions in Mpimbwe is now negligible: of the 187 livestock-keeping households, only 2 reported having lost any livestock to lions (a total of 5 livestock) in the preceding 12 months (2009–2010). Indeed over the same period spotted hyenas reportedly took more livestock than did lions and leopards combined (Kruskal–Wallis  $X^2 = 35.2$ , p < 0.001) and losses to leopards alone were higher than losses to lions (Kruskal–Wallis  $X^2$  = 145.5, p < 0.001; Fig. 2 shows the mean number of livestock lost to different causes. While it is possible, but unlikely, that Sukuma retaliate against lions for losses to other predators, it would seem the traditional motive for lion-killing is largely absent.

#### 3.2. Perceived change in motivations for lion-killing

Ninety six percent of 129 households characterized lion killing as having undergone change. Group 1 in the MNDS analysis (Stress



**Fig. 2.** Mean number of cattle and shoats (sheep + goats) reported to have been lost to sickness, spotted hyenas, lions and leopards per livestock keeping household in preceding 12 month period.

0.01, 2D, Fig. 3) represents householders' perceptions of current motives for lion-killing and is dominated by the reported perception that today lions are hunted in the KRE. In contrast group 2 represents householders' perceptions of 'traditional' motives for lion-killing and is dominated by the response 'livestock protection'. ANOSIM analysis confirmed that the clustering in the data between traditional and current responses differed significantly (R = 0.38, p < 0.001). Furthermore 72% of households perceiving a shift from avenging to hunting, said that the opportunity to acquire wealth through dancing was motivating the change. Clearly there has been a widespread shift in the motivation for lion-killing in Mpimbwe, as perceived by our interviewees.

#### 3.3. What predicts perceived change?

To determine which households perceive a change in lion-killing motives we analyzed 6 potential predictors: *Dancer visits, family lion dancer, wealth, residency time, distance PA* and *livestock lost to* 

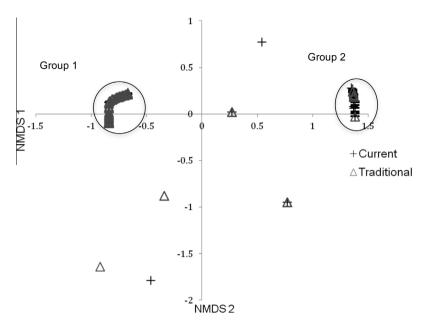


Fig. 3. Non-metric multi-dimensional scaling (NMDS) plot showing distinct clusters of traditional and current motives for lion killing (stress = 0.01).

predators. Our candidate model set was comprised of 42 models, which, after applying Richard's (2008) procedure of removing more complex models that were clearly not better, was reduced to two final models (Table 3). Model averaging applied to these two models (Table A.1) revealed that the variable *dancer visits* has the greatest influence (as based on summed AIC-weights) on whether households perceived a shift from avenging to hunting (summed model weight = 0.78, estimated regression odds ratio (OR) = 1.51). *Residency time* (summed model weight = 0.22, estimated OR for an increment of 10 years 1.22) also positively influenced the probability of *Change*. In short, households are more likely to perceive, recognize or admit to a change in lion-killing motivation if they are frequently visited by dancers, and if they have lived for a long time in Mpimbwe (Fig. 4a).

#### 3.4. What predicts which households are targeted?

We explored the potential effect of *wealth*, *residency time*, *family lion dancer* and *distance PA*. Eight candidate models were identified which were reduced to 3 (Table 3) following application of Richard's procedure. Three variables were retained in the final model

#### Table 3

Candidate models identified for each analysis within 6  ${\rm AIC}_{\rm c}$  units of the model with the lowest  ${\rm AIC}_{\rm c}.$ 

	-2Log link	AIC <sub>c</sub>	$\Delta AIC_{c}$	Weight		
Perceived shift fron	Perceived shift from avenging to hunting. Response = Change/no change					
DV <sup>a</sup>	-109.82	223.7	0	0.78		
RT <sup>b</sup>	-111.12	226.3	2.59	0.22		
Dancer targeting. R	esponse = visit/no v	visit				
W <sup>c</sup> +FLD <sup>d</sup> +RT	-104.17	216.6	0	0.71		
FLD + RT	-106.8	219.7	3.18	0.15		
FLD + W	-106.85	219.8	3.26	0.14		
Rewarding. Response = rewarded/not rewarded						
Ch <sup>e</sup> + FLD + DV	-77.56	165.61	0	0.34		
Ch + DV	-78.67	165.62	0.01	0.34		
DV	-79.8	165.77	0.16	0.32		

<sup>a</sup> Dancer visits.

<sup>b</sup> Residency time.

<sup>c</sup> Wealth.

<sup>d</sup> Family lion dancer.

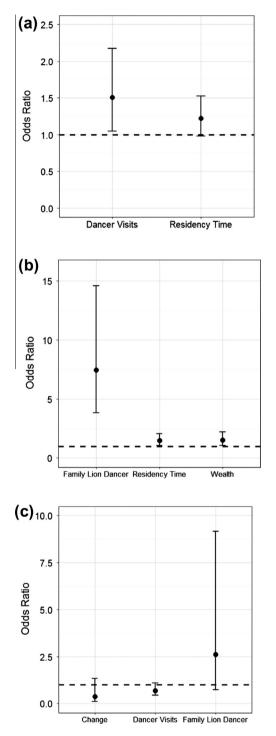
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set: *family lion dancer, wealth,* and *residency time.* All had positive regression coefficients indicating higher values were associated with a higher probability of being targeted (Fig. 4b, Table A.1). The odds ratios for these three predictors were 7.46, 1.54 and 1.49 respectively (where that for residency time refers to an increment of 10 years). In short, a dancer targets households that have more dancers amongst their extended kin, that are wealthy, and that have been settled in Mpimbwe for a long time. The summed model weights for these predictors were 1.0, 0.86 and 0.85 respectively.

#### 3.5. What predicts rewarding behaviour?

A total of 128 visits by dancers were reported by 71 households, of which 96 were rewarded and 33 were not. On the basis of cost/ benefit considerations (see Table 2) we included six variables in our global model. Of these six we expected three predictors to encourage reward giving (*wealth, family lion dancer, livestock predation*) and three to discourage it (*distance PA, dancer visits* and *change*). Rewarding is relatively cheaper for wealthy households, relatively more worthwhile for households that perceive their stock to be at risk (given previous losses and the belief that lionkilling is effective), and perhaps relatively more attractive to households who have dancers among their kin. Conversely households may be disinclined to reward a dancer if they are a frequent target of dancers, the further they live from a protected area boundary, or if they perceive a change from avenging to hunting.

Three candidate models incorporating only three of the 6 predictors were identified (Table 3). The model averaged parameter estimates for this set indicated that *dancer visits* (OR = 0.69, summed model weight = 1) and *change* (OR = 0.38, summed model weight = 0.68) reduced the probability of rewarding (Table A.1). Conversely having a lion dancer amongst one's kin (*family lion dancer*) increased the probability of rewarding the dancer (OR = 2.61, summed weight = 0.34). In short, dancers are less likely to be rewarded by households that perceive a change in contemporary dancers' motivation (avengers to hunters), and by those that are most frequently visited. Dancers are more likely to be rewarded by households that have dancers among their extended kin (Fig. 4c). The confidence intervals for these effects all include 1.0,



**Fig. 4.** Odds ratios (ORs) with 95% confidence intervals derived from modelaveraged coefficients for the predictors of (a) households reporting change in lion killing motives, (b) households targeted by lion dancers and (c) households rewarding a dancer. Dotted reference line at OR = 1.0 (no effect).

so the evidence for their influence is not as strong as for the other responses.

#### 4. Discussion

Where lions kill livestock or people there is an obvious motive for local communities to kill lions. Irrespective of the real or perceived damage caused by lions, such situations provide strong incentives for lion-killing that are often explained as acts of protection but are additionally motivated by recognition, status and material reward. Such reward systems can support lion-killing *even after the threat has diminished*, only exacerbating the pressure on an already locally rare population, as is the case of lions in KRE. In our study area we found that lion-killing was not directly linked to episodes of stock killing, a worrying observation and contrary to the pattern reported hitherto for East Africa; in fact there were almost no stock losses to lions, yet lion-killing persists. The conservation challenge now shifts to understanding the persistence of the cultural traits of rewarding of lion killers in Tanzania's largest livestock-keeping group, so as to leverage useful information with which to devise strategies targeted at stopping this practice.

#### 4.1. Motive change and household targeting in lion dancers

The shift from avenging to hunting is widely perceived and acknowledged in the majority of sampled Sukuma households. That households most frequently visited by dancers, or with a long history in Mpimbwe, are more aware of this shift most likely reflects their greater exposure.

Our finding that dancers target households that have a lion dancer among their kin, that are wealthy, and that have been long settled in Mpimbwe also has intuitive rationale. Contemporary dancers align traditional sensitivities (they visit households with a history of lion dancing that are perhaps more sympathetic towards dancers) with economically strategic behaviour (they target households that are rich and well established to maximize rewards), as is expected if lion-killing is primarily motivated by making money.

#### 4.2. Rewarding lion killing

Although these results are less well statistically supported, rewards are more forthcoming from households that have dancers among their extended kin, and less forthcoming in households that perceive a change in contemporary dancers' motivation from avenging to hunting, and by those that are most frequently visited. The first predictor suggests a persistence of mutual rewarding behaviour among cliques of families that engage in lion dancing; households within these cliques are perhaps the most traditional (although we have no measure of this) and least willing to jeopardize their social networks (crucial to food security in this population, Hadley et al., 2007) as a result of refusing a dancer. While such dynamics likely constitute an obstacle to behavioural change, the latter two predictors are more encouraging. There is evidence of donor fatigue, insofar as households visited by a greater number of dancers are less likely to provide gifts. Gifts (typically large, consisting of one or more cows, sometimes with a calf) cannot be offered on a regular basis, thereby limiting lion-killers' economic incentives to dance at much-visited households. Even more encouraging, we found clear reluctance to offer rewards in households acknowledging the shift from avenging to hunting. Indeed interviewees, both men and women, expressed disapproval of dancers who arrived, touting costumes adorned with claws and teeth taken from lions killed deep inside KNP, and called them "wafeki", a ki-swinglish neologism implying they are cheats meriting no reward.

#### 4.3. Cooperation and harnessing collective action for lion conservation

Cooperation and collective action lie at the heart of community security (Mathew and Boyd, 2011) as well as community management of natural resources (Ostrom, 2000; Borgerhoff Mulder and Coppolillo, 2005). Cooperation is dependent on most individuals upholding the rules of engagement (Jones et al., 2008) and the

Table A.1	
Estimated regression coefficients derived from model averaging final model set.	

	Number of qualifying models	Estimate b	SE	z value	Summed AIC-weight
Perceived cho	ange in drivers of lion killing. Response = Change/n	o change			
DV <sup>a</sup>	1	0.41	0.19	2.19	0.78
RT <sup>b</sup>	1	0.02	0.02	1.76	0.22
Lion dancer t	argeting. Response = visit/no visit				
FLD <sup>c</sup>	3	2.01	0.34	5.88	1
W <sup>d</sup>	3	0.43	0.19	2.29	0.86
RT	1	0.04	0.02	2.35	0.85
Rewarding. R	esponse = rewarded/not rewarded				
DV	3	-0.37	0.23	1.6	1
Ch <sup>e</sup>	2	-0.96	0.64	1.5	0.68
FLD	1	0.96	0.64	1.5	0.34

<sup>a</sup> Dancer visits.

<sup>b</sup> Residency time.

<sup>c</sup> Family lion dancer.

<sup>d</sup> Wealth.

e Change.

punishment of defectors (Boyd and Richerson, 1992; Boyd et al., 2010). As dancers hunt rather than avenge, households are starting to refuse to offer rewards. This provides an intriguing leverage point for conservation interventions, to which we now turn.

Sukuma, like other pastoralist populations, have strong cultural institutions to ensure community security and the provision of public goods (Paciotti and Hadley, 2004; Paciotti et al., 2005). Cooperating over the rewards given to avengers should be seen in this light. As households withdraw from rewarding dancers, whether this is because they view dancers as hunters rather than avengers, because lions are no longer viewed as a threat to livestock, or for entirely independent reasons (such as the payments being too onerous), this cooperation is starting to erode. Indeed, in the disgust and annoyance some interviewees voice regarding "wafeki", we are seeing an emerging realignment of community collective action against those that break the rules and kill lions deep inside the national park, lions that cannot reasonably be viewed as constituting a threat. We call this a "realignment" because in the past community collective action supported the rewarding of avengers, whereas nowadays community collective action increasingly appears to punish (or at least negatively sanction the rewarding of) hunters.

This locally-emerging development, specifically the antipathy community members feel for "wafeki" and the resolution of households to deny them rewards, holds potential for a powerful grassroots conservation movement. Accordingly we have mounted a campaign (*Watu, Simba na Mazingira* – People, Lions and the Environment) to spread awareness that young men are hunting lions (and demanding payments) for personal gain rather than avenging for perceived common good. This campaign capitalizes on the frustration of households that have spotted this trend and refuse to offer rewards. The program is successfully campaigning to have sanctions on non-retaliatory lion-killing, and the reward of hunters, formalized within village bylaws, and is working on scaling up to all of Mpimbwe (Genda et al., 2012). This is good news for lion conservation in one of the species' most important national strongholds on the continent.

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#### Appendix A

See Table A.1.

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