

Human–wildlife conflict, benefit sharing and the survival of lions in pastoralist community-based conservancies

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Summary

1. Like many wildlife populations across Africa, recent analyses indicate that African lions are declining rapidly outside of small fenced areas. Community conservancies – privately protected areas that engage community members in conservation – may potentially maintain wildlife populations in unfenced pastoralist regions, but their effectiveness in conserving large carnivores has been largely unknown until now.

2. We identify drivers of lion survival in community conservancies within the Masai Mara ecosystem, Kenya, applying mark–recapture analyses to continuous sight–resight surveys. We use the number of livestock and human settlements as proxies for potential human–lion conflict whilst controlling for environmental variables and lion socioecology.

3. Average lion densities within the Mara conservancies between 2008 and 2013 (11–87 lions 100 km⁻²) were 2.6 times higher than those previously reported in 2003. Survival rates varied amongst prides and were highest for lions utilizing central regions of conservancies.

4. The number of livestock settlements (bomas [corrals] and manyattas) that were not members of a conservancy, and that fell within a pride home-range, had a large negative effect on female survival and was the most influential external predictor in models. These non-conservancy settlements accounted for 37.2% of total observed variation in survival, whereas conservancy settlements, which benefit financially from wildlife through their membership, had no effect on lion survival.

5. Internal drivers of survival agreed with known ecology and social behaviour including age plus a negative effect of male takeovers on cub survival < 6 months. Vegetation cover, prey availability and the density of grazing livestock within a pride's range did not explain patterns in lion survival.

6. *Synthesis and applications.* We show that lion densities have increased substantially within the Mara conservancies over the last decade and suggest that the creation of community conservancies has benefitted their survival. This suggests that lions can survive outside of fenced areas within pastoral regions if communities gain benefits from wildlife. We highlight the importance of expanding existing conservancies beyond their current geographical and political scope and forming buffer zones if wildlife ranges outside them. We suggest that changing attitudes to predators should be a key goal of community-based conservancies. Further work is recommended to identify what specific aspects of conservancy membership promote lion survival.

Key-words: Community conservation, conservation benefits, livestock, Maasai Mara, mark–recapture, pastoralism, pastoral settlements, protected areas, retaliation, sight–resight

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Introduction

Large predators in Africa have declined in recent decades, largely due to human impacts (Woodroffe 2000). African lion *Panthera leo* populations have declined by 70% from an estimated 100 000 in the 1960s and suffered an 83% reduction in range (Nowell & Jackson 1996; Bauer & Van Der Merwe 2004; Riggio *et al.* 2012). Outside national parks and managed hunting concessions, most free-ranging lions exist within private conservation regions and pastoralist rangelands (Nowell & Jackson 1996; Riggio *et al.* 2012). The most rapid declines have occurred where there is both a predominance of pastoralism or agriculture and little financial value to be gained from wildlife (Frank *et al.* 2006; Kissui 2008). Sustaining lion populations in pastoralist regions is complex because lions cause significant economic damage through livestock depredation, injure or kill people and are often killed in retaliation, usually through spearing or poison (Ogada *et al.* 2003; Woodroffe & Frank 2005; Frank *et al.* 2011). Effective lion conservation outside of protected areas centres around mitigating or managing this conflict (Ogada *et al.* 2003; Hazzah, Borgerhoff & Frank 2009; Hemson *et al.* 2009).

Key to protecting lions is the establishment and effective management of protected areas (Nowell & Jackson 1996; IUCN 2006; Riggio *et al.* 2012). However, rapid human population growth has led to an increase in human activities in rangelands bordering many reserves, leading to encroachment and habitat loss and increasing the risk of retaliatory killings of lions from livestock depredation, thereby reducing their efficacy for conservation (Woodroffe & Ginsberg 1998; Parks & Harcourt 2002; Balme, Slotow & Hunter 2010). Providing cultural and economic incentives for coexisting with lions is critical to their conservation in human-dominated landscapes (Brockington 2004; IUCN 2006; Dickman 2010). Such incentives may be best achieved through community-based conservancies which involve local people in tourism and wildlife management (Groom & Harris 2008; Hemson *et al.* 2009; Lindsey, Románach & Davies-Mostert 2009). However, these regions inherently support pastoralism, and thus offer potential for conflict between wildlife and people, and may not exclude all human activities that negatively impact large carnivores (Parks & Harcourt 2002; Bamford, Ferrol-Schulte & Wathan 2014). Conflict mitigation strategies such as compensation schemes may not be effective if they do not also promote livestock husbandry practices which reduce depredation and thus retaliatory killings (Bulte & Rondeau 2003; Woodroffe *et al.* 2006; Maclellan *et al.* 2009). Furthermore, wildlife and land management policies may not be uniform across connected conservancies, effectively fragmenting landscapes further (Lamprey & Reid 2004; Dolrenry *et al.* 2014).

In order to understand if, and how, community conservancies contribute to lion conservation, it is important to understand which aspects of conservancy management, for example control of livestock and human

densities, may affect lion survival whilst controlling for environmental variables (Harvey & Gittleman 1982; Whitman *et al.* 2007; Gastone *et al.* 2010). Here, we use continuous sight-resight data to estimate numbers and assess the survival of lions within community conservancies north of the Masai Mara National Reserve. We test the impact of aspects of pastoralism – specifically the presence of pastoralist settlements and their livestock – and determine whether conservancy membership increases lion survival whilst controlling for potentially influential environmental and human influences. We also identify conservancy management practices which may minimize human–lion conflict and help sustain viable lion populations.

Materials and methods

STUDY AREA

Kenya's Masai Mara National Reserve (MMNR, 1530 km²) lies between latitudes 1°00' and 2°00' S and longitudes 34°45' and 36°00' E and adjoins Tanzania's Serengeti National Park to the south. The north-western border connects with the community-based wildlife conservancies of the former Koiyaki-Lemek Group Ranch (Mara North, Lemek, Olare Orok and Mara Naboisho Conservancies) totalling ca. 1000 km² (Fig. 1). The region is predominantly savanna grassland, scattered *Croton* scrub and *Acacia sp.* woodland. Rainfall is bimodal, featuring short (November–December) and long (March–June) rains. Diverse assemblages of resident and migratory wildlife occupy the conservancies and surrounding pastoral lands during the dry season spanning July–October (Brotten & Said 1995; Bhola *et al.* 2012). The Mara conservancies are managed for wildlife, with 64% of households gaining an income from wildlife tourism, but cattle, sheep and goat pastoralism is the economic base for 94% of households (Nyariki, Mwang'ombe & Thompson 2009). Between 1977–2009, both resident and migratory wildlife utilizing the conservancies declined by 60–70% as a result of increased human activities, progressive displacement by livestock and intensive agricultural development north of the conservancies (Sinclair *et al.* 2007; Ogutu *et al.* 2009, 2011; Bhola *et al.* 2012).

LION MONITORING

Lions ($n = 382$) belonging to 13 prides were catalogued and monitored continuously between July 2008 and July 2013 within the Musiara region of the MMNR and six adjoining Mara conservancies within the former Koiyaki-Lemek Group Ranch (Fig. 1). Lions were identified using whisker spot patterns (Pennycuik & Rudnai 1970) and resighted ($n = 6360$) during daytime tourist game drives led by safari guides. Guides were trained in lion identification and lion identities were verified from photographs. Sightings at bomas and manyattas (defined below) were also used if the pride could be verified. At all sightings, the location, number and identity of all animals and the sex of animals >1 year of age were recorded. Approximate date of birth was determined by size, maternal dependency and mane development. Pride membership was determined by associated females and their dependent offspring (Schaller 1972). We used encounter rates to determine monitoring efficiency; if we encountered no new resident lions in

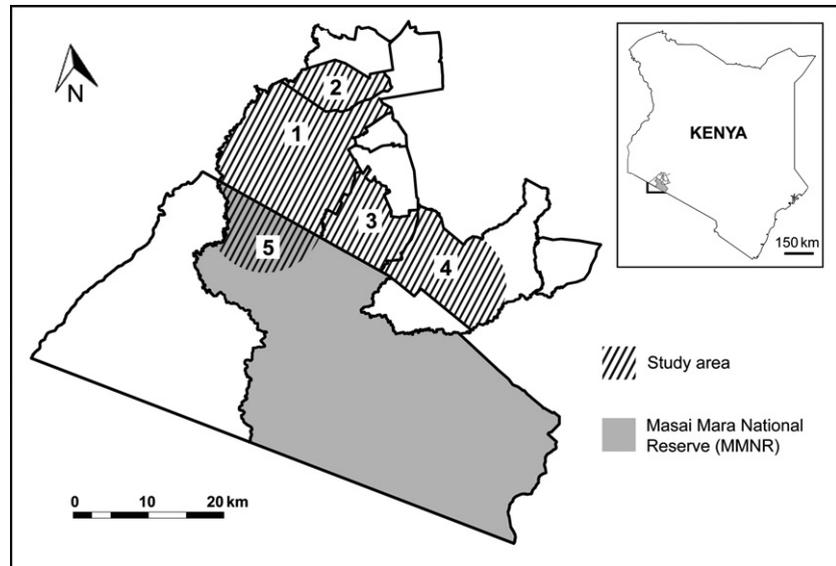


Fig. 1. Map of the study area lying between latitudes 1°00' and 2°00' S and longitudes 34°45' and 36°00' E: 1) Mara North Conservancy (MNC); 2) Lemek; 3) Olare Orok Conservancy (OOC); 4) Mara Naboisho Conservancy; and 5) Masai Mara National Reserve; Musiara (MMNR).

six months of monitoring, we deemed our survey to be exhaustive (Ogutu *et al.* 2006; see Fig. S1 in Supporting Information). We calculated lion density as the average number of resident adults and subadults per 100 km².

HOME-RANGE ANALYSIS

Lions are highly territorial and habitat features within their home-ranges are likely to affect their survival (Packer *et al.* 2005). Given that opinions differ on the most appropriate home-range determination methods, and considering that only daytime observations were available and nocturnal ranges of lions often exceed daytime ranges, we estimated the home-range of each pride in six different ways in order to calculate spatially dependent anthropogenic and environmental covariates (Appendix S1). For each home-range method, we did not exclude any apparent outliers in order for us to consider all settlements within the entire range that may suffer from lion attacks on livestock (Kissui 2008; Hazzah, Borgerhoff & Frank 2009). All geographical analyses were conducted using ArcMap version 10.1 (ESRI 2011).

SETTLEMENTS

We used the number and type of settlements within each pride's home-range as a measure of potential human–lion conflict. Settlements were classified into three types: houses (dwellings without livestock enclosures), bomas (livestock enclosures without dwellings) and manyattas (communal livestock enclosures including dwellings). Settlement locations were plotted using DigiGlobe satellite images from 2012 (Google Earth 2014; Bing Maps 2014). Additionally, houses and bomas were scored as small (1), medium (2) or large (3), and manyattas were scored by the number of dwellings that they contained. Bomas plus manyattas were collectively deemed 'livestock settlements'. In order to quantify the potential effects of settlements housing livestock, plus the potential effects of conservancy membership, as those without membership may receive less benefits from tolerating lions (Kissui 2008; Hazzah, Borgerhoff & Frank 2009), we quantified settlements using four different metrics. We calculated (i) the total number of

houses within the home-range that had conservancy membership, taking into account their size (S_{IN}); (ii) the total number of livestock settlements that had conservancy membership, taking into account their size and/or the number of dwellings (MB_{IN}); (iii) the total number of houses within the home-range that were not part of a conservancy, taking into account their size (S_{OUT}); and (iv) the total number of livestock settlements that were not part of a conservancy, taking into account their size and/or the number of dwellings (MB_{OUT}). A settlement was deemed to have conservancy membership if it was located within a conservancy boundary unless we were informed otherwise. This division of settlements allowed us to differentiate between the different modes of human–lion interaction such as the extent of range overlap and tolerance versus intolerance as a function of benefit sharing.

PREY AND LIVESTOCK DENSITY

Livestock and prey species population estimates were acquired from aerial surveys conducted by the Directorate of Resource Surveys and Remote Sensing of Kenya (DRSRS) from 2008–013. Transect, counting and population estimation methods used are detailed in Norton-Griffiths (1978). To account for seasonal shifts in population estimates due to variances in the time of sampling between years, and also because data resolution was not consistent across all regions, all counts were averaged over the entire study period to provide a relative measure of prey availability between pride home-ranges. For each home-range, we estimated (i) migratory prey density (number km⁻²) and (ii) resident prey density. Livestock abundance was estimated separately from prey availability as (iii) livestock density. This range of different measures allowed us to accurately quantify the potential effect of different prey species on lion survival, plus the potential positive or negative effects of grazing livestock present within the home-range.

ENVIRONMENTAL VARIABLES

Daily precipitation at -1.464477 S, 35.26336 E was recorded using a standard metric rain gauge to measure seasonal rainfall.

The percentage of woody cover within each home-range that exceeded 0.4 m in height was calculated as a minimum cover requirement for lions as an ambush predator (Elliott *et al.* 1977; Hopcraft, Sinclair & Packer 2005). The percentage of woody cover was calculated by ground-truthing a structural vegetation map developed by Reed *et al.* (2009). The horizontal cover available to ambush predators was measured at 1840 points that included all of the vegetation types outlined by Reed *et al.* (2009) and is described in greater detail in Hopcraft, Sinclair & Packer (2005) and Hopcraft *et al.* (2012). The number of river confluences was also calculated as a metric for prey catchability (Hopcraft, Sinclair & Packer 2005). These variables were averaged over the study period in cases where multiyear data were available.

ANALYSIS 1: SURVIVAL ANALYSIS

Adult females and their dependent offspring of eight prides, for which monitoring continued for at least 24 months (340 individuals), were included in the survival analysis. Adult males (>3.5 years) were not included in the survival analysis because they could not always be assigned to individual prides and often moved separately from pride females; this prevented spatial covariates from being applied. Births and deaths were included, but immigrations were not as these mostly comprised transitory animals. Microsoft Excel (2007) and R (R Development Core Team 2008) were used to create binary capture histories. A survival interval of 6 months (January–June; July–December) was chosen for accuracy of ageing and homogenization of sampling effort. Program MARK (Burnham & Anderson 2002) and package RMark (Collier & Laake 2013; Laake *et al.* 2013) were used to estimate the survival (ϕ) and capture probability (p) for individual lions using a live-encounter Cormack–Jolly–Seber (CJS) model for open populations (Cormack 1964; Jolly 1965; Seber 1965). We determined resight probability in order to accurately inform survival models.

We fixed p to 0 and ϕ at 1 when individual prides were not monitored. Likewise, p and ϕ were fixed for prides not initially

monitored to allow survival to vary over time when monitoring began. To account for known social and behavioural drivers of survival (Schaller 1972; Packer & Mosser 2009), a base model was constructed first using social and individual covariates (pride and age class – sex was not included for dependents due to small sample sizes; Table 1). We considered four different age-class structures to account for age-related behavioural and maturation variances (Vanderwaal, Mosser & Packer 2009). Pride male takeover (MT) events were allowed to affect small cub (<6 months) and large cub (6–12 months) survival due to probable infanticide (Pusey & Packer 1994). All covariates within the base model were allowed to vary over time. We used the corrected Akaike Information Criterion (AIC_c) for model selection to account for small sample sizes (White & Burnham 1999). The biologically plausible models within 4 AIC_c of the top model were then run with external covariates (Table 1) to test the role of anthropogenic and environmental variables on lion survival. Within RMark, we used program RELEASE (Burnham *et al.* 1988) to test for overdispersion of the global model (Table S3). As the results indicated a reasonable fit (Table S3), we proceeded with a value of 1 for the variance inflation factor c . We first ran 453 competing models – six home-range measures in combination with all non-correlated variables and biologically plausible interactions – to determine if and how the effect of spatial covariates differed between the methods of home-range calculation. We then proceeded with models using only the selected home-range measure ($n = 78$; see Results: home-range selection). In order to identify the strongest predictor variables, we used the relative importance weights (w_i) which are the Akaike weights summed across all models in which each predictor i occurred, with each covariate represented equally across all models to ensure that summed weights were reflective of covariate strengths and not the number of models they appeared in (Burnham & Anderson 2002). We used model averaging to guard against overfitting, deemed necessary due to the exploratory nature of our study and the number of models run (Burnham & Anderson 2002).

Table 1. Covariates used in modelling apparent survival and sight–resight probability of lions, classified as internal (relating to lion social ecology) and external (environmental and anthropogenic covariates)

Classification	Description	Covariate	
Internal	Pride grouping	G	
	Cubs vulnerable to infanticide (≤ 6 months)	C	
	Individuals > 6 months	NC	
	Age category in years: cubs <1, subadults 1 < 3.5, adults ≥ 3.5 yrs	A3 _A	
	Age category in years: cubs <1, subadults 1 < 4, adults ≥ 4 yrs	A3 _B	
	Age category in years: cubs <1, dependent subadults 1 < 2.5, independent subadults 2.5 < 3.5, adults ≥ 3.5 yrs	A4 _A	
	Age category in years: cubs <1, dependent subadults 1 < 2, independent subadults 2 < 3, adults ≥ 3 yrs	A4 _B	
	Occurrence of a male takeover	MT	
	External: anthropogenic	Number of conservancy member settlements, not housing livestock	S _{IN}
		Number of non-conservancy member settlements, not housing livestock	S _{OUT}
Number of conservancy member settlements housing livestock		MB _{IN}	
Number of non-conservancy member settlements housing livestock		MB _{OUT}	
External: environmental	Livestock density (km ²)	LS	
	Prey density: migrants only (km ²)	P _M	
	Prey density: residents only (km ²)	P _R	
	Average percentage vegetation cover	H	
	Home-range size (km ²)	HR	
	Number of river confluences	C	
Average rainfall per 6-month period (mm)	R		

ANALYSIS 2: MALE TENURE

Exploring the effects of pastoralism and environmental covariates on male survival was not possible because male home-ranges vary extensively over time (Funston *et al.* 2003; Loveridge *et al.* 2009). However, male tenure is an important driver of female social dynamics and cub survival both directly and indirectly (Packer & Pusey 1983; Whitman *et al.* 2007). We therefore undertook a separate analysis, constructing generalized linear models with a gamma error distribution and a log-link function (Bates *et al.* 2014) to estimate the length of male tenure (days) as a function of the number of females in the pride, home-range size, environmental variables (vegetation cover, river confluences, prey density) and anthropogenic variables (livestock density and conservancy and non-conservancy settlements). The coalition group and pride association were set as random effects to allow us to quantify variation between groups. Both univariate linear and quadratic models were constructed using each covariate and the models ranked in terms of AIC_c. The AIC_c best-supported model was then expanded by adding the covariate in the second best model, plus its interaction with the covariate in the best model, and noting the change in AIC_c. If the AIC_c for the new model reduced relative to the best model, then the new covariate was kept in the model; otherwise, it was deleted and the covariate in the next best model similarly added. This procedure was repeated sequentially until all covariates had been considered. The denominator degrees of freedom for F-tests of the effects in the final AIC_c-selected best model were synthesized using the Kenward-Roger approximation due to the small sample size ($n = 16$).

Results

Survival rates (ϕ), densities and compositions of the eight study prides are shown in Table 2. Our estimates of lion densities (lions 100 km⁻²) in the conservancies were dramatically higher than the 4.60 100 km⁻² estimated by Ogotu, Bhola & Reid (2005) for 2003 and generally increased over time from 2008 to 2012: 10.39, 14.00, 12.21, 17.15, 17.84, respectively. Average density across all the conservancies from 2008–2012 was 11.87 lions 100 km⁻². Survival varied amongst prides within the same conservancies and was highest for lions in the MMNR and those utilizing central regions of conservancies (Table 2; Fig. 2: dashed lines).

Table 2. Density (100 km²), home-range size (km²), the number of conservancy member settlements and the number of non-member conservancy settlements (both scored for size and calculated for the home-range: see Materials and methods), survival (ϕ) and sex and age compositions of study prides within the Mara conservancies averaged for the whole study period (2008–2013)

Region	Density (/100 km ²)	Pride	Home-range (km ²)	Member settlements	Non-member settlements	Adults		Subadults		Cubs	Survival (ϕ)	SE
						Female	Male	Female	Male			
MNC	8.15	River	104.55	490	71	2	2	2	2	5	0.608	0.135
–	–	Cheli	81.57	1	0	4	3	3	1	5	0.969	0.024
Lemek	8.62	Kicheche	119.25	281	76	6	2	1	1	4	0.623	0.080
Musiara	8.61	Marsh	149.12	267	11	8	4	4	5	9	0.905	0.031
OOC	20.36	Moniko	59.56	0	0	7	2	2	3	5	0.745	0.072
–	–	Engoyonai	80.30	111	0	6	2	3	3	6	0.784	0.073
Naboisho	9.54	Enoolera	112.06	15	440	3	3	1	0	3	0.586	0.159
–	–	Enesikiria	147.43	0	0	4	5	2	3	6	0.909	0.040

HOME-RANGE SELECTION

The importance of spatial variables included via model selection, using AIC_c, did not differ when their coefficients were calculated using five out of six home-range measures (KDE₁₅₀₀, KDE_{ad hoc}, MCP, MCP₁₅₀₀ and k -LoCoH₁₅₀₀; see Supporting Information: Supplementary methods). Models deriving from these five measures identified the number of livestock settlements in a pride's home-range that did not have conservancy membership as the strongest external predictor of lion survival (MB_{OUT}). Variable weighting across all 453 models also produced similar results. Only the home-range estimated using k -LoCoH differed, identifying vegetation cover as the most influential external driver of survival ($w_H = 0.270$; 16% total observed variation) followed by non-conservancy livestock settlements. We thus present results from models using KDE₁₅₀₀ home-range calculations ($n = 78$), a current and widely recognized home-range calculation method for which model selection showed the most support.

RESIGHT PROBABILITY

The best age-class predictor for resight probability combined dependent and independent subadults together and defined adults as over 4 years old (A3_A; Table 1). Resight probability varied with pride membership (G) and differentially over time (T) for each pride, and thus, detectability of lions was not consistent across the population. All survival models therefore contained the same variables for resight probability, defined as $p A3_A + T * G$.

DRIVERS OF LION SURVIVAL

Table 3 details all models within 4 AIC_c of the top model plus the next best model for comparison ($n = 5$). The best model of lion survival accounted for 24.8% of total explained variation across 78 models (AIC_c = 1017.26, d.f. = 75). The parameter estimates, their standard errors and upper and lower confidence intervals of the coefficients of the top model are shown in Table S2. The

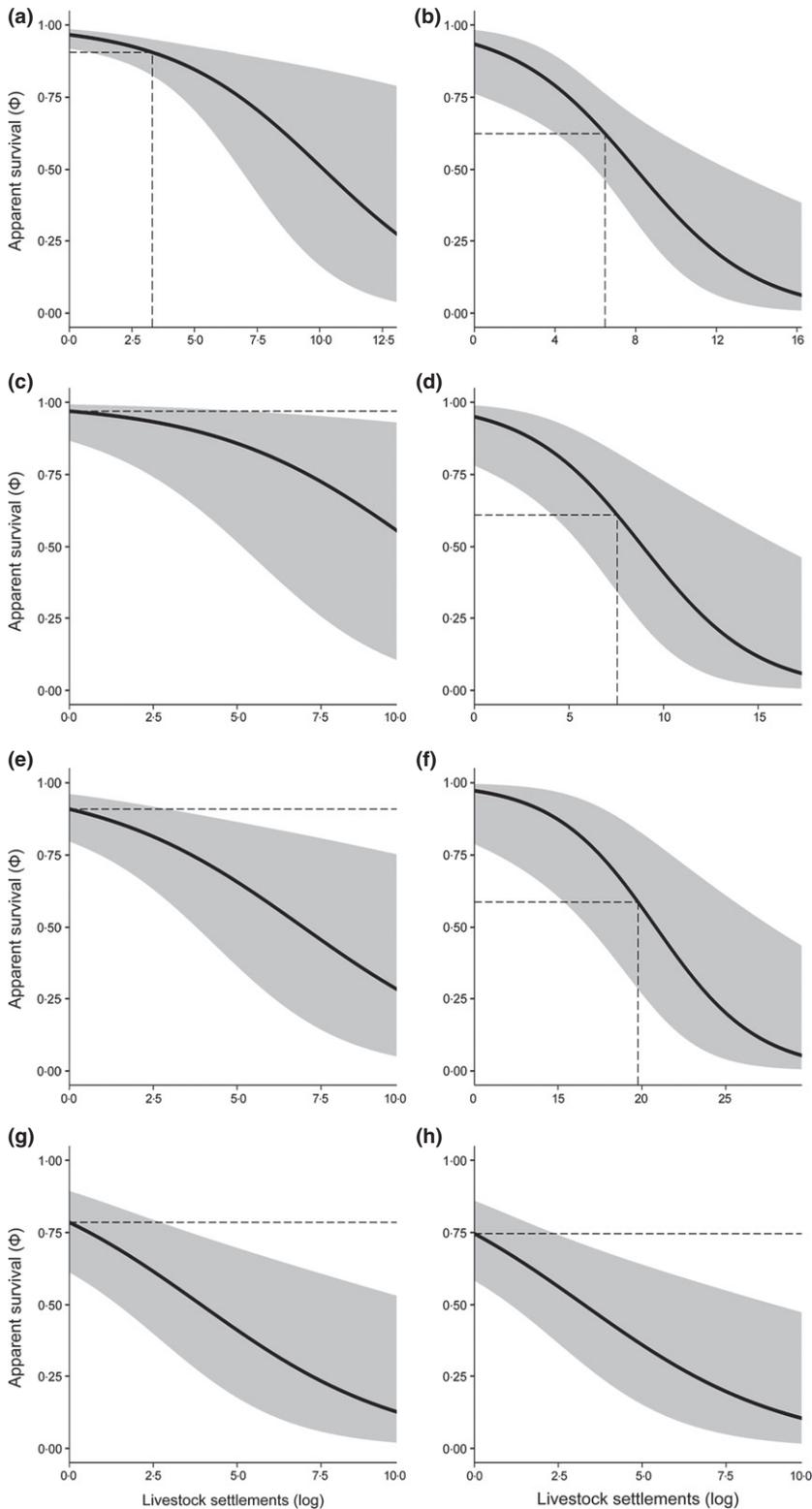


Fig. 2. Predicted survival of female lions in relation to the log number of livestock settlements within their home-range that do not belong to a conservancy (bomas scaled by their size plus manyattas scaled by houses they contain). SEs are shown in grey. Settlement densities ± 2 standard deviations of observed figures are predicted for eight prides within (a) the Masai Mara National Reserve and (b–h) the Mara conservancies. Dashed lines indicate apparent survival at current settlement numbers – no vertical line is presented where settlements are not present and survival is read at the interception of the survival curve at the y axis. See Table 2 for values.

occurrence of a male takeover affected the survival of young cubs <0.5 years ($\Delta AIC_c = 52.87$, d.f. = 1). The effect varied by pride, but was mostly negative; cub survival was lower on average when takeovers occurred (min = 0, mean = 0.47, SE = 0.11) than when resident males held a pride (min = 0.17, mean = 0.74, SE = 0.07).

Survival rates were not consistent across prides nor age classes ($\Delta AIC_c = 29.42$, d.f. = 12).

The effect of external covariates (included both additively and in biologically justifiable interactions) was quantified by Akaike weight (w_i) and is shown in Table 3. The number of livestock settlements within a pride home-

Table 3. Modelling lion survival; for covariate explanation, see Table 1. Models are based on KDE₁₅₀₀ (see Materials and methods; Mogensén, Ogutu & Dabelsteen 2011) and agreed with weighting of covariates across all models. Top models within 4 ΔAIC_c are shown ($n = 4$; Burnham & Anderson 2002) plus the next best-supporting model for comparison (italics)

Model	k	AIC_c	ΔAIC_c	w_i	Deviance
1 $\varphi C + C^*G^*MT + NC^*G + A3_A + MB_{OUT} + A3_A^*MB_{OUT}$	75	1017.26	0	0.25	636.58
2 $\varphi C + C^*G^*MT + NC^*G + A3_A + L + HR$	75	1019.23	1.97	0.09	638.55
3 $\varphi C + C^*G^*MT + NC^*G + A3_A + MB_{OUT}$	74	1021.07	3.81	0.04	642.79
4 $\varphi C + C^*G^*MT + NC^*G + A3_A$	73	1021.18	3.92	0.03	645.29
5 <i>$\varphi C + C^*G^*MT + NC^*G + A3_A + MB_{OUT} + H$</i>	75	<i>1021.97</i>	<i>4.71</i>	<i>0.02</i>	<i>641.29</i>

Table 4. Total Akaike weights (w_i) of external covariates, their categories (*) and the percentage weight for each category (in bold). For variation in survival explained by external covariates, the number of non-conservancy livestock settlements within the pride range had the highest Akaike weight (31.1% of total variation). All non-conservancy settlements accounted for 37.2% of total explained variation, whereas, in contrast, settlements that were members of a conservancy only accounted for 10.1% of total explained variation

Covariate	Total weight (w_i)	Non-conservancy settlements	Environmental	Prey	Livestock	Conservancy settlements
Non-conservancy livestock settlement count (MB_{OUT})	0.439	*				
Home-range size (HR)	0.196		*			
Livestock density km^{-2} (L)	0.160				*	
Non-conservancy settlement count (S_{OUT})	0.103	*				
Vegetation cover (H)	0.101		*			
River confluences (C)	0.086		*			
Resident prey density km^{-2} (P_R)	0.083			*		
Migratory prey density km^{-2} (P_M)	0.080			*		
Conservancy livestock settlement count (MB_{IN})	0.076					*
Conservancy settlement count (S_{IN})	0.072					*
Rainfall (R)	0.062		*			
		37.2%	30.5%	11.2%	11.0%	10.1%

range that did not have conservancy member status (MB_{OUT}) had a negative effect on survival and was the most influential external predictor when included with an interaction with age ($\Delta AIC_c = 3.92$, d.f. = 1; $w_{MB_{OUT}} = 0.439$), also featuring in the top model. Non-conservancy settlement measures together (MB_{OUT} , S_{OUT}) accounted for 37.2% of total observed variation across all models. The effect was more negative for adults ($\beta = -0.145$ compared to $\beta = -0.331$ for subadults and adults, respectively). Fig. 2 shows predicted survival for each pride in relation to varying numbers of non-conservancy livestock settlements. In contrast, no measures of settlements that had conservancy membership (MB_{IN} , S_{IN}) had an effect on survival (MB_{IN} : $\Delta AIC_c = -2.38$, d.f. = 1) and accounted for only 10.1% of explained variation across all models. Livestock density (LS) also had no effect on survival ($\Delta AIC_c = -2.11$, d.f. = 1), accounting for 11.0% of total explained variation.

Despite featuring in the second best-supported model (but note ΔAIC_c from the top model = -1.97), home-range size did not have an effect on survival (HR; $\Delta AIC_c = -1.50$, d.f. = 1). Prey density also did not have an effect on survival ($\Delta AIC_c = -2.11$, -2.16 , d.f. = 1 for P_M and P_R , respectively), nor did prey catchability estimated as the number of confluences within the home-range (C ; $\Delta AIC_c = -2.12$, d.f. = 1), the percentage of veg-

etation cover (H ; $\Delta AIC_c = -1.55$, d.f. = 1) or rainfall (R ; $\Delta AIC_c = -2.38$, d.f. = 1).

MALE TENURE

The number of females in a pride had the greatest strength of support for predicting male tenure length ($\Delta AIC_c = -4.74$ d.f. = 1). The AIC_c , ΔAIC_c , Akaike weights and likelihood values of models within 4 ΔAIC_c of the best-supported model are shown in Table S1. Adding additional terms to the top model did not increase model fit. Only home-range size and the number of conservancy settlements had reasonable quadratic relationships with tenure length.

Discussion

Lion populations are declining rapidly across Africa except in small fenced regions, with a 37% chance that lions in East Africa will decline by half in two decades (Bauer *et al.* 2015). Our analysis provides insights on factors affecting lion survival in human-dominated landscapes, and importantly, indicates that community-based conservancies may play a critical role in the conservation of lions outside of fenced and protected reserves, giving

potential hope for free-ranging lions despite the concerns and predictions of Packer *et al.* (2013) and Bauer *et al.* (2015). Exactly how community-based conservancies should be managed to promote the survival of threatened species has been hotly debated, yet discussions are supported by little empirical evidence. This analysis suggests that the proportion of human residents holding conservancy membership is a critical factor.

We found healthy lion populations within the conservancies north of the MMNR at densities of 8.20–20.36 lions 100 km⁻². Although different methodologies were used, these results suggest a significant population growth from 4.60 lions 100 km⁻² reported by Ogotu, Bhola & Reid (2005), for 2003, before the conservancies were established. The relative weights of environmental and human variables as identified by the best model indicate that, within our study region, human–wildlife conflict plays a more significant role in lion survival than does their environment. We attribute this to retaliatory killings due to livestock depredation as the negative effect was more pronounced when only bomas and manyattas were considered. Indeed, retaliatory lion killings have been identified as the most significant threat to lion populations (Frank *et al.* 2006). From 2008–2013, we were aware of 28 lion killings, three of which were poisonings; this is almost certainly an underestimate as lion killing is illegal and kept secret by perpetrators and authorities. Whilst we provide evidence that increasing pastoralist populations may negatively impact lion survival, more importantly we demonstrate that these effects may be lessened by promoting conservancy membership. This is a vital finding as human populations are predicted to increase across the Mara ecosystem (Lamprey & Reid 2004; Kolowski & Holekamp 2006; Ogotu *et al.* 2011; Bhola *et al.* 2012).

The influential internal drivers of survival including age and the detrimental effects of a male takeover agree with known lion ecology and social behaviour as described by Schaller (1972) and subsequent studies (Harvey & Gittleman 1982; Packer & Mosser 2009), indicating that our models are robust. The number of females in a pride as a major driver of male tenure length has obvious biological support in terms of an individual's reproductive success. Interestingly, we found little support for the effects of resource availability on lion survival or on male tenure length. Within savanna environments, prey availability may only impact survival when they are unusually scarce (Kissui & Packer 2004) possibly explaining why measured declines in local herbivores, driven by increasing pastoralism and agricultural development, may not yet be limiting regional lion populations (Ogotu *et al.* 2011; Bhola *et al.* 2012). The weak support for individual environmental variables also suggests that conflict mitigation should be the primary focus of lion conservation efforts and that this may be more critical in this region than controlling livestock grazing intensity or reducing habitat degradation

(Frank 1998; Ogotu, Bhola & Reid 2005; Frank *et al.* 2006).

Growth of human settlements is strongly correlated with species declines and has been linked to wildlife declines in the region (Nyariki, Mwang'ombe & Thompson 2009; Ogotu *et al.* 2011; Bhola *et al.* 2012). However, effective management of human–wildlife conflict may be more important than managing human density when conserving large carnivores (Linnell *et al.* 2001). The balance between valuing wildlife and the perceived and realized threat of predators is key in determining the outcomes of conflict (Dickman 2005; Hazzah, Borgerhoff & Frank 2009; MacLennan *et al.* 2009). Our results indicate that if the predicted rise in human populations occurs without expanding conservancy membership, and the associated financial benefits, regional lion populations will be significantly threatened. Crucially, as the negative effect of settlements on survival was mitigated by conservancy membership, we suggest that associated benefits such as the sharing of tourism revenues may significantly reduce the frequency and/or severity of reaction to livestock depredation by lions. From our analysis, it is not clear whether this is due to enhanced livestock protection and decreased depredation, or from a change in values and an increased tolerance for lions. Kolowski & Holekamp (2006) found no regional effect of enhanced livestock protection (improved fences, use of watchdogs, increased human activity) on livestock losses, which suggests that conservation benefits and the distribution of these benefits, enabled by conservancy membership, result in a change in attitudes towards predators. If lions benefit pastoralists financially, both the frequency and severity of retaliation for depredation may be reduced (Dickman 2005; Hemson *et al.* 2009; Bamford, Ferrol-Schulte & Wathan 2014). The Mara conservancies increase and stabilize the distribution of profits from wildlife, most likely promoting tolerance (Thompson *et al.* 2009). Some conservancies have also begun boma improvement and compensation programmes and are employing ranger teams; however, these strategies have not been evaluated in terms of their effect on mitigating retaliatory killings of lions (Hazzah *et al.* 2014). Although we have uncovered a strong effect, it is clear that further work is needed to identify the social, economic and political aspects encapsulated under 'conservancy membership' that are driving this effect. Additionally, our low sample size ($n = 8$ prides of 340 individuals), although typical of large carnivores, could be increased in order to explain more variation in models and strengthen these preliminary findings. We suggest future input from social scientists to measure the attitudes of member and non-member pastoralists towards wildlife and attempt to quantify the true cost of predators with reliable data on depredation events.

In this study, the number of livestock had no impact on lion survival even though this has correlated with large carnivore declines elsewhere (Hazzah, Borgerhoff & Frank 2009; MacLennan *et al.* 2009; Ogada 2014). In this region,

livestock grazing may benefit lion populations indirectly by maintaining sward palatability and attracting prey (Brotten & Said 1995; Toit 1999; Odadi *et al.* 2011). Ogotu, Bhola & Reid (2005) observed that wild prey biomass density was 2.6 times higher in the conservancies than in the Reserve and higher densities of small and medium herbivores utilize conservancy land (Bhola *et al.* 2012). It should also be noted that our measures of livestock density, derived from annual aerial counts, were both spatially and temporally coarse; further work addressing finer-scale movements is recommended in order to identify possible patterns of displacement.

Whilst our analysis shows support for the creation of community conservancies, it also indicates that individual conservancies in the region are not large enough to completely protect resident lion populations due to edge effects (Woodroffe & Ginsberg 1998) – lions whose territories contain non-conservancy settlements, often outside of conservancy boundaries, suffer a reduction in survival. Whilst male tenure length was not affected by the presence of settlements, males were observed to have different home-ranges to females, further suggesting that the inferred lethal impact of non-conservancy settlements operates on a spatial level. We recommend that survival analyses for male lions be conducted and that home-ranges be related temporally to the spatial distribution of settlements in order to empirically evaluate these preliminary findings. The tendency of the Mara conservancies to follow political boundaries rather than geographical constraints on animal movements may reduce their efficacy as a unified conservation area for lions. Buffer zones – and their effective management – are often critical for conserving large carnivores in small and unfenced protected areas (Balme, Slotow & Hunter 2010; Bamford, Ferrol-Schulte & Wathan 2014). The Mara conservancies are effectively a buffer zone between the MMNR and agricultural areas to the north, but have proven to be effective conservation areas in their own right and would benefit from extended buffer zones of their own.

CONSERVANCY MANAGEMENT RECOMMENDATIONS

We have documented far higher lion densities in the Mara conservancies than earlier reported (Ogotu, Bhola & Reid 2005), and our data on the positive impact of conservancy membership suggest that geographical expansion of the Mara conservancies would further protect this lion population. To minimize edge effects, conflict mitigation at conservancy boundaries should be a primary focus of conservation efforts. If settlements are relocated during conservancy formation, creation of settlement-free zones should cover full lion home-ranges when feasible. Unification of conservancies and harmonization of management practices across existing entities would provide more uniform protection for lions and regional consistency in standards of livestock management. Finally, we urge that consistent and reliable monitoring of large carnivores con-

tinues as these conservancies develop both geographically and politically.

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Data accessibility

Data available from Dryad Digital Repository doi:10.5061/dryad.35h47 (Blackburn *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary methods.

Fig. S1. Proportion of resident lions encountered over time within the study region.

Table S1. Male tenure length model results.

Table S2. Survival estimates for covariates from the top model.

Table S3. Results from RELEASE goodness-of-fit test.