Title: The relative effects of prey availability, anthropogenic pressure and environmental variables on lion (*Panthera leo*) site use in Tanzania's Ruaha landscape during the dry season

Authors: Leandro Abade[1,2], Jeremy Cusack[3], Remington J. Moll[2], Paolo Strampelli[1], Amy J. Dickman[1], David W. Macdonald[1], Robert A. Montgomery[1,2]

Institutional affiliations:

[1.] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Abingdon Road, Tubney, Abingdon, OX13 5QL, UK

[2.] Research on the Ecology of Carnivores and their Prey Laboratory, Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA

[3.] University of Stirling, 3A149, Stirling, FK9 4LA, UK

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Abstract

African lion (*Panthera leo*) populations have been reduced by almost half in the past two decades, with national parks and game reserves maintaining vital source populations, particularly in East Africa. However, much of the habitats necessary to support lion populations occur in unprotected lands surrounding protected areas. There is an ongoing need for understanding the ecological determinants of lion occurrence in these unprotected habitats, where lions are most vulnerable to extinction. This study evaluated variations in lion site use along a gradient of anthropogenic pressure encompassing the Ruaha National Park, Pawaga-Idodi Wildlife Management Area (WMA) and unprotected village lands via camera-trapping. We collected lion occurrence data in the dry seasons of 2014 and 2015, and modelled lion site use as a function of environmental and anthropogenic variables under a Bayesian framework. We recorded 143 lion detections within the national park, 14 in the WMA, and no detections in village lands. This result does not imply that lions never use the village lands, but rather that we did not detect them in our surveys during the dry season. Our findings suggest that lion site use was primarily associated with high seasonal wild prey biomass in protected areas. Thus, we infer that human-induced prey depletion and lion mortality are compromising lion site use of village lands. Seasonal prey movements, and a corresponding concentration inside the park during sampling, could also play an important role in lion site use. These findings reinforce the need to secure large-bodied prey base to conserve lions, and the importance of protected areas as key refugia for the species.

Keywords: Bayesian, conservation, occupancy modelling, human-carnivore conflict, Ruaha

Introduction

Protected areas, such as national parks, act as vital refugia for wildlife, serving as protection for large-scale ecological processes and ecosystem functions (Woodroffe & Ginsberg 1998; Le Saout *et al.* 2013). However, sustained human activities around protected areas contribute to their fragmentation (Wittemyer *et al.* 2008), creating a mosaic of often too small and/or isolated protected areas to effectively conserve large wide-ranging mammal species (Crooks *et al.* 2011; Lindsey *et al.* 2017). For instance, land use change around protected areas can alter immigration/emigration rates (Cushman *et al.* 2015), limit the genetic diversity of wildlife populations (Frankham, Bradshaw & Brook 2014), and ultimately population dynamics (Cushman *et al.* 2015). These issues are particularly apparent in Africa, where human population growth has rapidly intensified conversion of wilderness and greatly fragmented protected areas (Wittemyer *et al.* 2008). Correspondingly, large mammal populations have declined by almost 60% in the past 40 years, apart from in intensively managed and often fenced ecosystems in southern Africa (Craigie *et al.* 2010). Consequently, human encroachment and habitat conversion around protected areas present some of the greatest conservation challenges of the 21st century (Woodroffe & Ginsberg 1998).

Large carnivore persistence is particularly affected by human encroachment and habitat conversion around protected areas (Woodroffe & Ginsberg 1998). In these areas, large carnivores experience high mortality, and are imperilled by various sources of human-induced mortality including conflict-related killings (Dickman *et* *al.* 2014), illegal trophy-hunting (Loveridge *et al.* 2016), and bushmeat poaching (Lindsey *et al.* 2017). The high offtake observed in these areas can affect the demographic structure of and induce source-sink dynamics in carnivore populations and drive populations to local extinction (Woodroffe & Ginsberg 1998; Loveridge *et al.* 2010). Paradoxically, given large home range requirements and wide ranging tendencies, much of the habitat necessary to sustain viable large carnivore populations occurs outside of protected areas (Nowell & Jackson 1996). Thus, the fate of large carnivore populations may lie in the often unprotected and largely human-dominated habitat surrounding protected areas (Crooks *et al.* 2011; Carter & Linnell 2016).

Habitat located outside protected areas is particularly crucial for African lions (*Panthera leo*), as approximately 44% of the species range is associated with habitat that has no official protected status (Lindsey *et al.* 2017). African lion populations have declined by almost half in the last 20 years, with threats including habitat loss, prey depletion, conflict-related mortality, trade in lion body parts, and poorly-regulated trophy hunting (Bauer *et al.* 2015; Lindsey *et al.* 2017). Apart from trophy hunting, all these sources of mortality are more likely to occur outside strictly protected habitats where intense human activities interfere with lion movement patterns, dispersal ability, and demographics (Cushman *et al.* 2015; Loveridge *et al.* 2016). In fact, one study suggests that lions cannot persist in human-dominated landscapes when they reach a minimum density of 25 people/km2, a threshold likely relates to intense land-use conversion, prey depletion, and habitat degradation (Riggio *et al.* 2012; Lindsey *et al.* 2017). Given prevailing anthropogenic disturbance, these human-dominated landscapes represent the areas where lions and other large carnivores are most vulnerable to mortality and extinction risk (Loveridge *et al.* 2016; Lindsey *et al.* 2017). The predicted increase in human population growth in Africa, which is likely to double by 2050 (PRB 2016), will intensify human-lion interactions, and exacerbate competition over finite resources such as prey and space around protected areas, with an expected increase in conflict and its ensuing detrimental effects on lion survival. Thus, determining the extent to which lions can occupy these human-dominated areas is of major importance, as such habitats are likely to become increasingly important for their conservation.

Here we used a camera-trapping based survey to investigate the influence of environmental and anthropogenic variables on lion site use across a gradient of anthropogenic pressure in Tanzania's Ruaha landscape during the dry seasons of 2014 and 2015. We hypothesised increased lion site use in areas: *i)* closer to the Great Ruaha river (Abade, Macdonald & Dickman 2014b; Cusack *et al.* 2016) and surface water (Davidson *et al.* 2013; Oriol-Cotterill *et al.* 2015); *ii*) further from households and in areas of low human and livestock density (Everatt, Andresen & Somers 2014; Oriol-Cotterill *et al.* 2015); *iii*) closer to ranger posts, due to increased surveillance that might result in lower rates of lion human persecution or poaching of lions (Henschel *et al.* 2016); i*v*) increased prey biomass (Hayward & Kerley 2005; Davidson *et al.* 2013); and *v*) of increased vegetation cover, given its influence on determining prey catchability (Hopcraft, Sinclair & Packer 2005) and lion hunting success (Davies *et al.* 2016) in savannah ecosystems (Table 1).

The Ruaha landscape represents one of the largest strongholds for lion populations (Riggio *et al.* 2012), as well as a region where lions experience some of the highest known rates of conflict-related mortality in East Africa (Abade, Macdonald & Dickman 2014a; Dickman 2015). Despite its significance for lion conservation globally (Riggio *et al.* 2012), the paucity of information about the spatial ecology and distribution of lions in this landscape has been suggested to hinder conservation planning for the species by the Tanzania Wildlife Research Institute, which has listed this area as a national priority for lion research (TAWIRI 2009). Thus, the data generated by our study can be used to support strategies aiming at promoting conservation of lions and potentially other large carnivores in human-dominated landscapes, both locally and where there is overlap between lions and people.

Materials and Methods

The Ruaha landscape

Tanzania's Ruaha landscape (Fig 1) spans over 50,000 km^2 and is composed of the Ruaha National Park (RNP), Game Reserves, Pawaga-Idodi Wildlife Management Area (WMA), and surrounding village lands. There are no fences separating RNP, WMA and village lands, and wildlife can move without restriction across these areas. Trophy hunting of wildlife is prohibited within RNP and in the surrounding village lands, but is permitted in the Game Reserves and in limited sections of the WMA. In the village lands, which contains over 60,000 people across 22 villages, carnivores are exposed to various sources of anthropogenic disturbance and mortality, including habitat conversions, intense human-carnivore conflict, bushmeat snaring, and killings for body parts (Abade *et al.* 2018). Human livelihood is primarily based on agriculture and domestic livestock rearing. Livestock herds are commonly found grazing without restriction across village land and WMA during the day, reportedly under the surveillance of herders and untrained guarding dogs. At night, the stock is typically housed in bomas, with cattle usually in a separate boma from smallstock (Abade, Macdonald & Dickman 2014a). Attitudes towards large carnivores among local people tend to be negative, principally due to the actual or perceived risk of depredation upon livestock (Dickman *et al.* 2014), even though carnivore depredation accounts for modest stock loss, particularly when compared to diseases (Dickman *et al.* 2014). Yet, carnivore attacks on livestock generate intense hostility and lead to high levels of retaliatory and preventative lion killings (Abade, Macdonald & Dickman 2014b; Dickman 2015).

The climate of the region is semi-arid to arid, and the vegetation is a mosaic of semi-arid savannahs and Zambesian *miombo* woodlands (Sosovele & Ngwale 2002). The village lands are primarily covered by rice and maize fields and grazing areas.

Lion occurrence data

We studied lion site use by deploying 127 non-baited, remotely triggered, single camera-trap stations (CTs) that sampled 11 areas across the Ruaha landscape during the dry seasons (May to December) of 2014 and 2015. In 2014, we used 42 Reconyx HC500 CTs, and sampled the Msembe area, near the park headquarters, where there is low anthropogenic pressure (Cusack *et al.* 2015). In 2015, we used 85 Bushnell Scoutguard CTs to extend our survey into 10 additional areas, including four sampling areas in RNP, two in the WMA, and four in the village lands (Fig 1). The CTs set up and trail placement followed the methodology described in Abade et al (2018). We used a pseudostratified method for deploying our CTs, ensuring a minimum 1.5–2 km distance between stations, and 15–20 km distance between sampling areas in 2015. The sampling areas were distributed across a three distance bins from the border of the national park (0–10 km; 10–20 km; >30 km) to examine potential spatial variation in lion occurrence. We set the CTs facing animal trails when the pre-defined GPS coordinates were found within 5 meters from the nearest open path showing signs of animal use. All the CTs were placed in trees or poles at a height of 0.3–0.5 meters off the ground. We visited the CTs every 30–50 days to retrieve data and service the traps.

We pooled lion occurrence data and analysed them in a single-season framework, as previous studies have found similar lion and other large carnivore detection and occupancy rates across dry seasons in Ruaha (Cusack *et al.* 2016; Abade *et al.* 2018). We collapsed the temporal sampling extent into seven-day bin intervals across a 32-week survey (~210 days) period. Due to the long duration of the survey, we relaxed the population closure assumption of the occupancy model (MacKenzie *et al.* 2006), and thus adjusted the interpretation of the occupancy parameter from true occupancy to proportion of site used by lions during the overall survey period, rather than the probability of continuous site occupation (MacKenzie *et al.* 2006). The lion occurrence data are available on GitHub following the link https://goo.gl/9NURjE.

Environmental and anthropogenic variables

We modelled lion site use based on ecologic variables of known influence on lion occupancy and spatial distribution (Table 1), while accounting for the effect of trail type (animal trails - AT; no-trails - NT; human-made roads - RD) on lion detection (Fig. 2). We created covariate rasters at a 1km^2 resolution. We first manually created shapefiles depicting households, the Great Ruaha river, and ranger posts by digitizing aerial imagery. We then created the rasters for distance to households, Great Ruaha river, and ranger posts rasters using the “Proximity” function in GDAL proximity module in QGIS (QGIS 2018). We calculated the human and livestock density rasters based on the numbers of people co-habiting each property mapped in the study site, and those of domestic stock owned per household through the kernel density estimator tool. We characterised vegetation cover based on the Vegetation Continuous Fields (VCF) data derived from the MOD44B product (Townshend *et al.* 2011) for the study period. The VCF data ranges from 0-100%, and provides information on the proportional percentage estimates for vegetation cover types (including woody and herbaceous vegetation, and bare ground) for each landscape pixel, with higher values associated with increased vegetation cover. We calculated the distance to surface water sources using the HubDistance function in QGIS. We only considered surface water sources that sustained water for over 6 months of the year, based on the water seasonality data from Peckel *et al.* (2016).

We calculated a temporal catch-per unit effort (CPUE) index of prey biomass for each CTs based on the number of independent records (> 5 min (Burton *et al.* 2012; Abade *et al.* 2018) for all large- and medium-bodied wild prey photographed during the survey. The principle behind CPUE is that the proportional representation the catch from a population should increase when population density or effort increases (Seber 1992). Thus, conceptually, CPUE could serve as an abundance index, and be used to detect variation in numbers as in abundance itself. We classified large prey as those herbivores with a mean body weight > 100 kg (Ripple *et al.* 2015), and medium prey as those weighing between 18 to 100 kg (Hayward & Kerley 2005; Owen-Smith & Mills 2008). Prey weight was based on the estimated average male body mass for each species (Tacutu *et al.* 2013). We calculated the CPUE index by multiplying the number of independent events at each station by the species average weight, divided by the CTs sampling effort, and standardised per 100 camera trap days (Burton *et al.* 2012; Abade *et al.* 2018). We considered independent detection events for lion and prey as those with > 5 minutes between records (Burton *et al.* 2012; Abade *et al.* 2018).

Prior to model fitting, we standardized all the covariates, and assessed them for multi-collinearity and correlation based on the results of Pearson correlation and variance inflation factor tests. We only used minimally correlated covariates (Pearson <0.7, VIF <3 (Zuur, Ieno & Elphick 2010); see Table S1; S2 in Supporting Information). Thus, we removed distance to the Great Ruaha river and livestock density from the analyses due to high correlation with the other covariates (Table S1, S2).

Model analyses and averaging

We used temporally replicated surveys (i.e. weeks) to estimate the latent, unobserved site use at each CTs Z_i, where $Z_i = 1$ if site i is used and 0 otherwise, and detection probability $p_{i,j}$, where $p_{i,j}$ is the probability that lions are detected at site i during replicate j, given site use (i.e., $Z_i = 1$) (MacKenzie *et al.* 2002; Tyre *et al.* 2003). We included a random intercept indexed for each of the sampling areas (Moll *et al.* 2016; Abade *et al.* 2018), to minimise the spatial autocorrelation among model residuals (Fig S1). Our final model for lion site use was:

$$\text{logit}(\Psi_\text{i}) = \alpha_\text{area} + \alpha_1\text{*Medium prey}_\text{i} + \alpha_2\text{*Large prey}_\text{i} + \alpha_3\text{*Distance household}_\text{i} + \alpha_4\text{*Distance ranger post}_\text{i} + \alpha_5\text{*VCF}_\text{i} + \alpha_6\text{*Distance surface water}_\text{i} + \alpha_7\text{*Density of humans}_\text{i}$$

(Eq. 1)

where Ψ_i represents the probability of lion site use at the i^th CT, α_area represents a random intercept indexed by area with estimated hyperparameters μ (mean) and τ^2

(variance), and $\alpha_{1,2,\ldots 5}$ represent the influence of associated covariates at the i^{th} CT (Table 1).

The final detection model was implemented as follows:

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_\text{k}{*}\text{Trail}_\text{i}$$

(Eq. 2)

where $p_{i,j}$ represents the detection probability at the i^{th} CT during survey j given site use (i.e., $Z_i = 1$), β_0 is the intercept, and β_k represents the effect of the k^{th} trail type on lion detection at each CT ($k = 3$), with animal trail as the reference category. To ensure that vegetation did not interfere with the probability of detecting wildlife, we conducted a *post hoc* analysis that included VCF as a covariate. This analysis revealed no effect of VCF on detection probability ($\beta_{VCF} = 0.05$, 95% credible interval = (-0.20, 0.26), inclusion probability = 0.03).

We fit the models using a Bayesian framework and Markov chain Monte Carlo (MCMC) simulations in R v.2.13.0 and JAGS (Plummer 2003) using the package 'R2jags' (Su & Yajima 2012). We estimated the effect of each covariate on site use through the Bayesian inclusion parameter w_c; (Kuo & Mallick 1998), which had a Bernoulli distribution and an uninformative prior probability of 0.5. The posterior probability of w_c corresponds to the estimated probability of any given covariate ('C') to be included in the best model of a set of 2^C candidate models (Royle & Dorazio 2008; Burton *et al.* 2012; Moll *et al.* 2016). We calculated model-averaged estimates for the covariate coefficients over the global models from MCMC posterior histories (Royle & Dorazio 2008). We used uninformative uniform priors and implemented the models using three chains of 500,000 iterations each, discarding the first 50,000 as burn-in, and thinned the posterior chains by 10. Uninformative uniform priors translate to posterior mean estimates that are strongly shaped by the data rather than prior assumptions. We assessed the convergence of the models by ensuring R-hat values for all parameters were <1.1 (Gelman & Hill 2007).

Results

We recorded 157 independent lion detections at 35 (28%) of the 127 CTs over a total of 12,987 camera-trap days. We documented the spatial variation in lion detections across sampling areas, with the highest number of detections (n=143; 91%) in RNP (Fig 1). The WMA had far fewer detections (n=14; 9%), and we did not detect lions in the village lands (Table 2). We recorded 17,143 independent events of lion prey, with 13,709 (80%) in RNP, 3,138 (18%) in the WMA, and 296 (2%) in the village lands (Table 3). Notably, there were no detections of several preferred lion prey species, such as buffalo, giraffe and zebra, on village lands (Table 3). We detected over 2,800 independent livestock events in 32 out of 35 village land CTs.

We found that lion site use was significantly influenced by increased biomass of large and medium prey (Table 4, Fig 3). Of these prey-related covariates, large prey had the stronger effect on lion site use, as indicated by its larger posterior mean and higher inclusion probability (w_c Large prey = 0.98; Table 4). We found a positive, albeit non-significant (i.e. large variation and credible intervals overlapping zero), association between lion site use and increased distance to households, ranger posts, and increased vegetation cover (Table 4, Fig 3). Similarly, we found a positive although non-significant correlation between lion site use and proximity to surface water on lion occupancy. Inclusion probabilities indicated that large and medium prey, and distance to household were the most common covariates included in the model (Table 4). Lion detection probability was lower at CTs placed off-trail in comparison to those on animal trails and human-made roads, but this effect was relatively weak overall (Table 4).

Discussion

In this study, we only detected lions in habitats that had a protected status, and comparatively higher wild prey availability. We did not detect lions in the unprotected village lands, despite their known presence in these areas, as evidenced by spoor, livestock depredations and conflict with people (Dickman 2015).

Lion site use was positively associated with higher levels of wild prey occurrence. More importantly, we found that wild large prey was the main determinant for site use during the dry season in comparison to other covariates, corroborating previous findings that showed large-bodied wild prey availability to shape lion spatial distribution and habitat use (Hayward & Kerley 2005; Davidson *et al.* 2013). Additionally, our findings are similar to those presented by Cusack et al. (2016) regarding the significant positive effects of large prey species on lion occupancy and detection in RNP. Thus, we suggest that plans to effectively conserve lions in Ruaha should prioritise protecting large wild prey base, given its strong influence on determining lion site use.

In this study, we detected no evidence of lion use of the village lands, which could indicate low lion population densities in these areas due to persecution, behavioral avoidance of such areas, or both. We have similarly observed low use of village lands for other large carnivores in this landscape (Abade *et al.* 2018). We suspect that the current rate of land conversion (Lobora *et al.* 2017), coupled with low prey availability, intense bushmeat poaching (Knapp, Peace & Bechtel 2017), pastoralism, and high levels of human-carnivore conflict (Abade, Macdonald & Dickman 2014a; Dickman *et al.* 2014) all help to limit lion site use outside protected areas. In this way, our results add to a growing body of research demonstrating the importance of protected areas as key refugia for lions (Bauer *et al.* 2015; Lindsey *et al.* 2017). We did not find significant influence of proximity to surface water on lion occupancy, although we observed a positive trend on lion site use closer to surface water. Surface water has been documented as an important predictor of lion spatial distribution across African semi-arid savannahs, especially during dry seasons (de Boer *et al.* 2010; Valeix, Loveridge & Macdonald 2012; Davidson *et al.* 2013; Oriol-Cotterill *et al.* 2015), and proximity to the Great Ruaha river has been highlighted as an important predictor for habitat suitability for large carnivores in Ruaha (Abade, Macdonald & Dickman 2014b). Thus, the lack of a relationship between lion site use and surface water is somewhat surprising. One possible explanation for these results could be associated with lions and prey relying in more ephemeral water sources than those considered here (i.e. < 6 months), which could be diluting the effects of surface water on site use. Additionally, information on artificial surface water such as bore holes and livestock ponds were not considered in this study due to lack of georeferenced data, and this could be contributing to hinder our understanding of overall surface water supply on prey and lion site use patterns during the dry season. Given the marked seasonality on the study site, we recommend that further studies should collect data across the rainy season in order to fully understand the relative influence of anthropogenic and environmental variables on lion site use in this area. Finally, despite the fact that collinearity prevented us from considering distance to the Great Ruaha river could not be included in the model due to collinearity with distance to ranger post (Table S1), we evaluated its effect in a *post hoc* analysis by replacing the ranger covariate with the Great Ruaha river covariate. The results illustrate that distance to the Great Ruaha river had a negligible effect on lion site use (posterior mean = 0.92, sd = 2.10, 95% credible interval = (-3.33, 4.60), inclusion probability = 0.45).

It is noteworthy that we did record 14 lion detections in the northern portion of the WMA in a region with minimal human and livestock activity, and where park and private anti-poaching patrolling are relatively common. Despite a lack of significant influence of ranger posts on lion site use, the known presence of patrolling could be helping to lessen poaching and grazing activities, and contributing to lion occurrence in this area.

Poaching and displacement by livestock are known factors contributing to prey depletion (Ripple *et al.* 2015), which can be even more detrimental to carnivores than direct anthropogenic mortality (Rosenblatt *et al.* 2016). These effects can alter lion populations (Henschel *et al.* 2016), and are likely limiting lion occurrence in the village lands. Furthermore, lions are exposed to high human-induced mortality around RNP due to intense conflict (Abade, Macdonald & Dickman 2014a; Dickman *et al.* 2014) . Since 2010, over 100 lions have been killed by humans in the village lands (Dickman, pers. obs.). Although the effect of such killings on lion populations in Ruaha is yet to be quantified, they might be contributing to reduced lion numbers in the village lands, and hence to the low detection and site use observed here. Of substantial concern is the potential for these killings to lead to source-sinks for lions locally, with possibility to affect the population within the national park as well, as observed elsewhere in Africa (Woodroffe & Frank, 2005; Loveridge *et al.* 2010; Loveridge *et al.* 2016). Increasing human tolerance of lions in village lands by translating their presence into tangible benefits to local communities could minimise carnivore persecution and mortality (Dickman *et al.* 2014). Additionally, efforts to sustain wild prey base within human-dominated landscapes should be considered given their important influence on defining lion and other carnivores site use. Increased wild prey availability in village lands could help to alleviate predation on domestic livestock, although it might also have the unintended consequence of increased conflict associated with livestock depredation. Furthermore, concerted efforts to systematically improve husbandry practices using predator-proof bomas (Abade, Macdonald & Dickman 2014a), and prevention of human-carnivore conflict, could lead to a substantial reduction in lion and other large carnivore mortality, and contribute to conservation of these species in village lands (Weise *et al*., 2018). Lastly, efforts to improve food security, diversifying access to protein sources other than wild prey, and minimizing the potential economic reliance on bushmeat trade by local villagers could help alleviating unsustainable bushmeat harvesting (van Vliet *et al.* 2016), as well as the ensuing negative effects of prey depletion on lion conservation.

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Figure 1. Location of the study site, and distribution of camera-trap stations (blue shaded circles) across the Ruaha landscape, southern Tanzania. 1-11 represents sampling areas: 1. Mdonya; 2. Kwihala; 3. Msembe; 4. Mwagusi; 5. Lunda-Ilolo; 6. Pawaga; 7. Lunda; 8. Idodi; 9. Malinzanga; 10. Nyamahana; 11. Magosi. The yellow shaded circles represent the number of independent detections of lions (*Panthera leo*) at each camera-trap station. Dark blue shaded circles correspond to camera-trap stations set up in year 1 (Y1) and light blue circles correspond to camera-trap stations set up in year 2 (Y2).

Figure 2. Set of covariates hypothesised to influence lion (*Panthera leo*) site use across Tanzania's Ruaha landscape. A. Distance to households; B. Distance to ranger posts; C. Vegetation continuous fields/vegetation cover; D. Density of people per household. Biomass index of large and medium prey (CPUE), and trail type not represented here.

Figure 3. Predicted association of the hypothesised covariates to the probability of site use (A-F) of lions (*Panthera leo*). The solid lines represent the posterior means, and the light grey lines represent the estimated uncertainty based on a random posterior sample of 200 iterations.

Table 1. Covariates predicted to influence lion site use in the Ruaha landscape, southern Tanzania.*Ψ*. probability of site use; *P*. probability of detection

Covariates	**Model type**	**Covariate Class**	**Expected Influence on Site Use**
Density of humans	*Ψ*	Anthropogenic	-
Density of livestock	*Ψ*	Anthropogenic	-
Distance to Great Ruaha	*Ψ*	Natural	-
Distance to household	*Ψ*	Anthropogenic	+
Distance to ranger post	*Ψ*	Anthropogenic	-
Distance to surface water	*Ψ*	Natural	-
Large prey	*Ψ*	Natural	+
Medium prey	*Ψ*	Natural	+
Vegetation cover	*Ψ*	Natural	+
Trail type	*P*	Natural	+

Table 2. Total number of independent lion detections per sampling areas used to model lion site use in the Ruaha landscape, southern Tanzania. *Σ of all independent events. CT effort (days): Number of active days of survey; each day = 24h.

Land-management	Area	CT effort (days)	Σ* Events
National Park	Kwihala	196	1
	Lunda-Ilolo	196	0
	Mdonya	226	5
	Msembe	7,447	136
	Mwagusi	173	1
Wildlife Management Area	Lunda	867	14
	Pawaga	738	0
Village land	Idodi	674	0
	Magosi	656	0
	Malinzanga	718	0
	Nyamahana	1,059	0

Table 3. Total number of independent prey detections according to each land use category surveyed. RNP: Ruaha National Park; WMA: Wildlife Management Area; VL: village lands

Species	**Land-management**		
	RNP	**WMA**	**VL**
Bushbuck	79	48	15
Buffalo	75	4	0
Bush pig	33	16	9
Duiker	199	71	61
Eland	46	3	0
Elephant	2,893	509	0
Giraffe	1,407	217	0
Grant's gazelle	59	37	0
Greater kudu	910	212	130
Hippo	392	1	0
Impala	6,779	1,849	34
Lesser kudu	213	113	46
Warthog	181	50	1
Waterbuck	39	5	0
Zebra	404	3	0

Table 4. Posterior means, standard deviations, 95% credible intervals (C.I.), and Bayesian inclusion parameters (w_c) of lion site use models fit to camera trap data from the Ruaha landscape, southern Tanzania. Note that $\boldsymbol{\beta}_1$ is absent since it was associated with the reference trail type (animal trail) and was thus set to zero.

Covariate	**Parameter**	**Mean**	**SD**	**95% C.I.**	w_c
Medium prey	α_1	1.8	1.05	0.03, 4.12	0.59
Large prey	α_2	3.19	1.11	1.01, 4.90	0.98
Distance to household	α_3	2.61	1.84	-2.04, 4.89	0.61
Distance to ranger post	α_4	0.97	2.08	-3.38, 4.53	0.41
Vegetation cover	α_5	1.16	0.78	-0.08, 3.06	0.39
Distance to surface water	α_6	-1.53	1.74	-4.55, 2.15	0.42
Density of humans	α_7	-2.18	1.67	-4.86, 0.81	0.38
Mean random intercept	α_{site}	-4.77	3.47	-12.35, 1.19	-
Intercept	β_0	-0.57	1.13	-3.25, 0.75	-
Trail type.N	β_2	-1.97	0.84	-3.89, -0.61	0.27
Trail type.RD	β_3	0.28	0.33	-0.37, 0.88	0.27
CTs occupied	Ψ	42.24	4.09	37.00, 53.00	-