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

4  
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25

26 **Abstract**

27

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

49

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

52

### 53 **Introduction**

54 Protected areas, such as national parks, act as vital refugia for wildlife, serving  
55 as protection for large-scale ecological processes and ecosystem functions  
56 (Woodroffe & Ginsberg 1998; Le Saout *et al.* 2013). However, sustained human  
57 activities around protected areas contribute to their fragmentation (Wittemyer *et al.*  
58 2008), creating a mosaic of often too small and/or isolated protected areas to  
59 effectively conserve large wide-ranging mammal species (Crooks *et al.* 2011; Lindsey  
60 *et al.* 2017). For instance, land use change around protected areas can alter  
61 immigration/emigration rates (Cushman *et al.* 2015), limit the genetic diversity of  
62 wildlife populations (Frankham, Bradshaw & Brook 2014), and ultimately population  
63 dynamics (Cushman *et al.* 2015). These issues are particularly apparent in Africa,  
64 where human population growth has rapidly intensified conversion of wilderness and  
65 greatly fragmented protected areas (Wittemyer *et al.* 2008). Correspondingly, large  
66 mammal populations have declined by almost 60% in the past 40 years, apart from in  
67 intensively managed and often fenced ecosystems in southern Africa (Craigie *et al.*  
68 2010). Consequently, human encroachment and habitat conversion around protected  
69 areas present some of the greatest conservation challenges of the 21<sup>st</sup> century  
70 (Woodroffe & Ginsberg 1998).

71 Large carnivore persistence is particularly affected by human encroachment  
72 and habitat conversion around protected areas (Woodroffe & Ginsberg 1998). In these  
73 areas, large carnivores experience high mortality, and are imperilled by various  
74 sources of human-induced mortality including conflict-related killings (Dickman *et*

75 *al.* 2014), illegal trophy-hunting (Loveridge *et al.* 2016), and bushmeat poaching  
76 (Lindsey *et al.* 2017). The high offtake observed in these areas can affect the  
77 demographic structure of and induce source-sink dynamics in carnivore populations  
78 and drive populations to local extinction (Woodroffe & Ginsberg 1998; Loveridge *et al.*  
79 *al.* 2010). Paradoxically, given large home range requirements and wide ranging  
80 tendencies, much of the habitat necessary to sustain viable large carnivore populations  
81 occurs outside of protected areas (Nowell & Jackson 1996). Thus, the fate of large  
82 carnivore populations may lie in the often unprotected and largely human-dominated  
83 habitat surrounding protected areas (Crooks *et al.* 2011; Carter & Linnell 2016).

84         Habitat located outside protected areas is particularly crucial for African lions  
85 (*Panthera leo*), as approximately 44% of the species range is associated with habitat  
86 that has no official protected status (Lindsey *et al.* 2017). African lion populations  
87 have declined by almost half in the last 20 years, with threats including habitat loss,  
88 prey depletion, conflict-related mortality, trade in lion body parts, and poorly-  
89 regulated trophy hunting (Bauer *et al.* 2015; Lindsey *et al.* 2017). Apart from trophy  
90 hunting, all these sources of mortality are more likely to occur outside strictly  
91 protected habitats where intense human activities interfere with lion movement  
92 patterns, dispersal ability, and demographics (Cushman *et al.* 2015; Loveridge *et al.*  
93 2016). In fact, one study suggests that lions cannot persist in human-dominated  
94 landscapes when they reach a minimum density of 25 people/km<sup>2</sup>, a threshold likely  
95 relates to intense land-use conversion, prey depletion, and habitat degradation (Riggio  
96 *et al.* 2012; Lindsey *et al.* 2017). Given prevailing anthropogenic disturbance, these  
97 human-dominated landscapes represent the areas where lions and other large  
98 carnivores are most vulnerable to mortality and extinction risk (Loveridge *et al.* 2016;  
99 Lindsey *et al.* 2017). The predicted increase in human population growth in Africa,

100 which is likely to double by 2050 (PRB 2016), will intensify human-lion interactions,  
101 and exacerbate competition over finite resources such as prey and space around  
102 protected areas, with an expected increase in conflict and its ensuing detrimental  
103 effects on lion survival. Thus, determining the extent to which lions can occupy these  
104 human-dominated areas is of major importance, as such habitats are likely to become  
105 increasingly important for their conservation.

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

119         The Ruaha landscape represents one of the largest strongholds for lion  
120 populations (Riggio *et al.* 2012), as well as a region where lions experience some of  
121 the highest known rates of conflict-related mortality in East Africa (Abade,  
122 Macdonald & Dickman 2014a; Dickman 2015). Despite its significance for lion  
123 conservation globally (Riggio *et al.* 2012), the paucity of information about the spatial  
124 ecology and distribution of lions in this landscape has been suggested to hinder

125 conservation planning for the species by the Tanzania Wildlife Research Institute,  
126 which has listed this area as a national priority for lion research (TAWIRI 2009).  
127 Thus, the data generated by our study can be used to support strategies aiming at  
128 promoting conservation of lions and potentially other large carnivores in human-  
129 dominated landscapes, both locally and where there is overlap between lions and  
130 people.

131

## 132 **Materials and Methods**

133

### 134 *The Ruaha landscape*

135 Tanzania's Ruaha landscape (Fig 1) spans over 50,000 km<sup>2</sup> and is composed  
136 of the Ruaha National Park (RNP), Game Reserves, Pawaga-Idodi Wildlife  
137 Management Area (WMA), and surrounding village lands. There are no fences  
138 separating RNP, WMA and village lands, and wildlife can move without restriction  
139 across these areas. Trophy hunting of wildlife is prohibited within RNP and in the  
140 surrounding village lands, but is permitted in the Game Reserves and in limited  
141 sections of the WMA. In the village lands, which contains over 60,000 people across  
142 22 villages, carnivores are exposed to various sources of anthropogenic disturbance  
143 and mortality, including habitat conversions, intense human-carnivore conflict,  
144 bushmeat snaring, and killings for body parts (Abade *et al.* 2018). Human livelihood  
145 is primarily based on agriculture and domestic livestock rearing. Livestock herds are  
146 commonly found grazing without restriction across village land and WMA during the  
147 day, reportedly under the surveillance of herders and untrained guarding dogs. At  
148 night, the stock is typically housed in bomas, with cattle usually in a separate boma  
149 from smallstock (Abade, Macdonald & Dickman 2014a). Attitudes towards large

150 carnivores among local people tend to be negative, principally due to the actual or  
151 perceived risk of depredation upon livestock (Dickman *et al.* 2014), even though  
152 carnivore depredation accounts for modest stock loss, particularly when compared to  
153 diseases (Dickman *et al.* 2014). Yet, carnivore attacks on livestock generate intense  
154 hostility and lead to high levels of retaliatory and preventative lion killings (Abade,  
155 Macdonald & Dickman 2014b; Dickman 2015).

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

159

#### 160 *Lion occurrence data*

161         We studied lion site use by deploying 127 non-baited, remotely triggered,  
162 single camera-trap stations (CTs) that sampled 11 areas across the Ruaha landscape  
163 during the dry seasons (May to December) of 2014 and 2015. In 2014, we used 42  
164 Reconyx HC500 CTs, and sampled the Msembe area, near the park headquarters,  
165 where there is low anthropogenic pressure (Cusack *et al.* 2015). In 2015, we used 85  
166 Bushnell Scoutguard CTs to extend our survey into 10 additional areas, including four  
167 sampling areas in RNP, two in the WMA, and four in the village lands (Fig 1). The  
168 CTs set up and trail placement followed the methodology described in Abade et al  
169 (2018). We used a pseudostratified method for deploying our CTs, ensuring a  
170 minimum 1.5–2 km distance between stations, and 15–20 km distance between  
171 sampling areas in 2015. The sampling areas were distributed across a three distance  
172 bins from the border of the national park (0–10 km; 10–20 km; >30 km) to examine  
173 potential spatial variation in lion occurrence. We set the CTs facing animal trails  
174 when the pre-defined GPS coordinates were found within 5 meters from the nearest

175 open path showing signs of animal use. All the CTs were placed in trees or poles at a  
176 height of 0.3–0.5 meters off the ground. We visited the CTs every 30–50 days to  
177 retrieve data and service the traps.

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

189

#### 190 *Environmental and anthropogenic variables*

191 We modelled lion site use based on ecologic variables of known influence on  
192 lion occupancy and spatial distribution (Table 1), while accounting for the effect of  
193 trail type (animal trails - AT; no-trails - NT; human-made roads - RD) on lion  
194 detection (Fig. 2). We created covariate rasters at a 1km<sup>2</sup> resolution. We first  
195 manually created shapefiles depicting households, the Great Ruaha river, and ranger  
196 posts by digitizing aerial imagery. We then created the rasters for distance to  
197 households, Great Ruaha river, and ranger posts rasters using the “Proximity”  
198 function in GDAL proximity module in QGIS (QGIS 2018). We calculated the human  
199 and livestock density rasters based on the numbers of people co-habiting each



200 property mapped in the study site, and those of domestic stock owned per household  
201 through the kernel density estimator tool. We characterised vegetation cover based on  
202 the Vegetation Continuous Fields (VCF) data derived from the MOD44B product  
203 (Townshend *et al.* 2011) for the study period. The VCF data ranges from 0-100%, and  
204 provides information on the proportional percentage estimates for vegetation cover  
205 types (including woody and herbaceous vegetation, and bare ground) for each  
206 landscape pixel, with higher values associated with increased vegetation cover. We  
207 calculated the distance to surface water sources using the HubDistance function in  
208 QGIS. We only considered surface water sources that sustained water for over 6  
209 months of the year, based on the water seasonality data from Peckel *et al.* (2016).

210 We calculated a temporal catch-per unit effort (CPUE) index of prey biomass  
211 for each CTs based on the number of independent records ( $> 5$  min (Burton *et al.*  
212 2012; Abade *et al.* 2018) for all large- and medium-bodied wild prey photographed  
213 during the survey. The principle behind CPUE is that the proportional representation  
214 the catch from a population should increase when population density or effort  
215 increases (Seber 1992). Thus, conceptually, CPUE could serve as an abundance  
216 index, and be used to detect variation in numbers as in abundance itself. We classified  
217 large prey as those herbivores with a mean body weight  $> 100$  kg (Ripple *et al.* 2015),  
218 and medium prey as those weighing between 18 to 100 kg (Hayward & Kerley 2005;  
219 Owen-Smith & Mills 2008). Prey weight was based on the estimated average male  
220 body mass for each species (Tacutu *et al.* 2013). We calculated the CPUE index by  
221 multiplying the number of independent events at each station by the species average  
222 weight, divided by the CTs sampling effort, and standardised per 100 camera trap  
223 days (Burton *et al.* 2012; Abade *et al.* 2018). We considered independent detection

224 events for lion and prey as those with > 5 minutes between records (Burton *et al.*  
225 2012; Abade *et al.* 2018).

226 Prior to model fitting, we standardized all the covariates, and assessed them  
227 for multi-collinearity and correlation based on the results of Pearson correlation and  
228 variance inflation factor tests. We only used minimally correlated covariates (Pearson  
229 <0.7, VIF <3 (Zuur, Ieno & Elphick 2010); see Table S1; S2 in Supporting  
230 Information). Thus, we removed distance to the Great Ruaha river and livestock  
231 density from the analyses due to high correlation with the other covariates (Table S1,  
232 S2).

233

#### 234 *Model analyses and averaging*

235 We used temporally replicated surveys (i.e. weeks) to estimate the latent,  
236 unobserved site use at each CTs  $Z_i$ , where  $Z_i = 1$  if site  $i$  is used and 0 otherwise, and  
237 detection probability  $p_{i,j}$ , where  $p_{i,j}$  is the probability that lions are detected at site  $i$   
238 during replicate  $j$ , given site use (i.e.,  $Z_i = 1$ ) (MacKenzie *et al.* 2002; Tyre *et al.*  
239 2003). We included a random intercept indexed for each of the sampling areas (Moll  
240 *et al.* 2016; Abade *et al.* 2018), to minimise the spatial autocorrelation among model  
241 residuals (Fig S1). Our final model for lion site use was:

242

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

246 (Eq. 1)

247 where  $\Psi_i$  represents the probability of lion site use at the  $i^{\text{th}}$  CT,  $\alpha_{\text{area}}$  represents a  
248 random intercept indexed by area with estimated hyperparameters  $\mu$  (mean) and  $\tau^2$

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

251 The final detection model was implemented as follows:

252

$$253 \text{ logit}(p_{i,j}) = \beta_0 + \beta_k * \text{Trail}_i$$

254 (Eq. 2)

255

256 where  $p_{i,j}$  represents the detection probability at the  $i^{\text{th}}$  CT during survey  $j$  given site  
257 use (i.e.,  $Z_i = 1$ ),  $\beta_0$  is the intercept, and  $\beta_k$  represents the effect of the  $k^{\text{th}}$  trail type on  
258 lion detection at each CT ( $k = 3$ ), with animal trail as the reference category. To  
259 ensure that vegetation did not interfere with the probability of detecting wildlife, we  
260 conducted a *post hoc* analysis that included VCF as a covariate. This analysis  
261 revealed no effect of VCF on detection probability ( $\beta_{VCF} = 0.05$ , 95% credible interval  
262 = (-0.20, 0.26), inclusion probability = 0.03).

263 We fit the models using a Bayesian framework and Markov chain Monte  
264 Carlo (MCMC) simulations in R v.2.13.0 and JAGS (Plummer 2003) using the  
265 package ‘R2jags’ (Su & Yajima 2012). We estimated the effect of each covariate on  
266 site use through the Bayesian inclusion parameter  $w_c$ ; (Kuo & Mallick 1998), which  
267 had a Bernoulli distribution and an uninformative prior probability of 0.5. The  
268 posterior probability of  $w_c$  corresponds to the estimated probability of any given  
269 covariate (‘C’) to be included in the best model of a set of  $2^C$  candidate models (Royle  
270 & Dorazio 2008; Burton *et al.* 2012; Moll *et al.* 2016). We calculated model-averaged  
271 estimates for the covariate coefficients over the global models from MCMC posterior  
272 histories (Royle & Dorazio 2008). We used uninformative uniform priors and  
273 implemented the models using three chains of 500,000 iterations each, discarding the

274 first 50,000 as burn-in, and thinned the posterior chains by 10. Uninformative uniform  
275 priors translate to posterior mean estimates that are strongly shaped by the data rather  
276 than prior assumptions. We assessed the convergence of the models by ensuring R-hat  
277 values for all parameters were  $<1.1$  (Gelman & Hill 2007).

278

## 279 **Results**

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

289 We found that lion site use was significantly influenced by increased biomass  
290 of large and medium prey (Table 4, Fig 3). Of these prey-related covariates, large  
291 prey had the stronger effect on lion site use, as indicated by its larger posterior mean  
292 and higher inclusion probability ( $w_c$  Large prey = 0.98; Table 4). We found a positive,  
293 albeit non-significant (i.e. large variation and credible intervals overlapping zero),  
294 association between lion site use and increased distance to households, ranger posts,  
295 and increased vegetation cover (Table 4, Fig 3). Similarly, we found a positive  
296 although non-significant correlation between lion site use and proximity to surface  
297 water on lion occupancy. Inclusion probabilities indicated that large and medium  
298 prey, and distance to household were the most common covariates included in the

299 model (Table 4). Lion detection probability was lower at CTs placed off-trail in  
300 comparison to those on animal trails and human-made roads, but this effect was  
301 relatively weak overall (Table 4).

302

### 303 **Discussion**

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

308 Lion site use was positively associated with higher levels of wild prey  
309 occurrence. More importantly, we found that wild large prey was the main  
310 determinant for site use during the dry season in comparison to other covariates,  
311 corroborating previous findings that showed large-bodied wild prey availability to  
312 shape lion spatial distribution and habitat use (Hayward & Kerley 2005; Davidson *et al.*  
313 *al.* 2013). Additionally, our findings are similar to those presented by Cusack *et al.*  
314 (2016) regarding the significant positive effects of large prey species on lion  
315 occupancy and detection in RNP. Thus, we suggest that plans to effectively conserve  
316 lions in Ruaha should prioritise protecting large wild prey base, given its strong  
317 influence on determining lion site use.

318 In this study, we detected no evidence of lion use of the village lands, which  
319 could indicate low lion population densities in these areas due to persecution,  
320 behavioral avoidance of such areas, or both. We have similarly observed low use of  
321 village lands for other large carnivores in this landscape (Abade *et al.* 2018). We  
322 suspect that the current rate of land conversion (Lobora *et al.* 2017), coupled with low  
323 prey availability, intense bushmeat poaching (Knapp, Peace & Bechtel 2017),

324 pastoralism, and high levels of human-carnivore conflict (Abade, Macdonald &  
325 Dickman 2014a; Dickman *et al.* 2014) all help to limit lion site use outside protected  
326 areas. In this way, our results add to a growing body of research demonstrating the  
327 importance of protected areas as key refugia for lions (Bauer *et al.* 2015; Lindsey *et*  
328 *al.* 2017). We did not find significant influence of proximity to surface water on lion  
329 occupancy, although we observed a positive trend on lion site use closer to surface  
330 water. Surface water has been documented as an important predictor of lion spatial  
331 distribution across African semi-arid savannahs, especially during dry seasons (de  
332 Boer *et al.* 2010; Valeix, Loveridge & Macdonald 2012; Davidson *et al.* 2013; Oriol-  
333 Cotterill *et al.* 2015), and proximity to the Great Ruaha river has been highlighted as  
334 an important predictor for habitat suitability for large carnivores in Ruaha (Abade,  
335 Macdonald & Dickman 2014b). Thus, the lack of a relationship between lion site use  
336 and surface water is somewhat surprising. One possible explanation for these results  
337 could be associated with lions and prey relying in more ephemeral water sources than  
338 those considered here (i.e. < 6 months), which could be diluting the effects of surface  
339 water on site use. Additionally, information on artificial surface water such as bore  
340 holes and livestock ponds were not considered in this study due to lack of  
341 georeferenced data, and this could be contributing to hinder our understanding of  
342 overall surface water supply on prey and lion site use patterns during the dry season.  
343 Given the marked seasonality on the study site, we recommend that further studies  
344 should collect data across the rainy season in order to fully understand the relative  
345 influence of anthropogenic and environmental variables on lion site use in this area.  
346 Finally, despite the fact that collinearity prevented us from considering distance to the  
347 Great Ruaha river could not be included in the model due to collinearity with distance  
348 to ranger post (Table S1), we evaluated its effect in a *post hoc* analysis by replacing

349 the ranger covariate with the Great Ruaha river covariate. The results illustrate that  
350 distance to the Great Ruaha river had a negligible effect on lion site use (posterior  
351 mean = 0.92, sd = 2.10, 95% credible interval = (-3.33, 4.60), inclusion probability =  
352 0.45).

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

359 Poaching and displacement by livestock are known factors contributing to  
360 prey depletion (Ripple *et al.* 2015), which can be even more detrimental to carnivores  
361 than direct anthropogenic mortality (Rosenblatt *et al.* 2016). These effects can alter  
362 lion populations (Henschel *et al.* 2016), and are likely limiting lion occurrence in the  
363 village lands. Furthermore, lions are exposed to high human-induced mortality around  
364 RNP due to intense conflict (Abade, Macdonald & Dickman 2014a; Dickman *et al.*  
365 2014) . Since 2010, over 100 lions have been killed by humans in the village lands  
366 (Dickman, pers. obs.). Although the effect of such killings on lion populations in  
367 Ruaha is yet to be quantified, they might be contributing to reduced lion numbers in  
368 the village lands, and hence to the low detection and site use observed here. Of  
369 substantial concern is the potential for these killings to lead to source-sinks for lions  
370 locally, with possibility to affect the population within the national park as well, as  
371 observed elsewhere in Africa (Woodroffe & Frank, 2005; Loveridge *et al.* 2010;  
372 Loveridge *et al.* 2016). Increasing human tolerance of lions in village lands by  
373 translating their presence into tangible benefits to local communities could minimise

374 carnivore persecution and mortality (Dickman *et al.* 2014). Additionally, efforts to  
375 sustain wild prey base within human-dominated landscapes should be considered  
376 given their important influence on defining lion and other carnivores site use.  
377 Increased wild prey availability in village lands could help to alleviate predation on  
378 domestic livestock, although it might also have the unintended consequence of  
379 increased conflict associated with livestock depredation. Furthermore, concerted  
380 efforts to systematically improve husbandry practices using predator-proof bomas  
381 (Abade, Macdonald & Dickman 2014a), and prevention of human-carnivore conflict,  
382 could lead to a substantial reduction in lion and other large carnivore mortality, and  
383 contribute to conservation of these species in village lands (Weise *et al.*, 2018).  
384 Lastly, efforts to improve food security, diversifying access to protein sources other  
385 than wild prey, and minimizing the potential economic reliance on bushmeat trade by  
386 local villagers could help alleviating unsustainable bushmeat harvesting (van Vliet *et*  
387 *al.* 2016), as well as the ensuing negative effects of prey depletion on lion  
388 conservation.

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

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

601

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

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614 **Table 1.** Covariates predicted to influence lion site use in the Ruaha landscape,

615 southern Tanzania.  $\Psi$ . probability of site use;  $P$ . probability of detection

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

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

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

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

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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



644 **Table 4.** Posterior means, standard deviations, 95% credible intervals (C.I.), and  
 645 Bayesian inclusion parameters ( $w_c$ ) of lion site use models fit to camera trap data from  
 646 the Ruaha landscape, southern Tanzania. Note that  $\beta_1$  is absent since it was associated  
 647 with the reference trail type (animal trail) and was thus set to zero.

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Covariate	Parameter	Mean	SD	95% C.I.	$w_c$
Medium prey	$\alpha_1$	1.8	1.05	0.03, 4.12	0.59
Large prey	$\alpha_2$	3.19	1.11	1.01, 4.90	0.98
Distance to household	$\alpha_3$	2.61	1.84	-2.04, 4.89	0.61
Distance to ranger post	$\alpha_4$	0.97	2.08	-3.38, 4.53	0.41
Vegetation cover	$\alpha_5$	1.16	0.78	-0.08, 3.06	0.39
Distance to surface water	$\alpha_6$	-1.53	1.74	-4.55, 2.15	0.42
Density of humans	$\alpha_7$	-2.18	1.67	-4.86, 0.81	0.38
Mean random intercept	$\alpha_{site}$	-4.77	3.47	-12.35, 1.19	-
Intercept	$\beta_0$	-0.57	1.13	-3.25, 0.75	-
Trail type.N	$\beta_2$	-1.97	0.84	-3.89, -0.61	0.27
Trail type.RD	$\beta_3$	0.28	0.33	-0.37, 0.88	0.27
CTs occupied	$\Psi$	42.24	4.09	37.00, 53.00	-

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