

1 **TITLE:** Habitat use responses of the African leopard in a human disturbed region of rural  
2 Mozambique

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26 **ABSTRACT**

27 Leopard (*Panthera pardus*) populations across Africa are increasingly exposed to high levels of  
28 anthropogenic disturbance, and information on habitat use responses of leopards in human-  
29 disturbed landscapes can help inform status assessments and guide conservation interventions.  
30 Unfortunately, however, few studies have investigated leopard ecology in human-disturbed  
31 landscapes, particularly in Africa. We employed camera-trapping and occupancy modelling to  
32 provide inferences on leopard habitat use in a National Park in Mozambique impacted by  
33 subsistence farming and bushmeat poaching. Replicated detection/non-detection occupancy  
34 surveys were used to estimate site use by leopards in a representative area of the park, and to  
35 investigate relative impacts of environmental, conspecific and anthropogenic factors on leopard  
36 occurrence. The proportion of sites used by leopards was estimated at 0.814 (SE = 0.093), which  
37 is approximately twice the occupancy previously reported for lion (44%) and cheetah (40%) in  
38 the same area. Leopard presence was not strongly predicted by any of the covariates, indicating  
39 there were no strong limiting factors. While leopards generally avoided human settlements and  
40 were positively predicted by prey, results suggest that there was sufficient prey and space for the  
41 species to use most available habitats. The greatest contributing factor to leopard habitat use  
42 was a positive correlation with bushmeat poachers and lions. It is possible that these other  
43 predators provide a more accurate indicator of prey availability than our single-species indicator  
44 based on camera trap data. This study provides important novel information on habitat use by  
45 leopards in a system disturbed by rural human subsistence activities in Africa.

46 **Keywords:** Camera traps; Human disturbance; Bushmeat poaching; Occupancy; *Panthera pardus*

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## 50 INTRODUCTION

51 Leopards (*Panthera pardus*) have disappeared from at least 48% of their historic African range  
52 (Jacobson *et al.*, 2016) and are increasingly patchily distributed in Africa, having been locally  
53 extirpated from areas that have undergone intense habitat conversion or are densely populated  
54 by humans (Hunter *et al.*, 2013). This has resulted in elevated conservation attention, and calls  
55 for more rigorous research to inform conservation and management decisions (Balme *et al.*,  
56 2014). Of further concern, the majority of leopards in Africa currently exist outside of parks and  
57 reserves (Hunter *et al.*, 2013), and current protected areas alone are insufficient in size to ensure  
58 the long-term viability of large carnivore populations (Swanepoel *et al.*, 2013). Improving  
59 knowledge on how leopards respond to human presence is therefore necessary to identify habitat  
60 requirements and limits of tolerance (Athreya *et al.*, 2013; Balme *et al.*, 2014), and to guide  
61 conservation in human-dominated regions (Carter *et al.*, 2015). Presently, however, there have  
62 been few such studies, particularly in Africa (but see Henschel *et al.*, 2011), and the limited  
63 information available indicates that limits of tolerance are highly regionally specific and likely to  
64 change over time (Henschel *et al.*, 2011; Carter *et al.*, 2015). More information is therefore needed  
65 from areas with different sources and levels of impact, to inform conservation planning and  
66 enable an adaptive management approach to the species' conservation.

67 Leopard distribution patterns can also be affected by competition with sympatric large carnivore  
68 species (Vanak *et al.*, 2013; Carter *et al.*, 2015), and understanding inter-species interactions  
69 between predators can be important for effective conservation planning (Linnell and Strand  
70 2000; Carter *et al.*, 2015). In many protected areas in Africa, leopards are at risk of  
71 kleptoparasitism, injury and direct mortality from lions (*Panthera leo*; Nowell and Jackson 1996).  
72 However, while lions can shape leopard habitat use (Maputla *et al.*, 2015), other studies have  
73 found little evidence of spatiotemporal avoidance by leopards (Vanak *et al.*, 2013; Maputla *et al.*,

74 2015), and uncertainty remains on the nature of these intraguild responses, particularly in  
75 human-impacted landscapes.

76 The goal of this study was to provide information on leopard occurrence, and to identify factors  
77 influencing habitat use by leopards, in a disturbed African landscape. Limpopo National Park  
78 (LNP) is a legally protected area in Mozambique that is unusual in being inhabited by both  
79 leopards and lions as well as by humans and free-grazing livestock. LNP borders on the Kruger  
80 National Park (KNP) in South Africa, and is part of the Great Limpopo Transfrontier Park  
81 (GLTP) and the wider Greater Limpopo Transfrontier Conservation Area (GLTFCA) (Fig. 1).  
82 In this context, a greater understanding of leopard ecological requirements can help conservation  
83 practitioners working in a wider matrix of protected areas connected by multiple-use landscapes  
84 (Balme *et al.*, 2007; Athreya *et al.*, 2013).

85 We applied a single-season occupancy modelling framework (MacKenzie *et al.*, 2002) to  
86 replicated detection/non-detection camera trap surveys to investigate site use by leopards across  
87 a 2 500 km<sup>2</sup> study area in LNP. We then used hierarchical ranking of covariates to assess the  
88 relative impacts of environmental, conspecific and anthropogenic variables on leopard site use.

89 FIGURE 1 HERE

## 90 MATERIAL AND METHODS

### 91 *Study area*

92 LNP is a 8,238 km<sup>2</sup> protected area in southern Mozambique, and together with Kruger National  
93 Park (KNP), South Africa, and Gonarezhou National Park, Zimbabwe, forms the Greater  
94 Limpopo Transfrontier Park (GLTP), part of the Greater Limpopo Transfrontier Conservation  
95 Area (GLTFCA), a mosaic of parks and reserves surrounded by areas lacking formal protection  
96 (Fig. 1). At the last published estimate, approximately 6,500 people inhabited eight villages within  
97 the core area of LNP (Fig. 2), and an additional 20,000 people resided in villages along the

98 Limpopo River, the park's eastern boundary (Huggins *et al.*, 2003). Pressures exerted from  
99 humans in the park include extensive free-grazing of livestock (including over 20,000 cattle;  
100 Stephensen, 2010), land clearing for subsistence agriculture, and 'bushmeat poaching' (Everatt *et*  
101 *al.*, 2014). Bushmeat poaching pressure in the park is high, with modelling of poaching activity  
102 suggesting that bushmeat poachers were using circa 80% of LNP in 2013 (Everatt *et al.*, 2014).  
103 Poaching techniques employed in the park include the setting of snares and traps, poisonings,  
104 and the use of bows and firearms. Recent evidence suggests the establishment of large-scale  
105 commercial bushmeat poaching operations in LNP (Everatt and Andresen, unpublished data).

106 The primary habitat in LNP consists of dry open deciduous tree savanna, or 'sandveld', with  
107 deep sandy soils covered predominantly by *Colophospermum mopane* thickets and low open  
108 woodlands, as well as seasonally flooded short-grass depressions ('pans'). Rainfall is distinctly  
109 seasonal, with 95% of the average 500 mm/year of rainfall occurring between November and  
110 April (Stalmans *et al.*, 2004; Cambule *et al.*, 2014). Large mammal populations in LNP were  
111 severely affected during the armed conflicts in Mozambique (1964-1974; 1980-1992; Hanks  
112 2000), and although there is some wildlife recolonisation occurring from neighbouring KNP,  
113 human presence in the park is currently acting as a barrier for the process (Everatt *et al.*, 2014;  
114 Lunstrum 2015). Twenty-two species of ungulate and 18 species of mammalian carnivore occur  
115 in the park, including leopards, lions, cheetahs (*Acinonyx jubatus*), spotted hyaenas (*Crocuta crocuta*)  
116 and wild dogs (*Lycan pictus*) (Andresen *et al.*, 2014).

### 117 ***Occupancy survey design***

118 Occupancy models use replicated detection/non-detection surveys to estimate the probability of  
119 detecting a species ( $p$ ), and derive unbiased probabilities of sites being used by the species ( $\Psi$ )  
120 (MacKenzie *et al.*, 2002). The following assumptions of an occupancy model were initially made:  
121 1) sites are closed to changes in occupancy (i.e. they are either occupied or not *by the species* for  
122 the survey duration); 2) species are not falsely identified; 3) detections are independent; and 4)

123 heterogeneity in occupancy or detection probability are modelled using covariates (MacKenzie *et*  
124 *al.*, 2006). However, given that we employed an approach where the occupancy estimator ( $\Psi$ )  
125 was interpreted as the *probability of site use*, rather than the proportion of area occupied  
126 (MacKenzie *et al.*, 2006), we were able to relax the closure assumption.

127 The camera-trap grid covered approximately one third of LNP (circa 2 500 km<sup>2</sup>). Due to large  
128 portions of LNP not being accessible as a result of very limited infrastructure, most sites were  
129 located in the central third of the park. Nevertheless, sampling occurred across the major  
130 environmental strata of the park, and followed a gradient of the main defining features present in  
131 LNP (including habitats, human settlements, drainage lines, and LNP and KNP boundaries) (Fig.  
132 2). Fifty-five sites were sampled over 12 months (November 1, 2011 - October 31, 2012).

133 FIGURE 2 HERE

#### 134 ***Data collection***

135 Data were collected through temporally-replicated detection/non-detection 7-day camera trap  
136 sampling occasions. A total of 55 stations, each comprised of one digital motion-activated  
137 camera with infra-red flash, were employed across a period of 12 months, from November 2011  
138 to October 2012. Camera stations were moved between sites during the survey period, as a  
139 result of logistical restrictions. Stations were active for a period ranging between 14 to 219 and  
140 days (2 to 30 occasions; mean = 9.9 occasions), and a minimum of 16 stations were deployed at  
141 any one time during the survey period. Unequal sampling across sites is accounted for in the  
142 modelling process (Mackenzie *et al.* 2002). In order to maximise the probability of detecting  
143 carnivores, cameras were placed along game trails, dirt tracks, waterholes and river edges.  
144 Cameras were deployed facing towards the path of movement, and checked regularly for data  
145 and malfunctions.

#### 146 ***Site use covariates***

147 We identified a total of six prey, sympatric competitor, landscape and anthropogenic covariates  
148 to explain heterogeneity in leopard occurrence in LNP (Table 1). For raster-layer based  
149 covariates (i.e. proximity to human settlement, proximity to rivers), values were calculated as the  
150 mean of all 30x30m pixels included in a 1 km<sup>2</sup> area around each camera-trap station, located at  
151 its centre. Following other authors, we considered this a meaningful scale to investigate the effect  
152 of site covariates on habitat selection by a large felid (Sunarto *et al.*, 2012; Everatt *et al.*, 2015;  
153 Tan *et al.*, 2017).

154 Prey resources available to leopards at sites were modelled through the probability of occurrence  
155 of a preferred prey species (*P*) of leopard, impala (*Aepyceros melampus*; Hayward *et al.*, 2006), which  
156 is also the most commonly consumed species in contiguous KNP (Bailey 1993). An impala  
157 occupancy model for LNP was borrowed from Andresen *et al.*, (2014), providing impala site use  
158 probabilities at each site for the same survey period. We assumed this covariate was biologically  
159 representative of the encounter probability of preferred prey for leopards. The influence of lion  
160 occurrence on leopard habitat use was modelled as site-specific probabilities of lion site use (*L*),  
161 which similarly were borrowed from the lion occupancy model of Everatt *et al.*, (2014), and used  
162 as a proxy for probability of leopard encounter with lions. Both impala and lion site use were  
163 modelled as point estimates for each site as a result of site use estimates being available at the  
164 level of the individual station. We reasoned that this would be a suitable way to assess the impact  
165 of their presence on leopard site use at the finer habitat-use scale employed.

166 Anthropogenic pressures that might affect leopard resource use were modelled using two  
167 covariates: proximity to agro-pastoralist settlements (*S*) and probability of bushmeat poaching  
168 (*B*). Settlement location data were extracted from a raster layer (Peace Parks Foundation,  
169 Stellenbosch), and site-specific estimates of proximity were calculated at each spatial scale as the  
170 mean Euclidean distance of each 30x30-m pixel in the 1km<sup>2</sup> area surrounding the camera-trap to  
171 the nearest settlement boundaries, using Spatial Analyst tool in ArcGis 10.2 (ESRI, Redlands,

172 California, U.S.A.). A bushmeat poaching occupancy model developed by Everatt *et al.*, (2014)  
173 provided the probability of poaching at each site.

174 In contiguous KNP, leopards preferentially inhabit perennial river riparian zones, as a result of  
175 higher prey density and stalking cover (Bailey, 1993). A covariate for availability of riparian  
176 habitat ( $R$ ) was therefore included for landscape features that facilitate capture of prey.  
177 Landscape data were extracted from a raster layer (Peace Parks Foundation, Stellenbosch), and  
178 site-specific average estimates of proximity to riparian areas were measured as the mean  
179 Euclidean distance of each 30x30-m pixel in the 1 km<sup>2</sup> area around the camera-trap station to  
180 rivers. Additionally, the effect of habitat type on leopard site use was also investigated. If a  
181 camera station was located in more open habitat (sandveld or alluvial plains) the site was  
182 assigned a value of '1', while if it was situated in thicker, partially closed habitat (mopane  
183 shrubveld, combretum/mopane ruggedveld, Lebombo hills; see Fig. 1) it was assigned a value of  
184 '0'.

### 185 ***Detection probability covariates***

186 Three detection covariates were identified to explain heterogeneity in detection probabilities  
187 between used sites. These were: whether the station was placed on a track, game trail, or  
188 riverbed; camera model; and season. The rationale for the inclusion of these covariates is  
189 reported as supplementary material.

190 TABLE 1 HERE

### 191 ***Occupancy analyses***

192 Maximum likelihood estimates for leopard detection probability ( $p$ ) and site use ( $\Psi$ ) were  
193 obtained using the single-season option in programme PRESENCE v9.3 (Hines, 2006).  
194 Following data collection, a single detection matrix was obtained by compiling detection histories  
195 of each sampled site ( $n= 55$ ), assigning a '1' for sampling occasions where leopards were detected



196 and a '0' if they were not. A two-step process was then followed. First,  $p$  was modelled using the  
197 most parametrised covariate model, to compare candidate detection models and identify that  
198 which better explained heterogeneity in detection probability (MacKenzie *et al.*, 2006; Karanth *et*  
199 *al.*, 2011). Following this, site use probability ( $\Psi$ ) was modelled by fixing the previously identified  
200 best detection model, and varying all possible combinations of site use covariates. Continuous  
201 covariates were standardised on a z-scale, and all covariates were tested for collinearity using  
202 Pearson's correlation test and not included in the same model if  $r > 0.6$  (Green, 1979). Models  
203 were ranked based on their Akaike Information Criterion (AIC), adjusted for small samples sizes  
204 (AICc; MacKenzie, 2006), and were considered to be strongly supported if they had a  $\Delta\text{AICc}$  of  
205  $< 2$ . Models that did not reach numerical convergence were excluded and not considered. In the  
206 event of no single model possessing an AICc weight of over 0.95, a final candidate set of all  
207 modes with  $\Delta\text{AICc} < 7$ , whose combined weights surpassed 0.95 (95% confidence set), was  
208 retained. The importance of individual variables in explaining heterogeneity in leopard  
209 occurrence was determined by the summed weights of models containing the variables  
210 (Mackenzie and Royle, 2005), while the sign of the untransformed  $\beta$ -coefficients of each  
211 covariate represented the direction of influence of the covariate (*i.e.* positive or negative).  
212 Average  $\beta$ -coefficient estimates ( $\bar{\beta}$ ) were obtained for each covariate by averaging values (with  
213 shrinkage) across all models within the final 95% candidate set, based on their relative weights.  
214 Covariates were deemed to have a robust impact if the  $\beta$ -coefficient  $\pm 1.96 \times \text{SE}$  did not include  
215 zero (MacKenzie and Bailey, 2004). Site-specific and overall estimates of  $\Psi$  and  $p$  were obtained  
216 by averaging values (with shrinkage) across models within the 95% confidence set, based on their  
217 relative weights. Goodness of fit was assessed through 10,000 bootstrap samples and Pearson's  
218 chi-squared tests for the most parametrised model (MacKenzie and Bailey, 2004).

## 219 **RESULTS**

220 A survey effort of 3932 camera-trap nights at 55 camera stations resulted in 161 leopard  
221 photographic events. Pooling these data into seven-day sampling occasions resulted in a  
222 combined total of 546 occasions at 55 sites (average: 9.9 occasions per site).

### 223 *Leopard occurrence and habitat use*

224 The model-averaged probability of detecting leopards given presence at a site was  $\hat{p} = 0.264$  (SE  
225 = 0.034). When accounting for detectability, the model averaged ( $\Sigma w > 95\%$ ) probability of site  
226 use was  $\hat{\Psi} = 0.814$  (SE = 0.093), meaning leopards were estimated to use circa 81% of the  
227 sampled sites. This estimate is circa 21% higher than the naïve site use estimate (0.600) that does  
228 not account for detection error. Detection covariates ‘track’ and ‘camera-trap model’ emerged  
229 with strong support when ranking detection models (complete ranking available as  
230 supplementary material). When ranking different combinations of site covariates, there was no  
231 covariate that could better explain leopard habitat use than the constant model, which received  
232 strong support ( $\Delta AICc = 0.00$ ; Table 2). The covariate most strongly correlated with leopard  
233 habitat use was lion occurrence ( $\Sigma w = 0.35$ ), followed by probability of bushmeat poaching  
234 ( $\Sigma w = 0.28$ ) and probability of impala site use ( $\Sigma w = 0.18$ ) (Table 3). Averaged  $\beta$ -coefficient  
235 estimates showed that leopard habitat use was generally positively associated with lion, as well as  
236 bushmeat and preferred prey (impala) probability of site use. Leopard habitat use was generally  
237 negatively associated with proximity to human settlements, and also generally positively  
238 associated with average proximity of the site to riparian habitat, and the site being in a partially  
239 closed rather than open habitat (Table 3). However, none of these site covariates had a robust  
240 impact on leopard habitat use. There was no evidence of lack of fit ( $P = 0.43$ ) or  
241 overdispersion ( $\hat{c} = 0.71$ ).

242 TABLE 2 HERE

243 TABLE 3 HERE

244 **DISCUSSION**

245 *Leopard occurrence and habitat use in Limpopo National Park*

246 Information on status and habitat use responses is necessary for informed evidence-based  
247 management, and for assessing the success of conservation initiatives (Gray and Prum, 2012).  
248 We used camera-trapping and occupancy modelling to provide inferences on the occurrence and  
249 habitat use of leopards in an anthropogenically disturbed African landscape, where a dominant  
250 competitor, the lion, is also present.

251 Our results reveal that occurrence and habitat use by leopards in LNP were not strongly  
252 predicted by any of the environmental, conspecific or anthropogenic covariates tested, with the  
253 constant model emerging with strong support. This corroborates findings by leopard habitat use  
254 studies in Asia, which indicated a similar lack of limiting factors (Steinmetz *et al.*, 2013; Athreya *et*  
255 *al.*, 2015; Carter *et al.*, 2015). Together with the relatively high estimate of proportion of sites  
256 used by leopards (81%), the results suggest there was sufficient prey and space available for  
257 leopards to use most available habitats in the study area.

258 Although no covariate had a robust impact on leopard space use, there was some support for  
259 positive associations with bushmeat hunting activity and lion site use. These positive associations  
260 between leopards and lions and bushmeat poachers could be indicating that these three  
261 predators are active in less-depleted areas of the park where their respective prey species remain  
262 most available. Marker and Dickman (2005) and Henschel *et al.* (2011) observed that poachers  
263 and leopards had overlapping dietary niches and hunted in similar areas, and in West-Central  
264 Africa Toni and Lodé (2013) found more evidence of leopard presence in poached areas.  
265 Poachers in LNP target medium-sized antelopes such as those in the preferred prey range of  
266 leopards, in accessible prey-rich habitats (Andresen and Everatt, unpublished data), and it is  
267 therefore possible that both are selecting for similar prey-rich locations. Moreover, the higher  
268 suitability of riparian habitats to both hunting by leopards and snaring by poachers could be a

269 further driver of this observed association, and it is possible that presence of snared carcasses  
270 from bushmeat poachers, and the associated scavenging opportunities, are also influencing  
271 leopard habitat use decisions.

272 We also found no indication of interspecific spatial exclusion between lions and leopards in  
273 LNP. On the contrary, the observed positive associations (Tables 2, 3) again suggest that both  
274 species could be selecting for less depleted patches, where their respective prey species remain  
275 more numerous. Contrasting results have been obtained regarding the effect of lions on leopard  
276 space use (Vanak *et al.*, 2013; du Preez *et al.*, 2015; Maputla *et al.*, 2015), and our study  
277 strengthens the hypothesis that spatial relationships between the two carnivores are context  
278 dependent. Density of the dominant competitor has been indicated as the strongest factor  
279 influencing the impact on a subordinate (Creel, Spong and Creel 2001), and the relatively low  
280 lion density in the park (0.99 lions per 100 km<sup>2</sup>; Everatt *et al.*, 2014) likely facilitates this  
281 coexistence (Creel *et al.*, 2001). In addition, the adaptability of leopards, in terms of both diet and  
282 behaviour (Karanth and Sunquist, 2000; Mills and Biggs, 1993), likely plays a role in enabling  
283 them to successfully compete for resources in areas of LNP where they overlap spatially with  
284 lions. Indeed, Everatt *et al.* (2014) showed that lion presence in LNP was strongly predicted by  
285 African buffalo presence (*Syncerus caffer*), suggesting that the observed lack of spatial separation is  
286 facilitated by hunting different prey, and Maputla *et al.* (2015) also identified diet partitioning as a  
287 potential factor in facilitating this coexistence in contiguous Kruger NP.

288 There was also a positive relationship between leopards and impala site use, suggesting that  
289 leopards could be making space use decisions based on impala presence. However, this  
290 relationship was not robust. Leopards have a wide dietary breadth (Hayward *et al.*, 2006; Owen-  
291 Smith and Mills, 2008; Hunter *et al.*, 2013), including the common duiker (*Sylvicapra grimmia*),  
292 another preferred leopard prey with broad habitat requirements and able to exist close to  
293 settlements in LNP (Andresen and Everatt, unpublished data; Estes, 1991; Hayward *et al.*, 2006).

294 In addition to enabling leopards to occur in relatively close proximity to human settlements, this  
295 likely also resulted in limiting the effect of impala site use on leopard habitat use decisions.  
296 Rather, it is possible that the positive associations observed between predators (including  
297 bushmeat poachers) are masking the effect of other prey species on leopard habitat use, with  
298 other predators acting as a proxy for overall leopard prey availability that was not accounted for  
299 in our prey model.

300 Results also reveal that leopards possess a higher tolerance of human presence than two  
301 sympatric predators in the park, lion and cheetah. Leopards were estimated to use circa twice the  
302 sites as either species in the sampled portion of LNP (leopards: 81%, *this study*; lions: 44%,  
303 Everatt *et al.*, 2014; cheetah: 40%, Andresen *et al.*, 2014). While leopards generally avoided  
304 coming into close proximity of agro-pastoralist settlements (no photographs of leopards were  
305 recorded by cameras located <5 km from village edge), beyond this distance villages had a  
306 negligible effect on site use. On the other hand, a robust negative correlation with settlements  
307 was the greatest predictor for both lions and cheetah. Additionally, while Everatt *et al.* (2015)  
308 found that lions strongly avoided sites with high probability of bushmeat poaching, our results  
309 indicate that leopards were associated with these areas. Our study thus reveals a greater level of  
310 adaptability by leopards than lions and cheetahs to human settlements and incidences of  
311 bushmeat poaching.

312 As pointed out by others (Tan *et al.*, 2017) one caveat of applying occupancy modelling to  
313 camera trap survey data is that detections occur at a point-scale (camera trap stations), while  
314 raster covariates (proximity to settlements and rivers) are measured at a different scale (the 1 km<sup>2</sup>  
315 area around each station). It is also important to point out that our results are relevant to the  
316 spatial scale used in the study (i.e. the 1 km<sup>2</sup> area around the stations), and the inferred  
317 relationships might differ at other spatial scales.

318 ***Conservation implications and recommendations***

319 Our findings show that leopards can persist in an African landscape impacted by subsistence  
320 agriculture, livestock and high incidences of bushmeat poaching, provided sufficient prey is  
321 available. The study provides support for the possibility of conserving the species in human-  
322 modified landscapes, as has already been suggested by others (e.g. Athreya *et al.*, 2013). Our  
323 results are particularly relevant in the context of conservation planning for leopards in the  
324 GLTFCA. Although landscape permeability between the protected areas in the GLTFCA is  
325 limited by growing human presence and disturbances in the non-protected areas (Andresen and  
326 Everatt, unpublished data), the ability of leopards to persist in human-impacted landscapes in the  
327 region suggests that the species could potentially maintain a connected meta-population across  
328 the wider GLTFCA.

329 Nevertheless, the fact that leopards regularly use the same areas as bushmeat poachers is of  
330 concern, given the high prevalence of wire snares in these areas, to which the species has been  
331 shown to be susceptible (Jacobson *et al.*, 2016). Furthermore, baited traps targeting carnivores  
332 have also been recorded (Andresen and Everatt, unpublished data). As a result, we believe that  
333 poaching could potentially be a concern for leopards in LNP, and requires further attention in  
334 the form of more data on impacts on this population. Future research should also include  
335 surveys among the human communities residing on the eastern border of LNP, to determine  
336 current levels of human-carnivore conflict in these areas, and whether these could be acting as  
337 attractive population sinks (Delibes *et al.*, 2001) for leopards dispersing from less impacted  
338 regions of the park. We also recommend large carnivore occupancy surveys in LNP every 4  
339 years, to monitor changes in leopard and other large carnivore presence and habitat use, as well  
340 as potential fluctuations in prey base and poaching intensity.

341 Finally, our findings provided further evidence for the context-dependency of habitat use and  
342 tolerance to human pressures exhibited by generalist species such as the leopard. Further studies  
343 investigating leopard spatial requirements and tolerance limits, in areas with a range of sources

344 and levels of impact, are needed to inform conservation planning in the rapidly changing African  
345 landscape, and will be key in allowing for an adaptive approach to the species' management  
346 (Marker and Dickman, 2005; Balme *et al.*, 2014).

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508 **FIGURE CAPTIONS**

509 **Fig. 1** Limpopo National Park in the context of the Greater Limpopo Transfrontier

510 Conservation Area (GLTFCA), comprising the Great Limpopo Transfrontier Park (GLTP; dark

511 grey) and other protected areas (lighter grey) surrounded by non-protected lands

512 **Fig. 2** Five-month home-range scale survey design in LNP. Surveyed sites (50 km<sup>2</sup> grid cells) are

513 overlaid over gradients of habitats and proximity to settlements. Inset map: LNP in relation to

514 other areas in the wider GLTFCA.

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529 **FIGURES**

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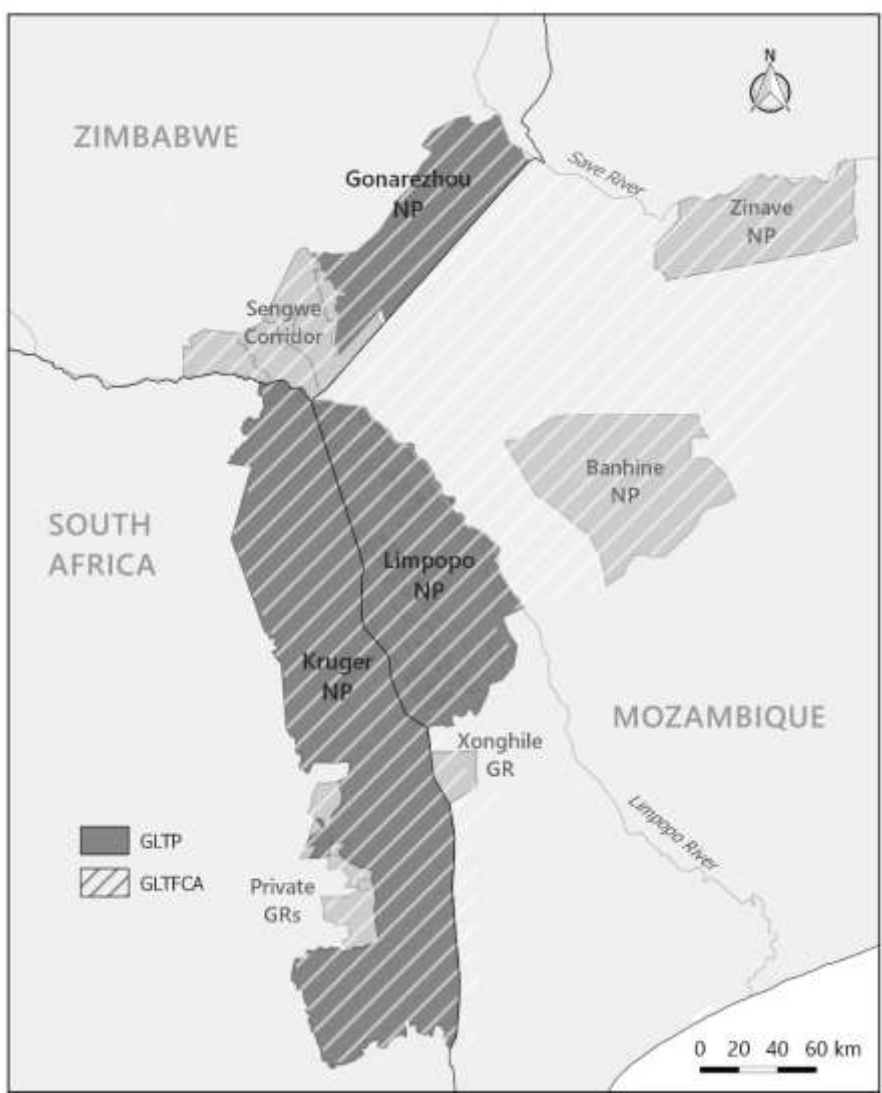
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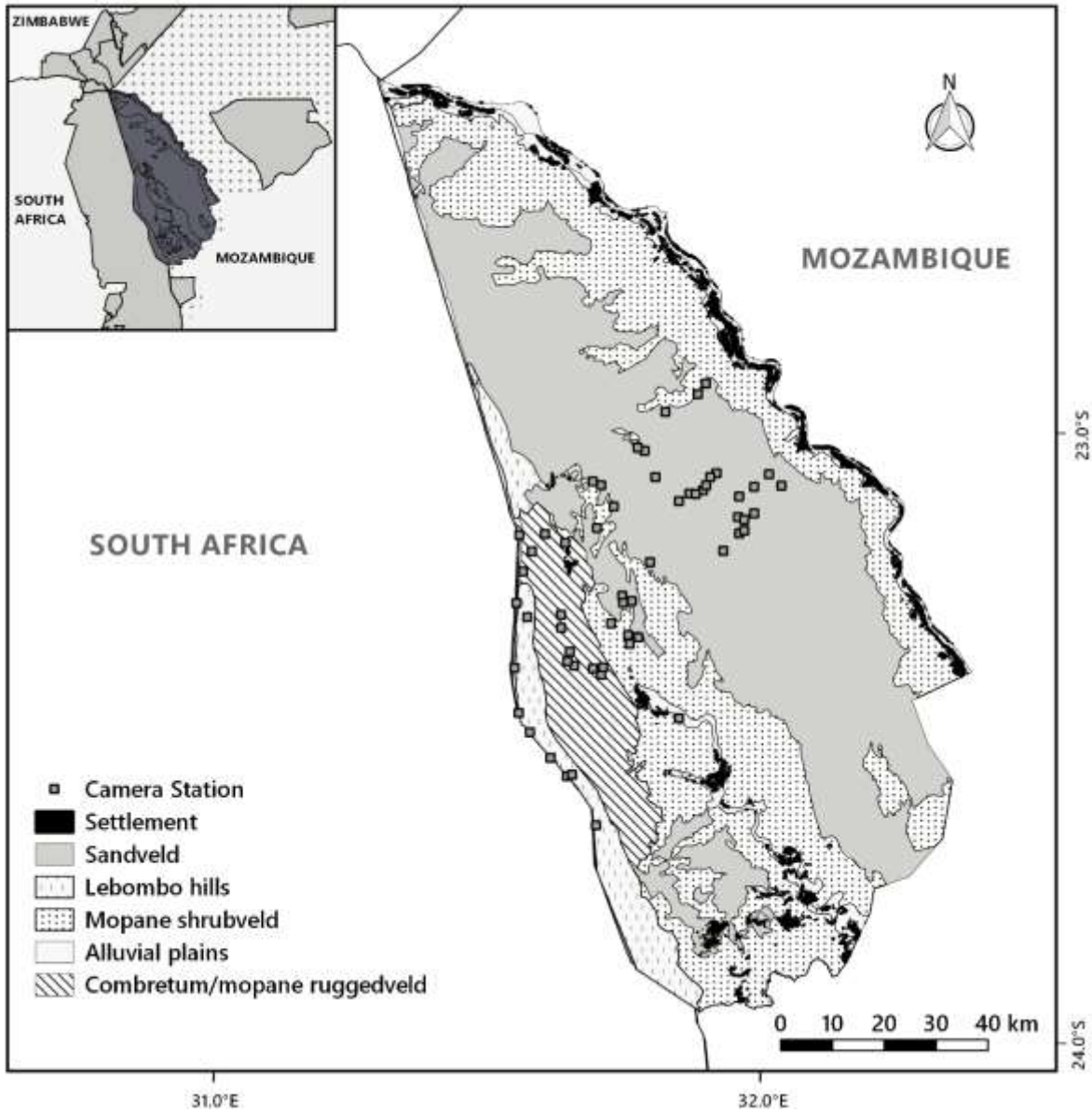
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Table 1 Site covariates Predictor variables expected to influence leopard site use, their relationship to leopard occurrence, and sampling range of values

Covariate (unit)	Key	Relationship to leopard occurrence	Sampling range (mean)
Preferred prey (PSU)	P	Availability of food resources	0.08 – 0.90 (0.45)
Bushmeat poaching (PSU)	B	Competition for prey, targeted/accidental snaring	0.07 – 0.99 (0.7)
Agro-pastoralist settlement (mean site proximity, km)	S	Persecution, loss of hunting cover	0.94 – 22.60 (11.60)
Riparian area (mean site proximity, km)	R	Landscape feature facilitating prey capture	0.17 – 5.58 (1.00)
Lion (PSU)	L	Competition for prey, predation	0.01 – 0.83 (0.47)
Habitat type (open vs. partially closed)	H	Potential preference for thicker habitat (hunting cover, protection)	1 (open), 0 (partially closed)

Table 2 Model selection for leopard site use ( $\Psi$ ). Final confidence set. Includes models for which  $\Sigma w > 0.95$ , plus the null model. Covariate key: probability of lion occurrence (L); probability of bushmeat poaching (B); proximity to agro-pastoralist settlements (S); probability of preferred prey (impala) occurrence (P); proximity to riparian habitat (R); habitat openness (H); camera-trap on track or riverbed (T); camera-trap model (C).

Models	AICc	$\Delta$ AICc	$W_i$	K	-2log
$\Psi$ (.), p(C,T)	463.01	0.00	0.16	4	454.21
$\Psi$ (L,B), p(C,T)	463.17	0.16	0.15	6	449.42
$\Psi$ (L), p(C,T)	463.75	0.74	0.11	5	452.53
$\Psi$ (P), p(C,T)	464.49	1.48	0.08	5	453.27
$\Psi$ (B), p(C,T)	464.82	1.81	0.07	5	453.60
$\Psi$ (R), p(C,T)	464.91	1.90	0.06	5	453.69
$\Psi$ (S), p(C,T)	465.39	2.38	0.05	5	454.17
$\Psi$ (L,R), p(C,T)	465.43	2.42	0.03	6	451.68
$\Psi$ (H), p(C,T)	465.43	2.42	0.05	5	454.21
$\Psi$ (L,H), p(C,T)	466.12	3.11	0.03	6	452.37
$\Psi$ (L,P), p(C,T)	466.15	3.14	0.03	6	452.40
$\Psi$ (P,R), p(C,T)	466.46	3.45	0.03	6	452.71
$\Psi$ (B,P), p(C,T)	466.58	3.57	0.02	6	452.83
$\Psi$ (P,H), p(C,T)	466.96	3.95	0.02	6	453.21
$\Psi$ (B,R), p(C,T)	467.14	4.13	0.02	6	453.39
$\Psi$ (B,S), p(C,T)	467.28	4.27	0.02	6	453.53
$\Psi$ (.), p(.)	483.38	20.37	0.00	2	479.15

$\Delta$ AICc = Difference between model AICc and that of model with the lowest AICc;  $W_i$  = relative model weight; k = number of parameters in the model; -2 log = twice the negative likelihood; (.) signifies constant parameter

Table 3 Relative summed model weights ( $\Sigma w$ ) and average  $\beta$ -coefficient estimates ( $\hat{\beta}$ ), with associated standard errors, of each covariate explaining leopard site use ( $\Psi$ ). Only models retained in the final confidence set ( $\Sigma w > 0.95$ ) were considered.

Site covariate	$\Sigma w$ (%)	$\hat{\beta}(SE_{\hat{\beta}})$
Lion	0.35	0.77 (0.49)
Bushmeat poaching	0.28	0.57 (0.45)
Preferred prey (impala)	0.18	0.42 (0.46)
Riparian habitat	0.14	0.33 (0.41)
Habitat openness	0.10	-0.05 (0.84)
Settlements	0.07	- 0.11 (0.46)

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564 SUPPLEMENTARY MATERIAL

565 Appendix I - Rationale for detection covariate choice

<b>Table A1</b> Rationale for detection covariate choice	
<b>Covariate</b>	<b>Rationale</b>
Station on track or riverbed	Considering that leopards use landscape features that facilitate movement when travelling (Hunter <i>et al.</i> , 2013), it was expected that cameras placed on roads, trails or riverbeds would have a higher probability of detecting an individual, given presence at a site. Sites where the camera station was located on a track, large game trail or riverbed were assigned a '1', while other stations a '0'.
Camera trap model	Two models were employed throughout the 5 month home-range scale study (Reconyx HC500 Wisconsin, USA, and Bushnell Trophy Cam Beijing, China), and each station received a '1' or '0' depending on the model used, respectively. During data collection for the 12-month study, Spy Point Tiny-W2 (Quebec, Canada) cameras were also active. Given the comparatively longer trigger and recovery times ( <a href="http://www.trailcampro.com/trailcamerareviews.aspx">http://www.trailcampro.com/trailcamerareviews.aspx</a> ), stations that employed Spy Point cameras were assigned a '0', while those that employed Reconyx and Bushnell cameras were pooled together and assigned a '1'.
Season	Variability in leopard detectability that might arise due to the effect of season was accounted for in the 12-month survey by assigning a '1' to wet season (November-April) occasions and a '0' to dry season (May-October) occasions.

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**Table A2** Model selection procedure for ranking of detection covariates. Covariate key: prob. of lion occurrence (L); prob. of bushmeat poaching (B); proximity to agro-pastoralist settlements (S); probability of preferred prey (impala) occurrence (P); proximity to riparian habitat (R); habitat openness (H); camera station on track or riverbed (T); camera-trap model (C); season, wet/dry (S)

Models	AICc	ΔAICc	W <sub>i</sub>	K	-2log
Ψ (L,B,P,S,R,H), p(C,T)	470.35	0.00	0.48	10	445.35
Ψ (L,B,P,S,R,H), p(T)	471.32	0.97	0.30	9	449.32
Ψ (L,B,P,S,R,H), p(C,T,S)	472.72	2.37	0.15	11	444.58
Ψ (L,B,P,S,R,H), p(T,S)	474.11	3.76	0.07	10	449.11
Ψ (L,B,P,S,R,H), p(S)	489.05	18.70	0.00	9	467.05
Ψ (L,B,P,S,R,H), p(.)	489.06	18.71	0.00	8	469.93
Ψ (L,B,P,S,R,H), p(C,S)	489.10	18.75	0.00	10	464.10
Ψ (L,B,P,S,R,H), p(C)	490.14	19.79	0.00	9	468.14

ΔAICc = Difference between model AICc and that of model with the lowest AICc; W<sub>i</sub> = relative model weight; k = number of parameters in the model; -2 log = twice the negative likelihood; (.) signifies constant parameter

571 **Appendix II – Hierarchical ranking of detection covariates**

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578 **Appendix III - Final candidate model sets (Σw>95%), and model-specific β-coefficients**

579 **(and associated standard error estimates) for covariates determining leopard site use (Ψ)**

**Table A3** Final candidate model sets (Σw>95%), and model-specific β-coefficients (and associated standard error estimates) for covariates determining leopard site use (Ψ)

Models	$\hat{\beta}_0(SE[\hat{\beta}_0])$	$\hat{\beta}_S(SE[\hat{\beta}_S])$	$\hat{\beta}_B(SE[\hat{\beta}_B])$	$\hat{\beta}_P(SE[\hat{\beta}_P])$	$\hat{\beta}_L(SE[\hat{\beta}_L])$	$\hat{\beta}_R(SE[\hat{\beta}_R])$	$\hat{\beta}_H(SE[\hat{\beta}_H])$
Ψ (.), p(C,T)	1.30 (0.48)	-	-	-	-	-	-
Ψ (L,B), p(C,T)	1.59 (0.64)	-	0.85 (0.52)	-	1.10 (0.58)	-	-
Ψ (L), p(C,T)	1.27 (0.46)	-	-	-	0.54 (0.41)	-	-
Ψ (P), p(C,T)	1.22 (0.47)	-	-	0.45 (0.45)	-	-	-
Ψ (B), p(C,T)	1.43 (0.58)	-	0.28 (0.36)	-	-	-	-
Ψ (R), p(C,T)	1.30 (0.47)	-	-	-	-	0.31 (0.41)	-
Ψ (S), p(C,T)	1.29 (0.49)	-0.09 (0.46)	-	-	-	-	-
Ψ (L,R), p(C,T)	1.30 (0.47)	-	-	-	0.60 (0.42)	0.41 (0.41)	-
Ψ (H), p(C,T)	1.31 (0.64)	-	-	-	-	-	-0.02 (0.92)
Ψ (L,H), p(C,T)	1.46 (0.70)	-	-	-	0.61 (0.46)	-	-0.37 (0.93)

$\Psi(L,P), p(C,T)$	1.22 (0.47)	-	-	0.19 (0.52)	0.45 (0.48)	-	-
$\Psi(P,R), p(C,T)$	1.21 (0.47)	-	-	0.47 (0.46)	-	0.33 (0.40)	-
$\Psi(B,P), p(C,T)$	1.32 (0.54)	-	0.24 (0.35)	0.45 (0.49)	-	-	-
$\Psi(P,H), p(C,T)$	1.31 (0.62)	-	-	0.47 (0.45)	-	-	-0.23 (0.89)
$\Psi(B,R), p(C,T)$	1.37 (0.53)	-	0.20 (0.38)	-	-	0.24 (0.47)	-
$\Psi(B,S), p(C,T)$	1.41 (0.57)	-0.13 (0.49)	0.29 (0.36)	-	-	-	-
$\Psi(., p(.))$	1.00 (0.39)	-	-	-	-	-	-

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