

**Environmental and anthropogenic drivers of African leopard *Panthera pardus*  
population density**

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## Abstract

Globally three quarters of large terrestrial mammalian predators are in decline and many populations are data deficient, including those of African leopards across much of their range. Here we assess the drivers of decline African leopard populations in 16 camera trap surveys covering a total area of 15 120 km<sup>2</sup>, across a gradient of anthropogenic impact, management and geography, in protected areas across the Zimbabwean component of the Kavango-Zambezi (KAZA) Transfrontier Conservation Area. Population density was calculated using spatially explicit mark-recapture estimators and Generalised Additive Models (GAM) were used to assess factors affecting population density. Density estimates ranged from 0.7 to 12.2 (mean  $2.9 \pm 2.7$ ) leopards/100km<sup>2</sup>. Leopard density was higher in wooded sites and rugged terrain but negatively affected by human factors including human appropriation of net primary productivity (HANPP), trophy hunting risk and bush-meat poaching. High lion densities (>6.0 lions/ 100km<sup>2</sup>) negatively affected leopard density. Annual rainfall over a gradient of ~ 300mm across survey sites was not influential in predicting population density.

Previous assessments of the drivers of declining leopard population density (CITES 1988), asserting that leopard densities can be predicted by annual rainfall and are unaffected by human disturbance in unmodified habitat are not supported by our findings. We recommend that the 1988 assessment, used to manage CITES leopard trophy hunting export quotas since the late 1980s, should be reviewed.

**Keywords:** African leopard, *Panthera pardus*, CITES, threats, trophy hunting

## 1. Introduction

Populations of large terrestrial carnivores are in decline (Estes et al. 2011; Ripple et al. 2014). Small population sizes, slow reproductive rates, requirements for extensive space, reliance on viable prey populations as well as their capacity to come into conflict with people make them particularly vulnerable to extirpation (Cardillo et al. 2004; Wolf and Ripple 2016). To halt and reverse declines there is an urgent need to better understand the biological and behavioural traits and habitat requirements that contribute to species vulnerability or resilience to human impact.

Globally, leopards are classed as Vulnerable by the IUCN and populations are declining (Stein et al. 2020) and now occupy only around 25% of the species' historical range (Jacobson et al. 2016). Of the eight Eurasian, Middle Eastern and Asian subspecies three are considered Critically Endangered (*P. pardus nimr*, *orientalis* and *melas*) and two endangered (*P. pardus saxicolor* and *kotiya*) (Jacobson et al. 2016; Rostro-García et al. 2016). Until recently, assessments of leopard conservation status in sub-Saharan Africa (*P. pardus pardus*) have considered populations to be relatively robust (Martin and de Meulenaer 1988). Nevertheless there is increasing evidence that African leopard populations are impacted by habitat conversion and prey depletion (Rosenblatt et al. 2016), poorly managed trophy hunting (Balme et al. 2012) and poaching for body parts and skins (Stein et al. 2020).

The leopard's transboundary distribution has also been recognized by the Convention on Conservation of Migratory Species of Wild Animals (CMS 2017), Appendix II, requiring coordinated conservation measures to be implemented by range states. They are listed on the Convention for the International Trade in Endangered Species (CITES) Appendix I, with only limited trade in hunting trophies of *P. pardus pardus* permitted, regulated by quotas for individual African range states. Current CITES leopard export quotas have been largely derived from estimates of sustainable hunting quotas based upon a the 1988 CITES assessment of continent wide leopard populations (Martin and de Meulenaer 1988).

Population estimates used in this assessment relied heavily on the assumption that leopard population density is closely correlated with rainfall and habitat type and utilisation models assumed that leopards occurred at maximum densities in unaltered habitat regardless of human activities. Despite being widely criticized (Bailey 1993; Jackson 1989; Norton 1990) the recommendations of this population assessment were largely adopted following

proposals at the 6th CITES Conference of Parties (CoP, CITES 1987) and were most recently reviewed at the 17<sup>th</sup> CoP (CITES 2016) and ratified at the 18<sup>th</sup> CITES CoP (Trouwborst et al. 2020).

Population estimates establishing baselines to inform management policy and against which to assess species status or recovery is often a prerequisite for successful conservation management and any utilization. However, robust population data for many carnivore species is often lacking because they are wide-ranging, elusive and occur at low densities making them challenging and costly to count (Karanth et al. 2010). Assessments of leopard population status have been hampered by limited range wide data (Jacobson et al. 2016). Although they are one of the most widely distributed Felids, studies of the species have a heavily geographic bias with half of all peer reviewed publications between 1982 and 2012 from five sub-Saharan African countries (South Africa, Namibia, Botswana, Kenya and Tanzania), with over half of these from South Africa (Balme et al. 2014). Published data from leopard populations from other parts of sub-Saharan Africa are more limited and this lack of evidence-based research greatly restricts evaluation of conservation status in the remainder of the species range.

In order to determine the salient predictors of African leopard population density, we surveyed, using camera trap surveys, 16 sites in Zimbabwe, falling largely within the Kavango Zambezi (KAZA) Transfrontier Conservation Area, a 520,000km<sup>2</sup> transboundary conservation area spanning Angola, Botswana, Namibia, Zambia and Zimbabwe. These sites were representative of a gradient of potential anthropogenic and environmental drivers of abundance in protected areas across African wooded savannah ecosystems. By understanding the drivers of leopard population density we aimed to identify threats that could impact the future conservation status of the species in protected wooded savannah ecosystems in central southern Africa.

## **2. Methods**

### **2.1. Study area**

To allow evaluation of the potential drivers of leopard population density, we surveyed 16 study sites in the northern and western of Zimbabwe (Figure S1), with variable levels of

protection (strict protection to consumptive utilisation), and a gradation of geographic and anthropogenic circumstances. Survey sites covered four national parks (strictly protected), two forest areas (forest product extraction and managed trophy hunting) and three safari hunting areas (managed trophy hunting). Annual trophy hunting quotas are allocated to areas where commercial utilisation is permitted (Safari Areas, Forest land, Communal and Private land). Zimbabwe has an annual CITES export quota of 500 leopards. However, between 1990 and 2018 this quota has never been met with only  $53 \pm 15\%$  (s.d.) of the annual quota exported (CITES 2020; Lindsey and Chikerema-Mandisodza 2012). Apart from Mana Pools National Park all survey areas fall within KAZA.

## **2.2. Camera trap survey**

Surveys of individually identifiable species from camera trap surveys, coupled with spatially explicit mark-recapture statistical methods have been shown to provide robust population density estimates (Balme et al. 2009a; Gopalaswamy et al. 2012). In this study a total of 797 camera trap stations were deployed across 16 survey sites between 2013 and 2019, covering a total of  $\sim 27,266 \text{ km}^2$  (Figure S1, Table S1). Each survey consisted of a mean of 44 (range 35-73) camera trap stations, with stations spaced in a predetermined grid approximately 4-5 km apart set, where possible, on trails and roads to optimise detection of large carnivores (duPreez et al. 2014). Each station consisted of paired trail cameras (white flash: Cuddeback models 1125, 1149 and C1, Non-Typical, WI, USA; Panthera V4, Panthera, NY, USA; black-flash: Stealthcam G42NG, Grand Prairie, TX, USA, used only in 2015 and 2016, making up  $\sim 20\%$  of camera units and were paired with white flash units where possible). For logistical reasons and to ensure between site comparability, surveys were undertaken during the dry season each year (April- early November) and deployed for a mean of  $48 (\pm 14 \text{ s.d.})$  trap nights. Camera batteries and memory cards were checked regularly throughout the survey and replaced when required. Images were downloaded, catalogued and archived at the end of each survey.

## **2.3. Density estimates**

### **2.3.1. Individual identification**

Images of the three most detected large carnivores (lion *Panthera leo*, spotted hyaena *Crocuta crocuta*, leopard) were extracted from the database. We considered each 24 hour period (12pm -12pm) as a sampling occasion, consecutive images of the same individual at the same location within the 24 hour period were defined as a single capture event. Animals were individually identified based on pelage patterns, whisker spots, unique scars and other physical features (Miththapala et al. 1989; Pennycuik and Rudnai 1970). Strampelli et al. (2022) have recently demonstrated the practicality of identifying lions from camera trap images. Images that could not be confidently identified (blurred, partial images) were discarded, although in practice most images could be assigned an individual ID (Table S4). Based on size and pelage characteristics, animals estimated to be dependent juveniles (leopard < 1year, hyaena <1 year, lion <2 years) were not included in analysis because of low recapture probabilities of juveniles (Karanth and Nichols 2002) and because high variability in juvenile recruitment and survival (Barthold et al. 2016) between years and sites can confound comparisons between surveys. For each survey, animal ID, trap location (detector number) and date were recorded in a matrix for analysis using spatially explicit mark-recapture software.

### 2.3.2. SPACECAP and secr validation

We used two spatially explicit population density models, using maximum likelihood-based inference implemented in the R package 'secr' (Efford 2017; Efford and Fewster 2013) and Bayesian inference implemented in the R package 'SPACECAP' (Gopalaswamy et al. 2012). At each survey site, a state-space mask was created to represent the available habitat for leopards with buffer distances (Table S1) calculated with the 'suggest buffer' function corresponding to  $4 \times \sigma$  (Efford, 2017). The number of iterations for all surveys was 60,000 and burn-in was increased for each survey to achieve model convergence up to a maximum of a ¼ of the number of iterations (15 000). For all datasets, data augmentation was five times the number of individuals identified. All site-specific models were tested with and without trap response and models were ranked based on their Akaike's Information Criterion (AIC; (Burnham and Anderson 2002)) and null model estimates from both maximum likelihood and Bayesian inference approaches compared. To evaluate the precision of density estimates we calculated the half relative confidence interval width

(HRCIW) (Dröge et al. 2020) providing a measure of the magnitude of population change that must occur for it to be detectable in subsequent surveys. Density surfaces were generated from SPACECAP for each survey site. Leopard density estimates were compared with those predicted by Martin and de Meulenaer (1988) for each survey site (see Supplementary material for methods).

## **2.3. Multi-scale modelling of the determinants of leopard density**

### **2.3.1 Model selection and evaluation**

A total of 14 covariates were selected *a priori* to identify the drivers of leopard density across the different sites (Table S2) and together with the SPACECAP density were extracted from each co-variate data layer at each of the 796 camera trap stations. To assess multi-scale relationships and identify the spatial scale at which both habitat and anthropogenic factors had the strongest effect on leopards densities (McGarigal et al. 2016) we transformed each continuous variable into six multi-scale covariates, using a moving window analysis with the focal statistic tool in ArcGIS (ESRI, window radius = 1 km, 5 km, 10 km, 15 km and 20km). Variables extracted from radii at each spatial scale surrounding each camera station were used to calculate the focal mean of all continuous predictors. For each covariate the optimal spatial scale for drivers of leopard densities was identified by the best fit (wAIC) from the competing univariate models (McGarigal et al. 2016). Finally, all environmental variables, at the most appropriate spatial scale, were standardised (mean-centred and divided by the standard deviation) before inclusion in the models.

Each covariate was inspected for significance using the log-likelihood ratio test of its univariate model. The retained set of covariates was then inspected for collinearity with a Pearson pairwise correlation matrix and the threshold of  $|r| \geq 0.7$  used to eliminate correlated predictors, using the wAIC of the univariate models to identify which variable to exclude from each pair of correlated variables. The remaining set of non-correlated and scale optimised predictors were then included in a Generalised Additive Model (GAM, with quasi-Poisson link, using the 'mgcv package in R, (Wood 2006), to describe the spatial variability in leopard density. This global model was inspected for spatial autocorrelation using a Global Moran I for regression residuals from its linear version and the spatial term

(Longitude, Latitude) was then added to the global model. Finally, the best model was selected based on the inspection of Akaike values (qAIC) (using 'qpcR' package in R) by sequentially removing each non-significant variable until the best performing, most parsimonious model was achieved. This model was then used to predict leopard densities across the whole surveyed area and the model validated firstly by the proportion of deviance explained, adjusted for the number of variables in the model and associated adj-R<sup>2</sup>, considered sufficient if adj-R<sup>2</sup> ≥ 0.1; and secondly, by using Pearson's product-moment correlation between the observed and the fitted densities (Lauria et al. 2011; Sguotti et al. 2016) to demonstrate correlations between survey data and predicted values. Possible overfitting of the model was suppressed by setting the basis dimension, or curve knots "k" to 5 following Wood et al., 2011 "*mgcv*" package and further increased the penalty on each model degree of freedom via "gamma =1.4" argument in gam (Wood et al., 2011 ) following Kim and Gu (2004) who show that the gamma argument is useful in suppressing overfitting, without degradation in the mean squared error (MSE) performance. Tests for overfitting of the model used a 5-fold cross validation to calculate R<sup>2</sup> (adj.) and proportion of deviance explained for training (80% data) and validation datasets (20% data), with outputs inspected for evidence of overfitting. To evaluate the relative contribution of each group of functionally distinct variables (habitat; anthropogenic factors; and sympatric competitors) to the global variance explained by the best model, we calculated the deviance explained (Wood 2006). Individual models excluding one functional set of covariates were run and respective deviance (DF) was related to both the null and full model deviances as follows:

$$DF = \frac{(D_{Excl} - D_{Full})}{D_{Null}}$$

Where D<sub>Excl</sub> is the deviance of the model excluding that variable; D<sub>Full</sub> is the deviance of the full model and D<sub>Null</sub> is the deviance of the null model.

Lastly, the difference between the full deviance of the most parsimonious model and the sum of each covariate-set-missing-models is taken as the shared variance explained by interacting covariates in the model.

### 3. Results



### 3.1 Individual identification of predators and leopard density estimates

A total of 428 leopards, 414 lions and 2367 spotted hyaenas were individually identified from camera trap images (Table S3). Leopard densities varied widely across the study area, ranging from 0.007 (SD  $\pm 0.009$ ) to 0.122 (SD  $\pm 0.009$ ) leopards per km<sup>2</sup>. Mean density across all sites was 0.0289 (SD  $\pm 0.0273$ ) leopards/ km<sup>2</sup> (Table 1). Population estimates, using the Bayesian framework (SPACECAP), conform to the reasonable probability that a population decline of more than 50% (HRCIW  $\leq 50\%$ ) would be detected in subsequent surveys, with a mean HRCIW of 36% (range 12-47%. Table 1). The HRCIW value decreased with increasing number of individuals detected in the survey. Although this is not true for all the surveys in this study, there is a strong support for the accuracy of the camera traps surveys being greater for more abundant species (Figure S2). Despite larger HRCIW values, the maximum likelihood “secr” density estimates were consistent with those obtained with the Bayesian, further validating the estimates obtained (Table 1).

### 3.2 Leopard density model

Multiscale variables were obtained by selecting the optimal scale at which each of the covariates was most influential. Overall, leopard densities were found to be best explained by vegetation cover at 20 km; spotted hyaena density at 1km; lion density at 20km; elevation at 5km; slope of elevation at 20km; maximum Human appropriation (HANPP) at 1km and road density at 20km (Table S2).

Collinearity ( $|r| \geq 0.7$ ) and significance from likelihood ratio tests resulted in the following variables being kept in the global model: Land Class; Tree cover; Spotted hyaena density; Lion density; total Organic carbon in soil; Slope of elevation; Human appropriation (HANPP); Rainfall; Trophy hunting risk and Hotspots of poaching. To control for overfitting, all covariate terms were constrained during smoothing (i.e.  $k = 5$ , Fisher et al. 2018) and the Akaike’s information criterion (QAICc, “*quasipoisson*” family which was found to better perform in modelling densities) was used to compare models and assess the relative strength of evidence for each model using the weights of AIC (wAIC). Given the collinearity found between Elevation, Human density, WDPA and the lack of significance of density of roads and distance to water and to roads all these variables were omitted from the global model. Survey area (Protected Area) was added as a random effect to control for site.

The global model was inspected for spatial autocorrelation (Global Moran I for regression residuals on the linear version of the model - statistic standard deviate = 0.1507, p-value < 2.2e-16) and the final model was adjusted to incorporate the interacting spatial term Latitude and Longitude to account for spatial autocorrelation. Non-significant variables in this model were then deleted stepwise and model performance (wAIC) improvement checked. The best model of leopard density omits both Tree cover and Rainfall. Finally, the density of leopards was best explained by a model including the spatial term, Land class, Spotted hyaena density and Lion density, total Organic carbon in soil, Slope of elevation, Human appropriation (HANPP), Trophy hunting risk, Hotspots of snaring and Survey area. Total Organic carbon and slope of elevation were both kept in the model even though not significant, as models including these covariates outperformed models with these variables omitted (Figure 1, Table S5 and S6). This final model had an adjusted  $R^2$  of 0.483 and total deviance explained of 57.7%.

Leopard density responded at broader scales to most of the covariates in analysis apart from Spotted hyaena density, which was found to be most influential at the 1km scale. In contrast Lion density was most influential at the 20km scale (Table S2). Leopard densities (Figure 1, 2) were higher at sites with higher spotted hyaena density and increased with lion density up to 0.06 lions/ km<sup>2</sup>, above which there is a steep decrease in leopard density. Leopard density was higher in woodland and lower in shrubland and bushed grassland and water dominated habitats. Although not significant, a positive relationship with both the total Organic carbon and the Terrain ruggedness was found. Higher Human appropriation of net primary productivity (HANPP) adjacent to the protected area, higher trophy hunting risk and sites that were significant hotspots of bush-meat poaching all have a negative influence on leopard density. Environmental covariates explained 19% of the total variance explained by the model, followed by the anthropogenic factors (7.4% of the total). Densities of intraguild competitors explained only 4% of the variance (Table S7). Similarity of  $R^2$  (adj.) and proportion of deviance explained from both the training (80%) and testing (20%) datasets ( $R^2$  (adj.) test = 0.52;  $R^2$  (adj.) train = 0.49 and Dev. expl. test = 0.60 and dev. expl. Train = 0.57) confirmed the absence of overfitting in our model. The final model was validated by Pearson's product-moment correlation demonstrating a strong positive

relationship between the empirically calculated densities per site and those resulting from predictions of the most parsimonious model ( $|r| = 0.681$ ;  $t = 26.201$ , d.f. = 793,  $p\text{-value} < 2.2e-16$ ).

## Discussion

Large, terrestrial predator population density is affected by environmental as well as by direct and indirect anthropogenic pressures (East 1984; Ripple et al. 2014). Environmental and ecological factors determining predator population density include bioclimatic and environmental conditions, such as rainfall, soil fertility, surface water availability, terrain (Bell 1982), prey biomass (Hatton et al. 2015) and competitors (Hayward and Slotow 2009; Linnell and Strand 2000). Anthropogenic factors include direct effects on populations such as over-exploitation, poaching, introduction of novel disease pathogens or invasive species and by indirect effects such as prey depletion, habitat loss and climate change (Owens and Bennett 2000; Ripple et al. 2014; Ripple et al. 2017; Woodroffe 2000). In this study we found that African leopard population densities were most negatively affected by anthropogenic threats (HANPP/ Hunting risk/Snaring) and high lion densities.

The status of sub-Saharan leopard populations and the ecological and anthropogenic drivers of population density need to be understood for populations to be adequately managed and protected. Across our survey sites we recorded leopard densities ranging from 0.7 to 12.2 leopards/ 100km<sup>2</sup>, with population estimates at 12 of 16 sites falling under 3.0 leopards/ 100km<sup>2</sup>. These latter densities are at the lower end of the scale of densities recorded for African leopards (Hunter et al. 2013) and fall below densities recorded in surveys of eutrophic savannah sites such as the Luangwa Valley (5.08-8.5 leopards/ 100km<sup>2</sup> (Rosenblatt et al. 2016) and  $11.8 \pm 2.6$  leopards/100 km<sup>2</sup> in Sabi Game Reserve, South Africa (Balme et al. 2019). However, low densities such as these may be typical of dystrophic savannah woodland sites (Bell 1982) and align with densities recorded at such sites elsewhere (densities ranging from 0.1 - 3.6 leopards/ 100km<sup>2</sup>, (Boast and Houser 2012; Stander et al. 1997; Stein et al. 2011; Strampelli et al. 2020).

Our findings suggest that a suite of factors best influence leopard population density with spatial variables providing the best explanatory power at large rather than small spatial

scales (Table S2), indicating the importance of landscape scale conservation for this species. Environmental and habitat features including Land class (habitat type), Terrain (slope) and soil nutrients (organic soil carbon) all positively affect leopard density, though none were overwhelmingly influential. Leopards are known to prefer closed habitats with wooded to intermediate vegetation cover and rugged terrain (Balme et al. 2007; Miller et al. 2018). These habitat features provide optimal conditions for hunting, concealment and refuge. Soil nutrient status is positively correlated with ungulate biomass and is likely to be a predictor of prey biomass (Bell 1982) and in turn predator population density (East 1984; Hatton et al. 2015). Surprisingly, annual rainfall was a poor predictor of leopard density. This is at odds with the suggestion that leopard population density can be predicted by rainfall (Martin and de Meulenaer 1988). If this were the case we would have expected rainfall, which varied from >750mm to <450mm across our survey sites to have more explanatory power and be influential in the final model predicting leopard density. While it is likely to be an ecological generality that herbivore biomass increases with rainfall across African savannah systems (East 1984) and thus ultimately influences predator numbers, it is also highly probable that other more proximate factors mask this relationship, particularly for predators potentially affected by anthropogenic activities.

Smaller carnivores within predator guilds are frequently impacted by interference competition with larger predator species (Ritchie and Johnson 2009). For instance, leopards have been shown to be affected by interference competition with tigers (*P. tigris*) where the two species are sympatric (McDougal 1988; Odden et al. 2010), though coexistence was facilitated by size of the prey base and habitat at other sites (Seidensticker 1976). In this study there was a positive relationship between the population density of spotted hyaenas and leopards suggesting that both predators are likely to be responding to similar environmental and anthropogenic drivers. This supports the suggestion that leopards are largely unaffected by competition for food resources with other large predators (Hayward and Kerley 2008). Leopards have been shown to be able to cope with kleptoparasitism by spotted hyaenas through temporal avoidance (Havmøller et al. 2020) and by caching kills out of reach in trees (Balme et al. 2017). Coupled with this, leopard body size overlaps sufficiently with that of hyaenas to limit interference competition via direct lethal confrontation (Bailey 1993).

On the other hand, the relationship between leopard and lion population densities was positive at low lion density but negative when lion density increased above  $\sim 6$  lions/100km<sup>2</sup>. The effect of lion density was most influential at the 20km scale suggesting that leopard-lion interactions might be mediated by leopard habitat selection at large spatial scales resulting in avoidance of areas where lions are abundant. Alternatively, leopard populations might be locally suppressed through direct mortalities from interference competition when lion density is high and interactions with lions are frequent. Evidence in the scientific literature for lion interference competition affecting leopard populations and/or habitat occupancy is, however, equivocal. Both leopard populations and behaviour have been shown to be impacted by high lion density (duPreez et al. 2015) with evidence that juvenile leopards may be vulnerable to lion predation (duPreez et al. 2014) as is the case for juveniles of other large carnivores such as cheetah (*Acinonyx jubatus*) and wild-dog (*Lycaon pictus*) (Durant et al. 2004; Groom et al. 2017). High juvenile mortality where interactions with lions is frequent could reduce population recruitment and ultimately population size. Similarly, adult leopards are occasionally killed by lions (Bailey 1993; Schaller 1972) and leopards have been shown to avoid lions at fine scales (Vanak et al. 2013), often favouring habitats that provide refuge sites (duPreez et al. 2015; Miller et al. 2018). Nevertheless, other studies have found little evidence of competitive exclusion of leopards by lions (Miller et al. 2018; Rosenblatt et al. 2016) and some have reported positive associations in the habitat occupancy of the two species (Allen et al. 2020; Strampelli et al. 2018). Lion-leopard competitive interactions are not well understood and are likely to be mediated by both habitat heterogeneity, prey resource abundance and spatio-temporal avoidance as is the case with large predator guild interactions in other areas (Karanth et al. 2017).

The effects of anthropogenic threats to carnivores are pervasive (Cardillo et al. 2004), such that, globally, more than three-quarters of large terrestrial predator species are in decline (Ripple et al. 2014). In this study leopard population density was noticeably impacted by anthropogenic factors. Increasing levels of habitat degradation in areas adjacent to the protected area sites had negative effects on leopard density. This accords with findings by other studies showing leopard occurrence to be negatively affected by human activity (Abade et al. 2018) and by edge effects imposed on protected areas by these activities

(Balme et al. 2010; Ngoprasert et al. 2007). Similarly, our results show that leopard population density was negatively affected by high levels of bush-meat poaching and by high trophy hunting quotas. Bush-meat poaching using wire snares is prevalent across many of the sites we surveyed, particularly those within the Sebungwe region of KAZA (Loveridge et al. 2020). Poaching causes both direct mortality of large predators and depletion of prey (Lindsey et al. 2013) and poses a significant threat to biodiversity (Ripple et al. 2016).

Excessive trophy hunting quotas to exploit large carnivore populations, without adequate assessment of population size and sustainability of offtakes, has been shown to be problematic (Brink et al. 2016; Creel et al. 2015; Packer et al. 2009) and leopard hunting quotas have been shown to be unsustainable in several African countries (Balme et al. 2009b; Caro et al. 1998; Pitman et al. 2015; Strampelli et al. 2020), with impacts exacerbated by high levels of retaliatory killing of animals in conflict with people (Swanepoel et al. 2011) and mismanagement of hunting offtakes (Spong et al. 2000). We found that high hunting quotas relative to estimated population size had a negative effect on leopard population density. Whilst, high annual hunting quotas do not necessarily equate to equivalently high hunting offtakes, they are generally indicative of hunting pressure on populations as evidenced by the fact that between 2009 and 2013 for ten Zimbabwean hunting concessions 83.1% (s.d.= 21.2; range: 33-100) of allocated annual quota was utilized (Table S8). These offtakes are comparable to the 45 -90% of annual leopard hunting quotas achieved in Tanzania (Spong et al. 2000).

These findings suggest that, across the landscape we surveyed, leopard populations may be less resilient in the face of human exploitation than has previously been assumed and populations may be depleted in hunting areas relative to areas that are more intensively protected. This accords with findings of other studies correlating leopard and other mammal population sizes with levels of protection (Searle et al. 2020; Stoner et al. 2007).

The results of this study reinforce several of the main criticisms of the 1988, CITES African leopard population assessment (Martin and de Meulenaer 1988). Firstly, in the wooded savannah sites surveyed here, spanning an annual rainfall gradient of ~ 300mm, rainfall was not found to be influential in predicting leopard population density. Secondly, in the intact habitat within formally protected areas surveyed, leopard populations were demonstrably affected by human activity, particularly over-exploitation through bush-meat poaching and

trophy hunting. These findings are at odds with the core assumptions of the 1988 CITES leopard population assessment that leopard population density is positively correlated with rainfall and leopards occur at maximum density in all unmodified habitat. Furthermore, density estimates based on extrapolations from vegetation type and rainfall generated by Martin and de Meulenaer (1988) exceed ours by a factor of between 1.4 and 13 at all but one site (Figure S3, Table S9), suggesting the 1988 CITES leopard population assessments may correspond poorly to contemporary estimates across the sites we surveyed. However, regardless of potential inaccuracies of previous assessments, and in the light of the clear impacts of human activity, including trophy hunting and accelerating threats to biodiversity emerging over the three decades since the 1988 assessment, there is an urgent case for revisiting sustainable management of leopard populations, both nationally and internationally.

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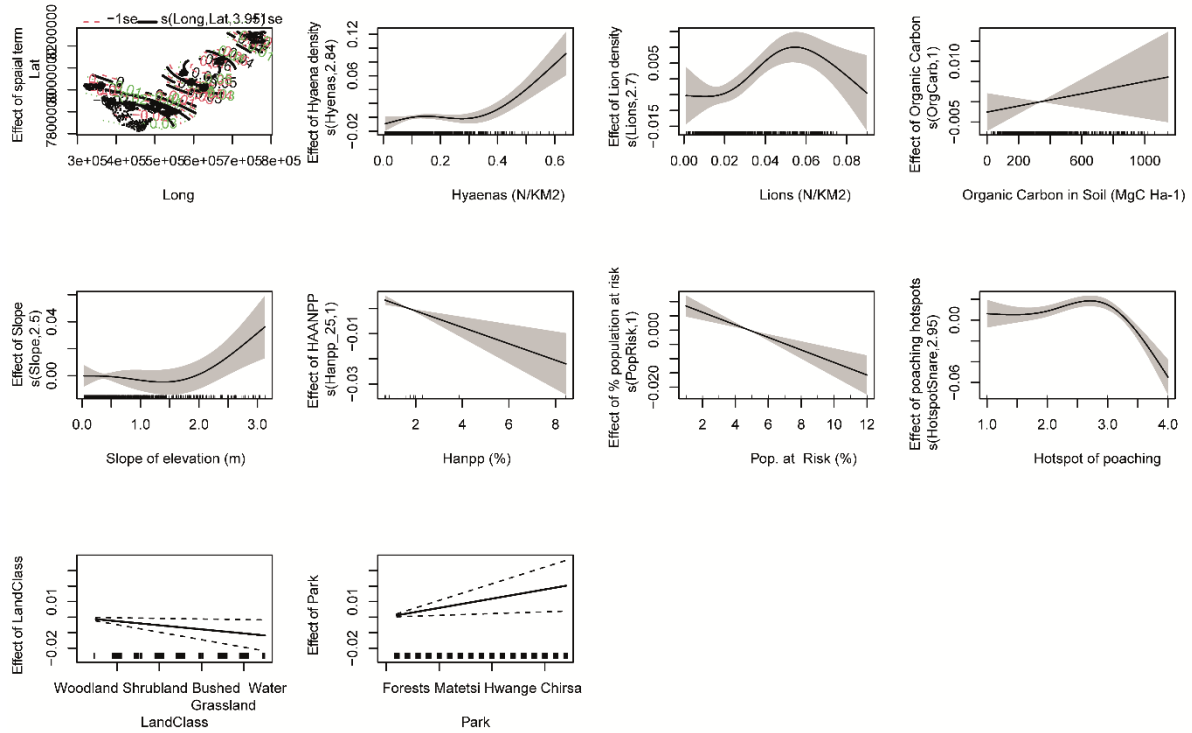
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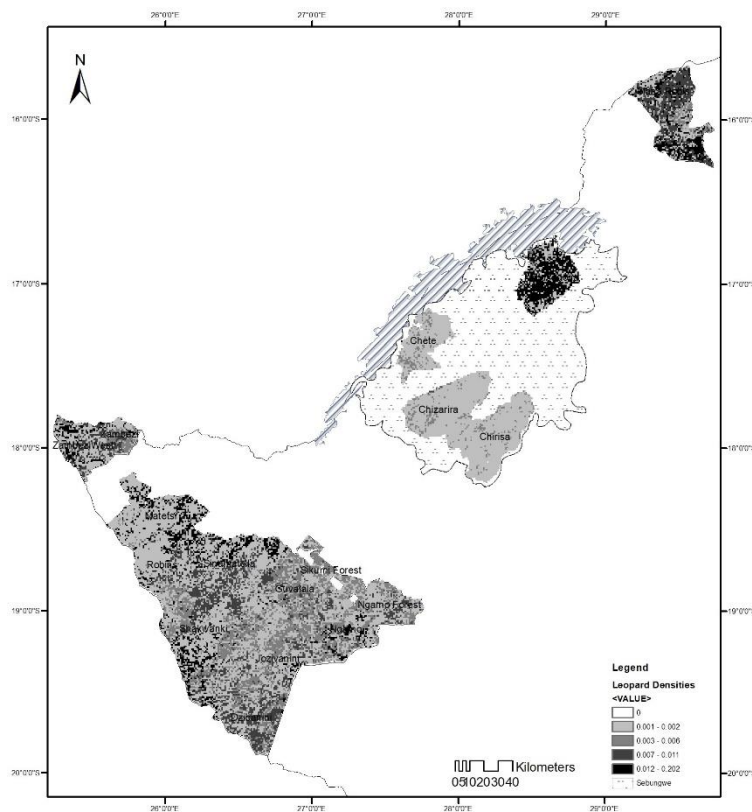
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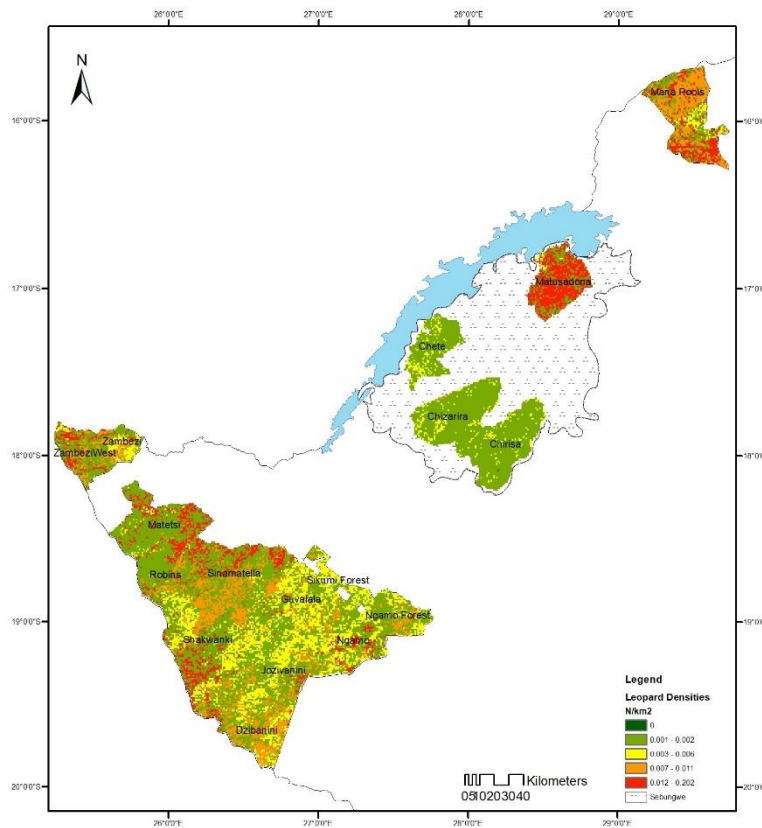
## Figures and Tables



**Figure 1.** Response curves of the continuous drivers of leopards densities in this study. Y-axis is the smoothed factor of leopard densities; X-axis is the covariate in analysis.



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667 **Figure 2:** Map of predicted leopard densities across the survey sites based on the GAM  
668 model

**Table 1:** Leopard densities calculated for each survey site using Bayesian (SPACECAP, Gopalaswamy et al. 2012) and Maximum Likelihood (SECR, Efford 2017) approaches. Spatial recaptures = detection of unique individuals at multiple locations in space; Sex ratio = ratio of Males/Females identified individuals; Density= number of individuals per km<sup>2</sup>, SD = standard deviation, SE = standard error, Max D= maximum density (upper 95% CI), Min D= minimum density (lower 95% CI), P-value = Bayesian P value, HRCIW = Half relative confidence interval width.

SURVEY	Area Type	Number of IDs	Spatial recaptures	Sex ratio (M/F)	SPACECAP						SECR				
					Density	SD	Min D	Max D	P Value	HRCIW	Density	SE	Min D	Max D	HRCIW
Mana Pools NP - North	National Park	35	9	0.6	0.04	0.01	0.03	0.05	0.58	29%	0.04	0.01	0.03	0.06	36%
Mana Pools NP - South		43	25	0.5	0.03	0.01	0.02	0.03	0.71	12%	0.03	0.01	0.02	0.04	35%
Matusadona NP		47	18	0.4	0.12	0.01	0.08	0.18	0.6	40%	0.1	0.02	0.06	0.15	49%
Chizarira NP		10	39	0.4	0.01	0.01	0.01	0.01	0.9	27%	0.01	0	0	0.01	63%
Zambezi NP		33	45	0.3	0.05	0.01	0.03	0.07	0.78	35%	0.04	0.01	0.03	0.05	37%
Hwange NP - Ngamo		17	18	0.3	0.02	0.01	0.01	0.03	0.57	42%	0.02	0.01	0.01	0.03	53%
Hwange NP – Dzibanini & Jozibanini		42	15	0.6	0.02	0	0.02	0.03	0.62	33%	0.02	0	0.01	0.03	39%
Hwange NP - Shakwanki		32	12	1	0.02	0.01	0.02	0.02	0.15	10%	0.03	0.01	0.02	0.05	43%
Hwange NP - Sinamatella		45	15	0.5	0.04	0.01	0.03	0.06	0.66	29%	0.04	0.01	0.03	0.06	33%
Hwange NP - Robins		16	9	2.2	0.01	0.01	0.01	0.02	0.64	45%	0.01	0	0.01	0.02	59%
Hwange NP - Guvalala		21	5	1.6	0.02	0.01	0.01	0.03	0.58	45%	0.02	0.01	0.01	0.04	60%
Ngamo & Sikumi Forests	Forest	15	13	0.7	0.01	0.01	0.01	0.02	0.64	47%	0.01	0	0.01	0.02	59%
Chete SA	Safari Hunting Area	11	16	0.8	0.02	0.01	0.01	0.03	0.7	44%	0.02	0.01	0.01	0.03	66%
Chirisa SA		9	14	0.3	0.01	0.01	0.01	0.01	0.76	45%	0.01	0	0.01	0.02	72%
Matetsi SA South (Unit 1-5)		26	18	0.6	0.02	0	0.01	0.03	0.56	33%	0.02	0.01	0.01	0.03	46%
Matetsi SA North (Unit 6-7)		16	10	0.3	0.03	0.01	0.02	0.04	0.49	42%	0.03	0.01	0.02	0.04	53%