Drivers of leopard (*Panthera pardus*) habitat use and relative abundance in Africa's largest transfrontier conservation area

Abstract

Transfrontier conservation areas (TFCAs) have the potential to provide havens for large carnivores while preserving connectivity across wider mixed-use landscapes. However, information on the status of species in such landscapes is lacking, despite being a prerequisite for effective conservation planning. We contribute information to this gap for leopard (*Panthera pardus*) in Africa, where the species is facing severe range contractions, using data from transect surveys of a 30,000km^2 area across Botswana and Zimbabwe in the Kavango-Zambezi (KAZA) TFCA. We used occupancy models to assess how biotic, anthropogenic, and management variables influence leopard habitat use, and N-mixture models to identify variables influencing the species' relative abundance. Leopard were detected in 184 out of 413 sampling units of 64km^2; accounting for imperfect detection resulted in mean detection probability $\bar{\bar{p}}$ = 0.24 (SD = 0.06) and mean probability of site use $\bar{\bar{\psi}}$ = 0.89 (SD = 0.20). Habitat use was positively influenced by prey availability and high protection. Relative abundance was best predicted by trophy hunting, which had a negative influence, while abundance was positively associated with high protection and availability of steenbok. Our findings suggest that securing prey populations should be a priority in conservation planning for leopard in Africa, and underline the necessity of preserving highly-protected areas within mixed-use landscapes as strongholds for large carnivores. Our findings also support calls for better assessment of leopard population density in trophy hunting areas, and illustrate the value of N-mixture models to identify factors influencing relative abundance of large carnivores.

Keywords

Habitat use; N-mixture models; occupancy models; relative abundance; transfrontier conservation area; trophy hunting

1. Introduction

Despite being widely considered one of the most adaptable of the world's large felids, the leopard (*Panthera pardus*) is classified as *vulnerable* by the IUCN (Stein *et al.*, 2016). In Africa, the species is primarily threatened by habitat loss and fragmentation (Di Minin *et al.*, 2016), prey depletion (Wolf and Ripple, 2016), and direct persecution by humans (Inskip and Zimmermann, 2009), which have collectively contributed to the species losing at least 48% of its historical range on the continent (Jacobson *et al.*, 2016).

As apex predators, leopards and other large carnivore populations require large, connected landscapes and viable prey populations to thrive (Crooks *et al.*, 2011). However, the connectivity beyond protected area borders required by these species is often at odds with the increased demand for land associated with growing and developing human populations (Di Minin *et al.*, 2016). The resulting habitat fragmentation has contributed to substantial range contractions for members of the large carnivore guild across the world (Wolf and Ripple, 2017). In light of this, there is a growing consensus that, while highly-protected areas remain a vital component of many large carnivore conservation strategies (Karanth and Chellam, 2009), small protected areas alone will not be sufficient to maintain viable populations of large carnivores into the future (Ripple *et al.*, 2014). A shift from the traditional protected area-centric approach to a landscape-level approach to conservation holds particular promise for leopards in Africa, the majority of which are believed to occur outside strictly-protected areas (Hunter, Henschel and Ray, 2013).

In Africa, transfrontier conservation areas (TFCAs) embody this movement, while emphasising the coupling of conservation with development initiatives. Defined as areas spanning international borders and encompassing multiple protected areas and land use types, TFCAs are managed as a single contiguous landscape for conservation (SADC, 1999). If effectively managed, TFCAs have the potential to protect large swathes of prime habitat and maintain connectivity within wider mixed-use landscapes, and thus provide havens for leopard within their contracting African range.

Until now, however, there has been relatively little effort to understand how leopards are faring across these larger conservation areas (Balme *et al.*, 2014; Jacobson *et al.*, 2016), with most research having been restricted to small, highly-protected reserves (but see Balme, Slotow and Hunter, 2010; Henschel *et al.*, 2011; Strampelli *et al.*, 2018). There is therefore a need to increase knowledge of the species within the context of large, mixed-use landscapes like TFCAs. Understanding how leopards adapt to different components of these modern mosaic landscapes is essential to inform management and conservation planning, evaluate the conservation effectiveness of different land-use types, and ensure the persistence of Africa’s leopard populations.

One land-use strategy of particular relevance to the leopard in Africa is trophy hunting, whereby a set quota of individuals may be hunted within a designated area each year. Trophy hunting has been used by conservation managers to attach economic value to wildlife areas by generating revenue for governments and local communities, and thus secure conservation benefits for natural habitats often unsuitable for photographic tourism (Lindsey, Roulet and Romañach, 2007). In the absence of viable conservation-oriented land use alternatives, trophy hunting is argued to therefore play an important role in preventing their conversion to agricultural land (Di Minin, Leader-Williams and Bradshaw, 2016; Dickman *et al.*, 2019). However, the practice can have detrimental long-term impacts on hunted populations if carried out unsustainably or combined with other sources of anthropogenic mortality (Packer *et al.*, 2010; Lindsey *et al.*, 2013). Information on these impacts is lacking even for species which have attracted considerable attention from policymakers (e.g. lion, *Panthera leo;* Macdonald *et al.*, 2017), and these gaps are greater still for leopard. Leopard populations within hunting areas should be assessed and monitored, and their habitat-use mechanisms understood, in order to ensure detrimental effects of hunting are avoided, and to inform sustainable and adaptive hunting management plans (Balme *et al.*, 2010).

We employed data from large-scale spoor surveys to investigate leopard status and habitat use across a mixed-use landscape within the southern Kavango-Zambezi (KAZA) TFCA. We used occupancy models to estimate the proportion of this landscape used by leopard, and assess how a suite of biotic, anthropogenic, and management variables influence habitat use for the species. We then employed novel N-mixture models to identify factors influencing relative abundance of leopard within the study area, and discuss the implications of our findings to highlight conservation priorities for leopard across modern African conservation landscapes.

2. Methods

2.1. Study area

At approximately 520,000km^2, KAZA is the world's largest terrestrial TFCA, encompassing 36 national parks and a host of other land uses, including unprotected land and communal areas (see Appendix A). The study area consists of approximately 30,000km^2 within the southern part of the TFCA, stretching across northeast Botswana and western Zimbabwe (Fig. 1). The area is generally water- and nutrient-poor due to its location in the Kalahari Basin, with an annual rainfall average of 500-700mm, although there are a large number of artificial waterholes across parts of the landscape. Vegetation is dominated by bushland savannah and woodland, interspersed with patches of grassland. Trophy hunting is permitted in Zimbabwe, and takes place across approximately 14% of the total study area. Leopard hunts follow an adaptive quota system for offtakes, with only males hunted. Although reinstated in 2019, trophy hunting was suspended in Botswana in 2014; while some data collection for this study was conducted prior to this ban, leopards were not hunted in this period.

2.2. Occupancy & N-mixture modelling

Occupancy models use patterns of detection and non-detection over multiple surveys (sampling occasions) of a sampling unit (site) to estimate detection probabilities (p), and consequently derive unbiased estimates of occupancy (ψ) (Mackenzie *et al.*, 2002). The occupancy framework allows the inclusion of covariates to explain heterogeneity in both occupancy and detection probability, facilitating insights into factors driving habitat use by species (MacKenzie *et al.*, 2006).

N-mixture models are a novel extension of occupancy models (Royle, 2004) which use counts of unmarked individuals to estimate site-specific abundance (λ). While a strict set of assumptions must be met for total abundance to be derived from such models, the N-mixture framework allows the effect of covariates on relative abundance to be explored, which can provide a more nuanced view of how a species is faring within different components of a landscape than measures of site use alone (Royle, 2004).

2.3. Data collection

We divided our study area into 8 x 8 km (64km^2) sites for both occupancy and N-mixture modelling (Fig. 2a,b), a scale we consider appropriate to capture second order selection (Johnson, 1980). As there is free movement of both leopard and their prey species among our sites, we relaxed the closure assumption of occupancy modelling by interpreting our state variable, psi (ψ), as the probability of site use instead of the probability of occupancy (Mackenzie, 2005).

Detection/non-detection data for leopard and other mammal species were collected across the study area from May 2012 to October 2015. Spoor survey transects (Fig. 1) were carried out by driving a vehicle at a low speed (~10km/h) along roads, fire-breaks and boundary cutlines, and recording any fresh spoor encountered. As highly-skilled local trackers assisted with spoor detection and identification, incorrect identification of tracks was highly unlikely. Surveys were started at first light to avoid disturbance and maximise visibility.

Sampling occasions consisted of both spatial replicates and temporal replicates of the same transects. Although the survey effort spanned multiple years, data collection within individual sites was restricted to a single year.

To avoid spatial dependence, we tested for independence by pooling detection/non-detection data into transects of increasing length, with any transect with at least one detection being assigned the value 1. Transects were increased by increments of 2km until the standard occupancy model without Markovian dependence (Mackenzie *et al.*, 2002) outperformed the model extended to account for Markovian dependence of detections/non-detections (Hines *et al.*, 2010), as per Henschel *et al*. (2016), using program PRESENCE (Hines, 2006).

2.4. Covariate selection

2.4.1. Detection covariate

Detection covariates are factors which are thought to potentially influence the probability of detecting a species given presence in a site (p). For both occupancy and N-mixture modelling, the number of 2km sections of transect per sampling occasion was modelled as a detection covariate (effort) to account for variation in total segment length after pooling to avoid spatial dependence.

Substrate quality was not included as a detection covariate, as it can be considered largely homogenous across the study area due to the prevailing soil type of Kalahari sand and the use of highly-skilled local trackers (Trans-Kalahari Predator Programme (TKPP), unpublished data).

2.4.2. Site use & relative abundance covariates

Site use covariates are factors hypothesised to influence the probability of a site being used by a species (ψ). Candidate variables which are believed to influence leopard spatial use were selected based on prior research wherever possible. The same variables were tested in N-mixture models of relative abundance (λ).

We hypothesised that leopard habitat use and relative abundance would be influenced by five metrics, represented by nine spatial covariates (further information on how covariates were calculated and the rationale behind their inclusion can be found in Appendix B):

- Water availability, quantified as the natural log of average pixel distance to nearest water point (name: *ln(water distance)*, hypothesised relationship: negative).
- Prey availability, quantified by developing models of the probability of site use by frequently taken prey species (as per Andresen et al., 2014; Everatt et al., 2014; Strampelli et al., 2018) using the spoor transect dataset, ensuring a measure of availability that accounts for imperfect detection. Probability of site use was modelled for four of the most frequently taken prey species by leopard (Hayward *et al.*, 2006): impala (*Aepyceros melampus; impala*, positive), common duiker (*Sylvicapra grimmia; duiker*, positive), steenbok (*Raphicerus campestris; steenbok*, positive), and warthog (*Phacochoerus africanus; warthog*, positive). Despite being considered an important prey species for leopard (Hayward *et al.*, 2006), our dataset contained insufficient detections of bushbuck (n = 20) for probability of site use to be modelled for the species. We hypothesised that habitat use by prey would be influenced by 13 spatial covariates (see Appendix C). The mean probability of site use for frequently taken prey was also calculated for each site, producing a variable reflecting general availability of these prey species (*all prey*, positive).
- Human disturbance, quantified as the natural log of average pixel distance to nearest settlement (*ln(settlement distance)*, positive).
- High protection, represented by the proportion of site highly protected (*protection*, positive), defined as areas subject to a high level of management and law enforcement activities (see Appendix A). Areas classified as being subject to high protection within the study area include National Parks (where only photographic tourism is permitted), Wildlife Management Areas, and a Safari Area (where limited trophy hunting is permitted; see Fig. 1 & Appendix A).
- Trophy hunting, represented by the proportion of site hunted (*hunting*, negative). At the time of data collection, trophy hunting of leopard was only permitted in the study area within Zimbabwe's Safari Areas, Conservancy Ranches, and Forest Areas (see Fig. 1 & Appendix A).

Covariate values for each site were extracted using ArcGIS Version 10.5.1 (ESRI, 2016) and QGIS Version 2.18.10 (QGIS Development Team, 2017).

2.5. Modelling approach

Analysis was conducted in R version 3.6.2 (R Core Team, 2017) using RStudio version 1.2.5033 (RStudio Team, 2015). Single-season, single-species occupancy models (Mackenzie *et al.*, 2002) were produced for each prey species and leopard in package *unmarked* version 0.12-3 (Fiske and Chandler, 2011). All continuous site use covariates were standardised on a z-scale prior to analysis.

Univariate models were ranked based on their Akaike Information Criterion (AIC) scores, corrected for small sample size (AICc) (Burnham and Anderson, 2002). Where covariate pairs were correlated by $|r| > 0.7$, the covariate with the highest-ranked univariate model was retained. For leopard, univariate model rankings were employed to determine which prey availability covariate best predicted leopard site use (ψ). We then held a global model consisting of all remaining site use covariates constant, while modelling the covariate hypothesised to affect detection (p), effort. The detection model with lowest AICc was then used to rank all possible additive combinations of site use covariates.

A final model set was produced for each prey species and leopard containing all models with ΔAICc < 2, representing models with substantial empirical support (Burnham and Anderson, 2004). Goodness of fit was assessed for the top-ranked and most parameterised models within this model set using the MacKenzie and Bailey goodness of fit test for single-season occupancy models based on Pearson's chi-square (MacKenzie and Bailey, 2004).

The relative importance of covariates was assessed by summing AICc weights of all models in the final model set in which that covariate was present (Burnham and Anderson, 2004). The direction of impact of covariates was represented by the sign of their beta coefficient estimates, and covariates were considered to have a significant impact if the 95% confidence interval of the beta coefficient ($\beta \pm 1.96$ SE) did not span zero. Predicted site use values for each site were extracted via model averaging of the final model set using package *MuMin* (Bartoń, 2013).

N-mixture models (Royle, 2004) were fitted to the leopard data to assess the relative influence of the nine candidate covariates on relative abundance (λ) across sites, following the same procedure as above but with input data comprised of count detections. Goodness of fit was assessed for the top-ranked model and the most parameterised model within the final model set using Sum of Squared Errors, Chi-square, and Freeman-Tukey tests.

3. Results

Repeated surveys of 5,055km of unique transects resulted in a total of 11,665km driven. We surveyed 474 sites over 286 days, with an average of 10.4km driven per site.

3.1. Prey site use

Results and discussion of prey site use modelling can be found in Appendix D. None of the models assessed for goodness of fit indicated lack of fit or overdispersion.

3.2. Leopard modelling

For leopard, spatial independence was achieved at 4km. Sites with only one sampling occasion were excluded from analysis, resulting in 413 sites. 285 leopard detections were obtained in 184 of the 64km^2 sites, giving a naïve occupancy of 0.45.

The mean probability of site use of the four frequently taken prey species ranked highest among covariates representing prey availability in the occupancy models, while probability of site use for steenbok ranked highest in the N-mixture models (see Appendix E). Effort had a significant positive impact on detection probability for both model types, and was retained as the detection covariate for all subsequent model testing.

Three models were retained in the final occupancy model set, and seven in the final N-mixture model set (Table 2). None of the models assessed for goodness of fit indicated lack of fit or overdispersion (see Appendix E).

3.2.1. Leopard site use

We estimated a mean detection probability of $\bar{p}$ = 0.24 (SD = 0.06) and a mean probability of site use of $\bar{\psi}$ = 0.89 (SD = 0.20) for leopard, which is approximately double the naïve occupancy estimate. Model-averaged estimates suggest a high level of habitat use by leopard across the majority of the study area (Fig. 2a).

The best predictors of leopard site use were high protection (summed model weight, $\Sigma w = 1.00$; Fig. 2c) and prey availability ($\Sigma w = 1.00$; Fig. 2d). Both had a positive effect, which was significant for prey availability (Table 3a). Site use was also generally negatively associated with distance to settlement ($\Sigma w = 0.37$), and generally positively associated with distance to water ($\Sigma w = 0.19$).

3.2.2. Leopard relative abundance

Our estimates of abundance produced using N-mixture models cannot be interpreted as absolute abundance, as individuals whose home range spans multiple sites would be included in the abundance estimate of multiple sites within their home range, and there is growing evidence that N-mixture models do not produce reliable absolute abundance estimates (Link *et al.*, 2018; Nakashima, 2020). Nevertheless, we use these models to make inferences about relative abundance across the study area (Fig. 2b). Overall, leopard abundance was highest across much of the study area in Botswana, and in Zimbabwe's Hwange National Park.

The best predictors of leopard relative abundance were trophy hunting ($\Sigma w = 1.00$; Fig. 2e) and high protection ($\Sigma w = 0.75$; Fig. 2f). Trophy hunting had a significant negative impact on abundance, while leopard abundance was positively associated with the level of protection, a relationship that was significant in one model (Table 3b). Although distance to water ($\Sigma w = 0.24$), availability of steenbok ($\Sigma w = 0.26$), and distance to settlement ($\Sigma w = 0.21$) all appeared in the final model set with consistent relationships to relative abundance, they did not show any robust relationship.

4. Discussion

4.1. General importance & impact

The widespread distribution estimated for leopard across the study area indicates that the species is faring relatively well within protected areas of the southern KAZA TFCA. This suggests that the KAZA TFCA has been successful in securing the continued persistence of the species in this region since its inception, and it will have an important role to play in preserving existing leopard habitat into the future.

Due to their scale, TFCAs have the potential to secure corridors for wildlife that may otherwise be lost to land-use conversion and fragmentation. Such landscape-scale connectivity is of particular value for large carnivores, whose wide-ranging behaviour and vulnerability to conflict mean that a lack of dispersal routes can result in population declines and eventual local extinctions (Winterbach *et al.*, 2013). The mosaic landscapes preserved through TFCAs can be especially important for species that are particularly vulnerable to intra-guild competition – such as the African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) – whose avoidance of areas with high densities of dominant competitors can force them into lesser- or non-protected land (Durant, 2000; Creel, 2001). Finally, large, appropriately-located tracts of interconnected land are necessary to support migratory species, which are an important component of the prey base for large carnivores in the region (Naidoo *et al.*, 2016). However, we are unable to make inferences about connectivity from this study, as occupancy modelling is not considered an appropriate proxy for landscape permeability across large scales (Zeller *et al.*, 2011; Pitman *et al.*, 2017), and less than 5% of our total survey effort was conducted in completely unprotected land. We therefore recommend further research to identify important corridors for wildlife populations within KAZA and other TFCAs, with a particular focus on assessments in completely unprotected land surrounding protected areas, and collaboration between researchers and land-use planners to ensure their integration into management plans.

Our analysis illustrates that sign-based occupancy modelling can be employed to monitor large carnivore habitat use across vast, mixed-use landscapes such as TFCAs (Thorn *et al.*, 2010). Insights provided by occupancy surveys can therefore be complementary to those obtained from more intensive survey efforts such as camera trap surveys, which can be used to produce robust population density estimates at finer scales.

This is the first study to employ N-mixture models to investigate relative abundance of leopard, and one of the first to do so for large carnivores (but see Belant *et al*., 2016). We believe this method holds promise as an efficient and cost-effective way to understand the factors affecting species' abundance over large scales. However, while we did control for spatial autocorrelation in our data, variation in leopard movement patterns across the study landscape may have resulted in artificially high relative abundance estimates in the more arid parts of our study area, where home ranges are likely to be larger (Rogan *et al.*, 2019). Thus, while we show that N-mixture models can provide useful insights through assessments of relative abundance, we echo calls against employing this methodology to obtain population estimates from spoor data (Link *et al.*, 2018; Nakashima, 2020).

4.2. Drivers of leopard habitat use & relative abundance

4.2.1. Availability of natural resources

Abundant prey are a key requirement for the survival of large carnivores, and prey base depletion is a major driver of global large carnivore population declines (Wolf and Ripple, 2016). In southern KAZA, leopard habitat use was strongly positively influenced by prey availability, confirming findings elsewhere in Africa (Burton *et al.*, 2012; Kane, 2014; Balme *et al.*, 2019). Our results suggest that it is the general availability of prey of preferred body size, and not of a specific species, that drives leopard habitat use at the scale considered. This is in keeping with the species' generalist feeding behaviour and ability to adapt their diet to a range of prey depending on available resources (Hayward *et al.*, 2006).

In contrast, relative abundance of leopard was better explained by the availability of a single prey species, steenbok. This could relate to steenbok having the highest probabilities of detection and site use across our study area, suggesting that it is the most widespread and readily available prey species of preferred body size for leopard regionally. While leopard have been shown to be able to subsist on smaller prey (Martins *et al.*, 2011), our results suggest that a relatively high availability of prey species within the preferred body size range may be necessary for higher densities of leopard to be supported. However, an important consideration to note is that our prey availability metrics reflect only presence, so any finer impact of prey abundance on leopard habitat selection and relative abundance will not be captured.

Our results suggest that leopard habitat use increases with distance from water. This finding is likely an artefact of the large number of water points at the northernmost part of our study area, parts of which are not highly protected and are therefore estimated to have a relatively low probability of site use. Nevertheless, this effect was not significant, in line with previous studies of leopard in Asia and elsewhere in Africa (Ngoprasert, Lynam and Gale, 2007; Constant, 2014; Kshettry *et al.*, 2017).

4.2.2. High protection

Leopard habitat use was positively associated with high protection, a relationship previously identified in Kenya's Maasai Mara (Madsen and Broekhuis, 2018). We also found a positive association between high protection and leopard relative abundance. The influence of protection may be direct, through the reduced risk of anthropogenic mortality in such areas, or indirect, through the role of protection in supporting higher densities of prey species. The latter mechanism was identified as more important in shaping leopard density in neighbouring Zambia (Rosenblatt *et al.*, 2016). However, these associations were not significant except in a single model, which may be a consequence of insufficient surveys being conducted in completely unprotected areas. Similarly, by grouping areas with a lower level of protection with unprotected areas, we may have failed to capture the importance of these partially-protected areas for leopard. Further conservation-oriented research should be carried out in such areas, as they are thought to contribute substantially to leopard range across Africa (Hunter, Henschel and Ray, 2013) and are particularly vulnerable to degazettement (Jones *et al.*, 2018).

4.2.3. Trophy hunting

Trophy hunting did not appear to have an influence on leopard occurrence. Moreover, given the importance of high protection in predicting habitat use by leopard, our results suggest that well-protected hunting areas may represent important areas of habitat for leopard in KAZA. However, results of N-mixture modelling suggest that trophy hunting may exert a top-down effect on this leopard population, even within highly protected hunting areas. The removal of mature individuals from a population via trophy hunting has been found to negatively impact abundance of hunted carnivore species elsewhere (Packer *et al.*, 2010; Lindsey *et al.*, 2013), and an inverse relationship between abundance and hunting offtake has been observed for lion in the study landscape (Loveridge *et al.*, 2016). Our findings suggest that similar population suppression mechanisms may be occurring in the study area for leopard.

4.2.4. Human disturbance

Habitat use by leopard was generally negatively associated with distance to human settlements. Although this contradicts findings from Angola (Petracca *et al.*, 2019), leopard have been shown to do particularly well near agricultural lands – which often coincide with areas of human settlement – in many other parts of their range (Athreya *et al.*, 2015), a pattern that has been attributed to higher prey availability in such areas (Constant, 2014). However, this result is likely to be an artefact of the large number of human settlements adjacent to the boundary of the highly-productive and relatively well-protected Hwange National Park at the south-eastern edge of our study area, where leopard site use and relative abundance were both estimated to be high. This hypothesis is supported by the lack of significance of this relationship. There is likely to also be a scale-dependency to this relationship, with finer-scale analysis more likely to show avoidance of human settlements by leopard, as found elsewhere (Strampelli *et al.*, 2018).

4.3. Conservation recommendations

The wide distribution and habitat tolerance of leopards within KAZA protected areas supports the continued movement towards conservation at the landscape-scale through initiatives such as TFCAs.

At the same time, our results highlight the importance of maintaining highly-protected core areas within these mixed-use conservation landscapes, as they provide areas of higher population abundance which can protect species against detrimental source-sink dynamics (Hansen, 2011). We recommend that further similar research be carried out as part of the transition to landscape-scale conservation to understand how other species are faring across different landscape components. TFCA partner countries should implement joint species-specific action and management plans, alongside landscape-level strategies, to ensure collaboration and uniformity of activities for managing key species across boundaries.

Given the importance of prey availability in shaping leopard habitat use, maintaining sufficient habitat to support prey populations should be a priority for the conservation of African leopard populations. Efforts should also focus on reducing bushmeat poaching of prey species, particularly as this brings the added benefit of reducing accidental snaring, which has severely reduced and even extirpated leopard populations in Asia (Rostro-García *et al.*, 2018; Rasphone *et al.*, 2019) and is a threat to leopard survival in Africa (Swanepoel *et al.*, 2015). These recommendations would benefit all large carnivore species in Africa, where 37% of prey species have decreasing population trends (Wolf and Ripple, 2016).

Our results suggest that trophy hunting can have both positive and negative impacts: well-protected hunting areas can offer valuable habitat for leopard (Lindsey, Roulet and Romañach, 2007; Di Minin, Leader-Williams and Bradshaw, 2016; Dickman *et al.*, 2019), but unsustainably high trophy hunting quotas may contribute to long-term leopard population declines (Packer *et al.*, 2009, 2010; Loveridge *et al.*, 2016). As such, quotas must be informed by robust estimates of population densities in hunting areas of the KAZA TFCA, ideally as part of a long-term monitoring effort with flexible quotas tied to annual population fluctuations (Balme *et al.*, 2010) and combined with meaningful community participation. Monitoring efforts should also be employed to identify any potential additional negative impacts of hunting on KAZA's leopard populations, such as disrupted dispersal patterns and inbreeding (Naude *et al.*, 2020), and reduced trophy size (Muposhi *et al.*, 2016), which can compromise the long-term sustainability of hunting activities. In recent years, camera trap surveys have been implemented across the study landscape to obtain density estimates for leopard, and findings are being utilised as part of adaptive quota management for leopard trophy hunting in Zimbabwe (ZPWMA, 2018); with the recent reinstatement of trophy hunting in Botswana, similar systems should also be integrated across the border. Given our evidence of trophy hunting influencing leopard abundance, we welcome these actions and recommend similar monitoring frameworks – for leopard and other hunted species – in other trophy hunting areas, to ensure activities are carried out without long-term detrimental effects to populations.

Supplementary Material

A description of land use designations in the study area (Appendix A), an overview and justification of leopard site use and relative abundance covariates (Appendix B), an overview and justification of prey site use covariates (Appendix C), prey site use analysis results and discussion (Appendix D), and detailed leopard site use and relative abundance analysis results (Appendix E) are available in the Supplementary Material.

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Figures & Tables

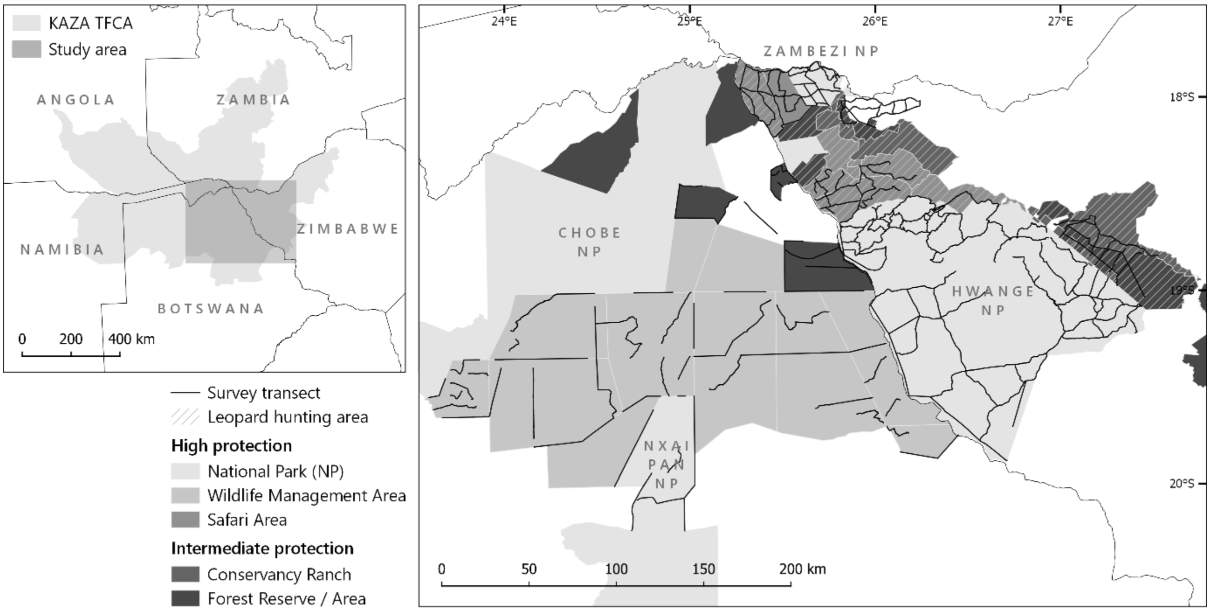

Figure 1: The study area within the KAZA TFCA (left); land use types in the study landscape and locations of survey transects (right). Protected areas are shown only in the study countries (Botswana & Zimbabwe). See Appendix A for a description of land use designations in place in the study area. Of the land use designations that permitted trophy hunting of leopard at the time of data collection, Safari Areas are classified as receiving high protection, while Conservancy Ranches and Forest Areas are classified as receiving intermediate protection.

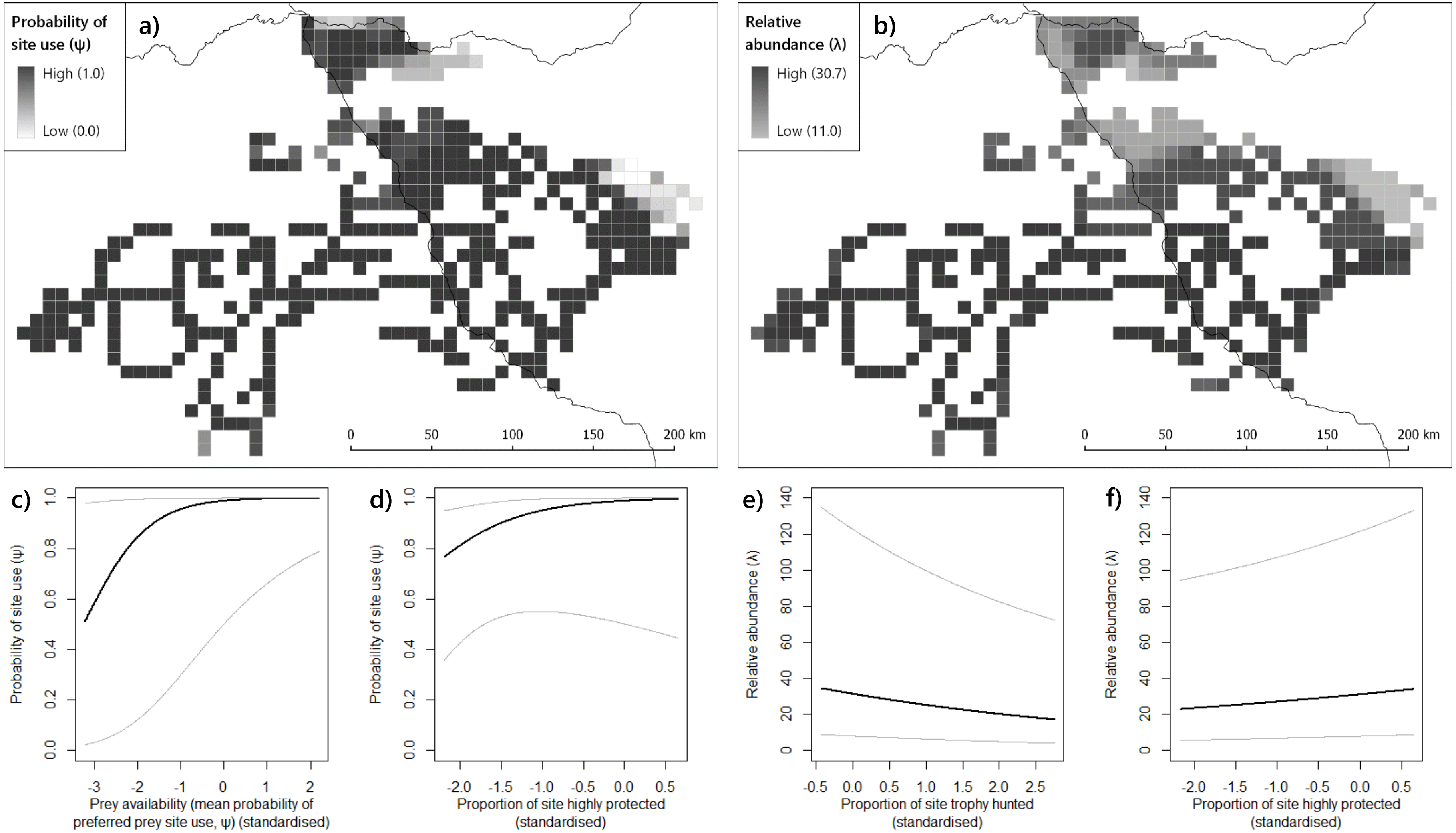

Figure 2: **Model-averaged estimates of leopard (a) site use ($\hat{\psi}$) and (b) relative abundance ($\hat{\lambda}$) for each site in the southern KAZA TFCA; estimates (with 95% confidence intervals) of leopard site use given variation in (c) prey availability, and (d) high protection, and relative abundance given variation in (e) trophy hunting, and (f) high protection.** Plots were produced using the top-ranked model based on AICc ranking (ψ(all prey + protection),p(effort) and λ(protection + hunting),p(effort)). Each covariate was predicted while holding the other at its mean value.

Table 2: Results of multivariate model selection estimating leopard (a) site use (occupancy models) and (b) relative abundance (N-mixture models) in the southern KAZA TFCA.

(a) Site use (occupancy)

	Model	nPars	-2*LogLike	AICc	ΔAICc*	AIC Wt
1	ψ(all prey + protection),p(effort)	5	1060.18	1070.33	0.00	0.43
2	ψ(all prey + ln(settlement distance) + protection),p(effort)	6	1058.41	1070.62	0.29	0.37
3	ψ(ln(water distance) + all prey + protection),p(effort)	6	1059.72	1071.93	1.60	0.19

(b) Relative abundance (N-mixture)

	Model	nPars	-2*LogLike	AICc	ΔAICc	AIC Wt
1	λ(protection + hunting),p(effort)	6	-676.87	1366.00	0.00	0.24
2	λ(ln(water distance) + protection + hunting),p(effort)	7	-676.31	1366.90	0.94	0.15
3	λ(steenbok + protection + hunting),p(effort)	7	-676.32	1366.90	0.97	0.15
4	λ(hunting),p(effort)	5	-678.47	1367.10	1.14	0.14
5	λ(ln(settlement distance) + protection + hunting),p(effort)	7	-676.58	1367.40	1.48	0.12
6	λ(steenbok + hunting),p(effort)	6	-677.62	1367.40	1.50	0.11
7	λ(ln(water distance) + ln(settlement distance) + protection + hunting),p(effort)	8	-675.74	1367.80	1.88	0.09

*All models shown are within ΔAICc < 2 from the top-ranked model.

Table 3: Parameter estimates (standard error in parentheses) of the final model set (ΔAICc < 2) for models estimating leopard (a) site use and (b) relative abundance in the southern KAZA TFCA.

(a)	**Site use (occupancy)**	**Intercept ψ**	**β ln(water distance)**	**β all prey**	**β ln(settlement distance)**	**β protection**	**Intercept p**	**β effort**
1	ψ(all prey + protection),p(effort)	4.42 (2.25)		**1.36 (0.56)**		1.48 (0.99)	-3.25 (0.55)	**1.11 (0.28)**
2	ψ(all prey + ln(settlement distance) + protection),p(effort)	4.75 (2.00)		**1.55 (0.60)**	-0.68 (0.61)	1.73 (0.94)	-3.25 (0.55)	**1.11 (0.28)**
3	ψ(ln(water distance) + all prey + protection),p(effort)	2.79 (1.39)	0.48 (0.45)	1.02 (0.53)		0.92 (0.51)	-3.23 (0.55)	**1.14 (0.28)**

(b)	**Relative abundance (N-mixture)**	**Intercept ψ**	**β ln(water distance)**	**β steenbok**	**β ln(settlement distance)**	**β protection**	**β hunting**	**Intercept p**	**β effort**
1	λ(protection + hunting),p(effort)	3.18 (0.62)				0.14 (0.08)	**-0.22 (0.08)**	-6.21 (0.77)	**0.90 (0.24)**
2	λ(ln(water distance) + protection + hunting),p(effort)	3.17 (0.62)	0.07 (0.07)			0.15 (0.08)	**-0.20 (0.08)**	-6.22 (0.77)	**0.91 (0.24)**
3	λ(steenbok + protection + hunting),p(effort)	3.17 (0.62)		0.09 (0.09)		0.13 (0.08)	-0.17 (0.09)	-6.22 (0.77)	**0.92 (0.24)**
4	λ(hunting),p(effort)	3.19 (0.63)					**-0.26 (0.08)**	-6.22 (0.78)	**0.91 (0.24)**
5	λ(ln(settlement distance) + protection + hunting),p(effort)	3.18 (0.61)			-0.06 (0.08)	0.16 (0.09)	**-0.24 (0.08)**	-6.20 (0.77)	**0.90 (0.24)**
6	λ(steenbok + hunting),p(effort)	3.18 (0.64)		0.11 (0.08)			**-0.20 (0.09)**	-6.23 (0.79)	**0.92 (0.24)**
7	λ(ln(water distance) + ln(settlement distance) + protection + hunting),p(effort)	3.16 (0.62)	0.09 (0.07)		-0.09 (0.08)	**0.18 (0.09)**	**-0.21 (0.08)**	-6.20 (0.77)	**0.91 (0.24)**

Beta coefficients (β) in bold indicate a significant impact on (a) probability of site use or (b) relative abundance in the model shown, as the 95% confidence interval (β ± 1.96 SE) does not span zero.