The influence of prey, pastoralism and poaching on the hierarchical use of habitat by an apex predator

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As an apex predator, habitat selection by African lions, *Panthera leo*, is primarily determined by bottom-up processes; however, increasing anthropogenic pressures may alter these relationships. Using camera traps and track surveys in the Limpopo National Park, Mozambique, we collected detection/non-detection data of lions and their prey and combined these with occurrence data on bushmeat poaching activities and spatial data on agro-pastoralist land use and other landscape features. We used hierarchical modelling within an occupancy framework to determine the relative influences of ecological variables on resource use and non-use by lions at two spatial scales. Habitat use by lions was most strongly influenced by the occurrence of their preferred prey across both spatial scales. However, lions were strongly negatively predicted by bushmeat poaching at the finer spatial scale and generally negatively predicted by agro-pastoralist activities at the coarser scale. Restricting our analysis to the home-range scale would have greatly underestimated the impact of bushmeat poaching on the ecology of lions. The results of our study illustrate the trophic dependency of prey resources to lions and the importance of considering scale when investigating species habitat use. Importantly, our study also demonstrates the limiting influence of bushmeat poaching on the use of habitat by an apex predator.

Key words: African lion, occupancy, African carnivore, bushmeat hunting, habitat ecology.

INTRODUCTION

Considering the biological constraints of obligate carnivory, the use of habitat by apex predators should be primarily predicted by bottom-up processes (Mitchell & Hebblewhite, 2012). However, competition with humans may alter trophic-based habitat relationships for predators, resulting in reduced habitat availability (Mitchell & Hebblewhite, 2012; Ripple *et al*., 2014). For instance, anthropogenic disturbance influences home-range level habitat selection by cougars, *Puma concolor*, (Dickson & Beier, 2002), wolves, *Canis lupus*, (Rich, Mitchell, Gude & Sime, 2012) and tigers, *Panthera tigris* (Barber-Meyer *et al*., 2013).

Competition with humans is recognized as the ultimate cause behind global predator declines (Ripple *et al*., 2014). However, many apex predator populations exist in human-dominated landscapes (Ripple *et al*., 2014) or are exposed to human pressures along reserve boundaries (Woodroffe & Ginsberg, 1998). Understanding how humans influence the use of habitat by apex predators is therefore important to improve species conservation and management. For example, knowledge of how humans alter trophic-based habitat relationships for apex predators is an important component of determining habitat suitability and population viability.

Habitat selection can be seen as a hierarchical process (Johnson, 1980), involving behavioural choices that span a continuum of time, space and ecological processes (Mitchell & Hebblewhite, 2012). Recognizing the scale dependency of variables on species fitness is important for conservation planning. Since species' fitness needs may differ with scale, investigations limited to a singular scale may fail to recognize the importance of key habitat components (Nams, Mowat & Panian, 2006). For instance, Ciarniello, Boyce, Seip & Heard (2007) demonstrated how delineating protected areas for grizzly bears, *Ursus arctos*, based on habitat selection at the third-order would have excluded important landscape features whose importance only became evident at the home-range scale.

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The contemporary distribution of the African lion, *Panthera leo*, is largely associated with the remaining extent of intact savanna (Riggio *et al*., 2012). At the home-range scale, lions may select for areas with relatively higher densities of large ungulates (Van Orsdol, Hanby & Bygott, 1985), and may select against areas with increased threat of human persecution (Ogutu, Bhola & Reid, 2005, but see; Woodroffe & Frank, 2005). Lion foraging success requires a combination of prey availability and suitable cover from which to attack (Hopcraft, Sinclair & Packer, 2005; Mosser, Fryxell, Eberly & Packer, 2009). At the fourth-order scale of habitat use, lions may select areas with preferred hunting features over areas with higher prey densities (Mosser *et al*., 2009; Davidson *et al*., 2013). Stalking and ambush cover are less limiting to lions in forested savannas (Funston, Mills, Biggs & Richardson, 1998; Hopcraft *et al*., 2005), than to lions on open plains (Hopcraft *et al*., 2005; Mosser *et al*., 2009).

The goal of this study was to determine the relative influence of bottom-up resource and top-down anthropogenic factors on the hierarchical use of habitat by lions in a system impacted by pastoralism and poaching. We considered the Limpopo National Park (LNP) in southwestern Mozambique as an ideal case study location because both lions and humans are resident in the park, and humans freely extract resources, including 'bushmeat', graze livestock, and are known to persecute lions (Everatt, Andresen & Somers, 2014). We measured habitat use by lions within an occupancy modelling approach that explicitly accounts for survey and site level species detectability (MacKenzie *et al*., 2002; Mitchell & Hebblewhite, 2012). Discreet occupancy models were also developed for the variables describing resources and threats encountered by lions in LNP. We predicted that habitat use by lions in LNP would reflect their ecological niche as an apex predator and be primarily predicted by bottom-up processes, but that the threats posed to lions by top-down anthropogenic pressures would strongly determine the use of habitat. In addition, we predicted that the relative importance of variables describing lion habitat would vary with scale.

METHODS

Study area

The study was conducted in a 2400 km^2 area of woodland savanna plains in Mozambique's Limpopo National Park (LNP) (UTM X 384502 UTM Y 7432635) (Fig. 1). LNP forms a component of the Greater Limpopo Trans-frontier Park (GLTFP) with Kruger National Park (KNP), South Africa and Gonarezhou National Park, Zimbabwe. Together these parks form the core of the Greater

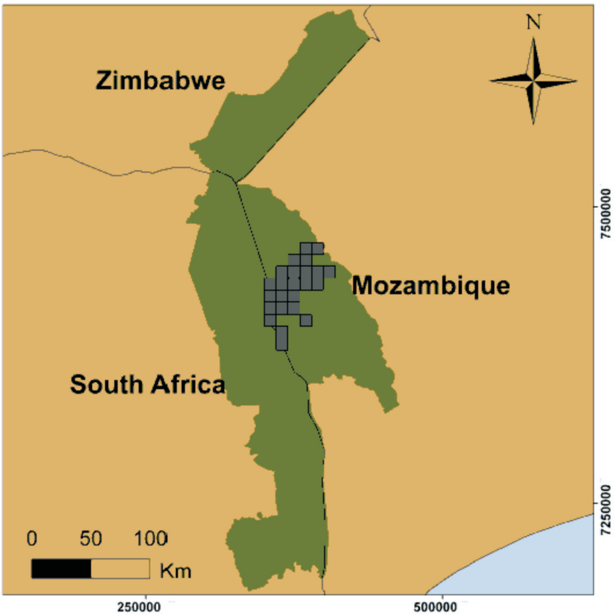

Fig. 1. Location of study area (squares) within Limpopo National Park, which forms the Mozambican component of the Greater Limpopo Trans-frontier Park (in green).

Limpopo Lion Conservation Unit (IUCN, 2006). The study area is bordered to the west by KNP and to the east by a near continuous band of agro-pastoralist settlements along the banks of the Limpopo River. There are additional smaller agro-pastoralist settlements situated within the study area. The human population is estimated at 6500 (in 2003) in LNP and 20 000 living in the eastern boundary villages (Huggins, Barendse, Fischer & Sitoi, 2003), together grazing over 20 000 cattle, *Bos primigenius* (Stephensen, 2010).

Wildlife in this region of Mozambique were largely decimated during 28 years of war (1964–1992) (Hatton, Couto & Oglethorpe, 2001). However, removal of portions of the South Africa–Mozambique border fence as part of the creation of the GLTFP in 2000 has provided opportunities for re-colonization of wildlife into LNP (Hanks, 2000), and currently 23 spp. of ungulates occur in the Park (Everatt, 2014). At the time of this study, the lion population in LNP was estimated at 66 individuals or a density of 0.99 lions/100 km^2 (Everatt *et al*., 2014).

Survey design

It is possible to examine habitat use at multiple spatial scales using sampling windows of differing, biologically relevant sizes (Baldwin & Bender, 2008; Sunarto *et al*., 2012). In this study, we examined habitat use by lions at two spatial scales equivalent to Johnson's (1980) second- and third-order of habitat selection. We defined second-order sampling sites as 100 km^2 grid cells, based on average home-range sizes of lions in the adjoining and contiguous KNP (Funston, Mills, Richardson & Van Jaarsveld, 2003.) (Fig. 1). Included within these grid cells we defined third-order sites as approximately 1 km^2, reasoning this size was biologically meaningful to the scale at which lions make short-term habitat-use decisions.

To quantify habitat use by lions we employed an occupancy modelling approach where the estimator (Ψ) was defined as the *probability of site use* (MacKenzie *et al*., 2006). We made the following assumptions; 1) species were not falsely identified, 2) detections were independent, 3) heterogeneities in occupancy or detection probabilities were modelled using covariates. It is important to note that the closure assumption could be relaxed because our estimator was *probability of site use* rather than *proportion of area occupied* (MacKenzie *et al*., 2006 p. 105).

Data collection

We collected the data from temporally replicated detection/non-detection camera trap and spoor surveys conducted from 9 September 2011 to 26 November 2012. We deployed digital motion cameras (15 Reconyx HC500 (Wisconsin, U.S.A.) (trigger time of 0.97 s, detection zone approximately 24 m), 7 Spy Point Tiny-W2 (Québec, Canada) (trigger time of 0.91 s, detection zone approximately 17 m), 10 Bushnell Trophy Cam (Beijing, China) (trigger time of 0.66 s, detection zone approximately 18 m) (http://www.trailcampro.com/trailcamerareviews.aspx) on dirt tracks, game trails and along river edges. In addition, we conducted track surveys on foot due to the lack of road networks in the study area. These surveys followed an obvious path of travel, (*i.e.* track, game trail or river edge) where substrate was adequate for tracking.

Sampling occasions at the home-range scale were represented by 189 temporally replicated 3 km transect samples (replicates separated by > 14 days) and 326, 14-day camera-trap samples for a combined mean of 21.6 samples per grid cell. Of the 24 grid cells, 23 were sampled with camera-traps (mean = 14 samples/grid cell, range = 3–30 samples/grid cell) and 23 were sampled with track surveys (mean = 8 samples/grid cell, range = 2–16 samples/grid cell). We note here that unequal sampling across sites is accounted for within an occupancy model (MacKenzie *et al*., 2002). In an effort to meet the assumption of independence between sampling occasions at the home-range scale, we pooled detections (within grid cells) when a camera-trap had sampled anytime 14 days prior to a track transect. Sample occasions at the short-term use scale were represented by 998 temporally replicated 1 km transects (232 sites; 638 samples) (replicates separated by 14 days) and 14 day camera-trap samples (82 sites; 360 samples) for a combined mean of 3.6 samples per site. Of the total 260 sites surveyed, 184 sites were sampled only by transects, 48 were sampled by transects and camera-traps, and 28 sampled only by camera-traps. The detection or non-detection of lions was recorded for each (14 day) camera trapping sample and each (1 km) track transect sample.

Identification of covariates

To explain habitat use by lions in a human-disturbed landscape, we considered five fitness-related covariates. These included: encounter

Table 1. Covariates expected to influence habitat use by lions.

Covariate	Key	Fitness value to lion	Description	Sampling range: short-term habitat use	Sampling range: home-range habitat use
Preferred prey	PP	Availability of preferred prey	Probability of buffalo site use	0.1–0.5 mean = 0.4	0.1–0.6 mean = 0.4
Alternate prey	AP	Availability of alternate prey	Σ Probability of warthog and impala site use	0.1–1.7 mean = 1.0	0.2 – 1.5 mean = 0.9
Bushmeat poaching	B	Targeted or accidental snaring	Probability of bushmeat poaching site use	0.0–1.0 mean = 0.6	0.1 – 1.0 mean = 0.6
Village	V	Persecution in defense of livestock	Proximity to agro-pastoralist settlements (km)	0.1–24.5 mean = 10.9	2.0 – 20.4 mean = 11.2
Riparian	R	Landscape feature facilitating prey capture	Amount of riparian area in site (# 30 × 30 m pixels)	0.0– 2.7 mean = 0.1	0.0 – 928.1 mean = 315.3

probability of lion's preferred prey, encounter probability of alternate prey, landscape features that facilitate prey capture (*i.e.* riparian areas), encounter probability of bushmeat poaching and agro-pastoralist use (Table 1).

Lions exhibit a strong preference for larger bodied prey including African buffalo, *Syncerus caffer*, (Hayward & Kerley, 2005). To quantify the influence of preferred prey availability on habitat use by lions, we used a probability of occurrence model for buffalo that was developed by Everatt *et al*., (2014) for the same survey area and time. Other species that lions are known to preferentially select for, including; giraffe, *Giraffa camelopardalis*, plains zebra, *Equus quagga*, and blue wildebeest, *Connochaetes taurinus*, (Hayward & Kerley, 2005), were excluded from the analysis because they have a limited distribution of occurrence in the study area (Stephensen, 2010). To quantify the influence of alternate prey availability for lions, we combined probability of site use for warthog, *Phacochoerus africanus*, (Supplementary information, http://dx.doi.org/10.6084/m9.figshare.1295207) and impala, *Aepyceros melampus*, (Andresen, Everatt & Somers, 2014) from models developed for the same survey and time. We assumed that the probability of prey occurrence (*i.e.* site use) is biologically representative of an encounter probability for lions. To quantify the influence of bushmeat poaching on habitat use by lions, we used a bushmeat poaching occupancy model developed by Everatt *et al*., (2014) for the same study area and time. Agro-pastoralist use was measured as the mean Euclidean distance to a settlement edge per 30 m × 30 m pixel in a grid cell (home-range analysis) or in a buffer (50 m diameter) placed around each camera station or track transect (short-term site use analysis) from a landscape raster (Peace Parks Foundation, Stellenbosch). We considered riparian areas as a proxy for landscape features that facilitate prey capture (Hopcraft *et al*., 2005), measured as the number of 30 m × 30 m pixels (per grid cell or buffer) overlapping either river (including drainage lines) or water (including pans) raster layers (Peace Parks Foundation, Stellenbosch). Analyses were made in the Spatial Analysis tool in ArcGIS 9.3.1. (ESRI, Redlands, California, U.S.A.).

Analytical methods

We constructed a detection/non-detection matrix for each site and spatial scale, recording a '1' or '0' where lions were detected or not detected, respectively. Following this, we constructed two survey-specific matrices for each analysis to account for differences in detectability between the two sampling methods used. In the first matrix a '1' was recorded where only the method 'track' was employed and a '0' where only cameras were employed. In the second matrix, a '1' was recorded where each method was used and data were pooled, and a '0' where only one method was used. The overlap of the two matrices therefore accounted for three sampling possibilities at each site; tracks only, cameras only and pooled samples. Additionally, we constructed season specific (wet *versus* dry) matrices, recording a '1' for surveys conducted during the wet season and a '0' for surveys conducted during the dry season. To account for variation in lion detection probability (p) the covariates 'track' and 'pooled' (hereafter referred to as method 'M') and 'season' were

Table 2. Results from discreet occupancy models describing the probability of detection ($\bar{\hat{p}}$) and probability of site use $\bar{\hat{\Psi}}$) by bushmeat poachers, buffalo, impala and warthog from camera trapping data in Limpopo National Park, September 2011 to November 2012.

	$\bar{\hat{p}}$	S.E.	$\bar{\hat{\Psi}}$	S.E.
Bushmeat poachers*	0.165	0.027	0.799	0.050
Buffalo*	0.368	0.041	0.416	0.084
Impala‡	0.285	0.038	0.482	0.090
Warthog†	0.336	0.035	0.513	0.049

From * Everatt *et al.*, (2014), ‡Andresen *et al.*, (2014), †Supplementary information http://dx.doi.org/10.6084/m9.figshare.1295207

included in all models describing lion site use (Ψ).

We estimated site occupancy (Ψ) and detection probability (p) using maximum likelihood functions (MacKenzie *et al.*, 2006) and the single season option in the program PRESENCE Version 5.5 (Hines, 2006). Continuous site covariates were standardized on a z-scale and all covariates were tested for collinearity using a cut-off of $r = 0.5$. Covariates found to be correlated were not included in the same models. All possible (non-correlated) combinations of occupancy covariates (Supplementary information, http://dx.doi.org/10.6084/m9.figshare.1295207) were considered for each analysis (home-range scale = 11 models, short-term site use scale = 16 models). We ranked models based on Akaike Information Criterion (AIC), using AICc adjusted for small sample size, with the sample size set as the number of sampling sites (Burnham & Anderson, 2002). Models with a ΔAICc <2 were considered to have strong support. We considered a candidate set of all models ΔAICc <7 whose combined weights ≥0.95 (*i.e.* 95% confidence set). AICc weights were used to determine the weight of evidence for each model, and were summed for each covariate in the 95% confidence set (Burnham & Anderson, 2002). Variables with high summed model weights were considered more important in explaining heterogeneity in occupancy. The direction of influence of individual covariates was determined by the sign of the β-coefficients (MacKenzie *et al.*, 2006). Covariates were considered to have strong or robust impact if $\beta \pm 1.96 \times$ S.E. from the top ranking model were not overlapping zero. We used a weighted model averaging technique to calculate overall parameter estimates (Burnham & Anderson, 2002). Finally, we performed a goodness of fit test using 10 000 bootstrap samples and a Pearson's chi-square statistic on the most saturated model (MacKenzie & Bailey, 2004).

RESULTS

We recorded a total survey effort of 5335 camera trap nights and 638 km of track surveys. After pooling sampling occasions, the final data set consisted of 251 sampling occasions at the home-range scale and 957 sampling occasions at the short-term site-use scale. Lions were detected on 35 (14 day) camera samples (from 664 lion photos) and 55 (1 km) track samples. We identified 19 individual lions from camera-trap images, with identification based on sex, age and distinguishing scars (Whitman & Packer, 2007). This number is therefore the minimum sample size of individuals considered in this habitat analysis. The probability of site use by lion's prey and by bushmeat poachers is summarized in Table 2.

Habitat use at the home-range scale

The model averaged probability of detecting lions where they occurred at the home-range scale was $\bar{\hat{p}} = 0.304$ (S.E. = 0.095). The covariate preferred prey was strongly supported and was the principal contributing factor to habitat use by lions at this spatial scale; the only model that emerged with a ΔAICc <2 was the univariate model Ψ(P)p(M+S) (Tables 3 & 4). Lions showed a strong use of sites with a greater probability of occurrence of their preferred prey (Tables 3 & 4). In addition, lions generally occurred at sites with a greater proportion of riparian areas that were further from villages with a greater probability of occurrence of alternate prey and lower probability of occurrence of bushmeat poaching (Table 4). There was no evidence lack of fit (p = 0.22) or over-dispersion (ĉ) = 1.20).

Habitat use at the short-term use scale

The model averaged probability of detecting lions where they occurred at the short-term use scale was $\bar{\hat{p}} = 0.230$ (S.E. = 0.038). The greatest contributing factors to habitat use by lions at this

Table 3. Summary of model selection procedure for factors influencing site use (Ψ) by lions at the home-range scale and at the short-term use scale. Covariates considered include; occurrence probability of preferred prey (P), occurrence probability of alternate prey (AP), occurrence probability of bushmeat poaching (B), distance from villages (V) and proportion of riparian area (W).

Model	ΔAICc	*w*	*K*	–2l
Home-range use				
Ψ(P)p(M+S)	0.00	0.372	6	151.44
Ψ(V)p(M+S)	2.47	0.108	6	153.91
Ψ(P+R)p(M+S)	2.89	0.088	7	150.27
Ψ(R)p(M+S)	3.45	0.066	6	154.89
Ψ(.)p(M+S)	3.52	0.064	5	158.57
Ψ(AP)p(M+S)	3.54	0.063	6	154.98
Ψ(P+B)p(M+S)	3.58	0.062	7	150.96
Ψ(AP+R)p(M+S)	4.18	0.046	7	151.56
Ψ(R+V)p(M+S)	4.21	0.045	7	151.59
Ψ(B+R)p(M+S)	5.50	0.024	7	152.88
Ψ(P+B+R)p(M+S)	5.72	0.021	8	148.50
Short-term use				
Ψ(P+B)p(M)	0.00	0.574	6	539.79
Ψ(P+B+R)p(M)	1.08	0.334	7	538.76
Ψ(P)p(M)	4.27	0.068	5	546.15
Ψ(P+R)p(M)	6.33	0.024	6	546.12
Ψ(.)p(M)	29.18	0.000	4	573.14

Detectability (p) varies with method (M) and season (S). Ψ(.) assumes site use is constant, ΔAICc is the difference in AICc values between each model with the low AICc model, *w* is the AICc model weight, *K* is the number of parameters in the model, and –2l is twice the negative log-likelihood value.

scale were the probability of occurrence of their preferred prey and the probability of occurrence of bushmeat poaching (Tables 3 & 4), where lions showed a strong use of sites with a greater probability of occurrence of their preferred prey and a strong negative use of sites with a greater probability of occurrence of bushmeat poaching (Tables 3 & 4). In addition, lions generally occurred at sites closer to riparian areas (Table 4). There was no evidence of a lack of fit (P = 0.41) or overdispersion (ĉ = 0.44).

Table 4. β-coefficient estimates for covariates influencing site use (Ψ) by lions in order of their summed model weights (Σw) at the home range use scale and at the short-term use scale.

Occupancy covariate	Σ model w (%)	β	S.E.
Home-range use			
Preferred prey	57.6	9.82*	4.73
Riparian	20.4	0.57	0.62
Villages	16.8	–1.12	0.64
Alternate prey	10.7	2.51	1.57
Bushmeat poaching	7.0	–1.13	1.69
Short-term use			
Preferred prey	99.9	8.62*	2.49
Bushmeat poaching	90.8	–1.50*	0.63
Riparian	35.9	0.56	0.46

*Indicates covariate has robust impact (β ± 1.96 × S.E. not overlapping 0).

DISCUSSION

In this study we considered use of habitat by an apex predator that co-occurs with human activities. Our results demonstrate that habitat use by lions is influenced by bottom-up resources and by top-down anthropogenic pressures (Fig. 2). In addition, we found that the limiting influence of bushmeat poaching was scale dependent, which has important conservation implications.

Habitat use by an apex predator was most predicted by bottom-up processes

Habitat use by lions in LNP was most strongly predicted by the occurrence of buffalo. The importance of this variable was indicated by the weight of evidence for models containing the buffalo covariate and by the strong positive influence of this covariate at the coarser home-range spatial scale. That the buffalo covariate was strongly determining across both spatial scales emphasizes the importance of this component of lion

Fig. 2. Habitat use by lions in the Limpopo National Park is influenced by bottom-up resources and by top-down anthropogenic pressures including pastoralism and bushmeat poaching.

habitat use (Rettie & Messier, 2000). These results suggest that lions in LNP are making behavioural choices to select habitat at the home-range scale that includes the limited distribution of buffalo herds in the park and then further selecting areas at a finer spatial scale that would increase their probability of encountering individual animals.

That habitat use by lions was strongly determined by the occurrence of prey resources agrees with trophic-based species-habitat relationships (Krebs, 2009; Mitchell & Hebblewhite, 2012). For instance, food resources were the primary predictor of second-order habitat selection by grizzly bears in the Canadian Arctic (McLoughlin *et al.*, 2002) and tigers in the Russian Far East (Miquelle *et al.*, 1999). Following this, predation risk by wolves was the primary predictor of second-order habitat selection by caribou, *Rangifer tarundus*, in northern Canada (Rettie & Messier, 2000) and predation risk by lions was the primary predictor of second-order habitat selection by zebra, giraffe and wildebeest on a reserve in South Africa (Thaker *et al.*, 2011).

Habitat use by an apex predator is influenced by top-down anthropogenic disturbance

Habitat use by lions in LNP was strongly negatively predicted by bushmeat poaching at the short-term use spatial scale. Bushmeat poaching may limit predator habitat by depletion of prey resources and by direct, targeted or non-targeted, persecution (Becker *et al.*, 2013; Lindsey *et al.*, 2013; Everatt *et al.*, 2014). During this study we found evidence of three lions that were killed by bushmeat poachers, thus reducing lion occurrence at these sites. In addition, by modelling prey occurrence, we were able to exclude the influence of prey depletion by bushmeat poaching, thus limiting our poaching covariate to describe the direct persecution of lions in LNP. However, applying this approach could mean that the total influence of bushmeat poaching (prey depletion and persecution) is underrepresented in our hierarchical ranking of explanatory covariates.

Finally, our results demonstrate the scale dependency of lion-habitat associations. While the importance of prey resources to the use of habitat by lions in LNP spanned the domain of both spatial scales examined, the limiting influences of the anthropogenic covariates varied with spatial scale. Our results show that considering habitat selection by lions only at the home-range scale would have greatly underestimated the direct impacts of bushmeat poaching on lion ecology. This is concerning because failing to recognize the impact of bushmeat poaching could lead to erroneous conclusions of lion habitat suitability and population viability.

Mechanisms responsible for the species-habitat relationships we present may include a behavioural or numerical response. Avoidance of pastoralism and bushmeat poaching by lions could indicate that lions possess a behavioural mechanism to reduce competition with humans (Schuette, Creel & Christianson, 2013). Alternatively, if reduced site use indicates a numerical response by lions then this could suggest that the human-impacted lands of LNP are acting as sink or as attractive-sink (Battin, 2004) habitat to the adjoining (source) habitat in KNP. In the context of acute continental range declines and the isolation of lion populations, sink habitats, although low in quality, may nonetheless be important to lion conservation by increasing lion range and maintaining genetic connectivity (Dolrenry, Stenglein, Hazzah, Lutz & Frank, 2014; Stoner *et al*., 2013). Under this scenario, LNP may offer range expansion and connectivity and thus play an important role in the viability of lions in the Greater Limpopo Lion Conservation Unit. Conversely, if lions are mistakenly selecting for human use areas (*i.e.* for cattle as prey and/or wildlife areas used by poachers) and suffering high levels of mortality, LNP could be acting as an attractive sink, which could reduce the viability of the greater lion population (Battin, 2004). Distinguishing between sink and attractive-sink habitats is therefore important for improving lion conservation prospects in the system.

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