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Large carnivores are key drivers of ecosystem structure and function, yet their populations are declining worldwide. African lion (*Panthera leo*) populations have decreased significantly in recent decades with an estimated 23 000 lions left in Africa. Successful conservation efforts rely on a sound understanding of how animals utilize their surrounding habitat. We used movement data from GPS collars to investigate patterns and drivers of seasonal space use by free-roaming lions in the Greater Mapungubwe Transfrontier Conservation Area (GM-TFCA). We developed individual and population-level resource utilization functions (RUF) from 2008 to 2015. RUFs relate non-uniform space use within a home range to landscape metrics in a multiple regression framework. We identified six landscape features hypothesized *a priori* to be good predictors of lion space use: land use, land cover, elevation, terrain ruggedness, distance to human settlements and rivers. Only elevation during the dry season was a significant factor detected for lion space use ($\hat{\beta}$ ± S.E.) (–0.278 ± 0.107, CI = –0.4881, –0.0676). Across seasons, lions varied in their avoidance of human settlements, but 12 of 18 (67%) individuals selected areas within their home ranges that were farther from human settlements. Lions moved randomly across the landscape independent of vegetation type regardless of season. In season-specific analyses, some lions avoided human settlements (dry season: 45%, [*n* = 10] utilized areas farther from settlements; wet season: 50% [*n* = 9]). The lack of avoidance of settlements by some lions in our study also confirms that individual variation among lions can lead to human–wildlife conflicts. Perhaps the most critical observation from our study is that individual lions acted very differently as they used the landscape, which suggests the need for management plans to be landscape and case-specific.

Keywords: African lion, Botswana, carnivore, *Panthera*, resource utilization, savanna, space use.

INTRODUCTION

Successful conservation efforts rely on a sound understanding of how animals utilize their surrounding habitat. Habitat selection by large carnivores has been widely investigated (Stephens & Krebs, 1986; Funston *et al.*, 2001; Crawshaw & Quigley, 1991; Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Mosser *et al.*, 2009; De Boer *et al.*, 2010; Vlaeix *et al.*, 2012; Petrunenko *et al.*, 2016) with prey abundance and catchability of prey (Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Hebblewhite *et al.*, 2005) being key factors in driving most large terrestrial carnivores in how they utilize the landscape. Like most large terrestrial carnivores, African lions (*Panthera leo*) are difficult to conserve in the wild because they require large home ranges, they have a diet that typically includes large prey, they occur at low densities and can pose a significant risk to human safety (Cardillo *et al.*, 2004; Cardillo *et al.*, 2005; Carbone *et al.*, 1999; Purvis *et al.*, 2000, Holmern *et al.*, 2007, Packer *et al.*, 2005; Hopcraft *et al.*, 2005). Consequently, lion populations have decreased significantly in recent decades, both in numbers and geographic range, with an estimated 23 000 free-ranging lions left in Africa (Riggio *et al.*, 2012; IUCN, 2013; Bauer *et al.*, 2015).

Lions are opportunistic stalk-and-ambush predators (Schaller, 1972; Van Orsdol, 1984; Hayward & Kerley, 2005) and select landscape features that

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increase hunting success and catchability of prey, such as dense cover, erosion gullies and watering holes (Funston *et al.*, 2001; Hopcraft *et al.*, 2005; Mosser *et al.*, 2009). As large and visible carnivores that are also found in groups, lions are particularly at risk from human persecution and frequently sustain high levels of anthropogenic mortality (Woodroff & Ginsberg, 1998; Woodroffe, 2000; Snyman *et al.*, 2015), leading to behavioural alteration with regards to proximity to humans (Oriol-Cotterill *et al.*, 2015). For example, Snyman *et al.* (2015) found that within an 11-year period at Botswana's Northern Tuli Game Reserve over 94% of adult lion mortality occurred outside protected area borders.

We investigated lion resource use in the Greater Mapungubwe Transfrontier Conservation Area (GM-TFCA) using resource utilization functions (RUF) (Marzluff *et al.*, 2004), also referred to as third-order habitat selection (Johnson, 1980). RUFs calculate a probabilistic measure of non-uniform space use within an animal's home range and then use a multiple regression framework to relate space use to landscape features while accounting for spatial autocorrelation among multiple consecutive locations from the same individual. Regression coefficients from the RUF can be used to draw inferences about the direction and magnitude of relationships between intensity of space use and values of selected resources at either an individual or a population level (Marzluff *et al.*, 2004, Kertson *et al.*, 2011). The primary objective of our eight-year study was to determine the potential effects of human development and landscape characteristics on seasonal land use of free-roaming African lions. Because lions are ambush predators (Schaller, 1972; Van Orsdol, 1984; Hayward & Kerley, 2005), we hypothesized that lions would closely associate with denser vegetation and rivers, where the catchability of prey is higher compared with non-riparian areas (Hopcraft, 2005). Additionally, we hypothesized that lions would avoid human settlements as these areas are perceived as sources of mortality (Woodroffe, 2001; Oriol-Cotterill *et al.*, 2015).

METHODS

Permission and ethical clearance for this research was granted by the Botswana Ministry of Environment, Wildlife and Tourism (EWT 8/36/4 XXXIII (48)). Within the GM-TFCA (4872 km^2), our primary study areas included in Botswana, the Northern Tuli Game Reserve (NTGR, 720 km^2); in South Africa, Mapungubwe National Park (MNP,

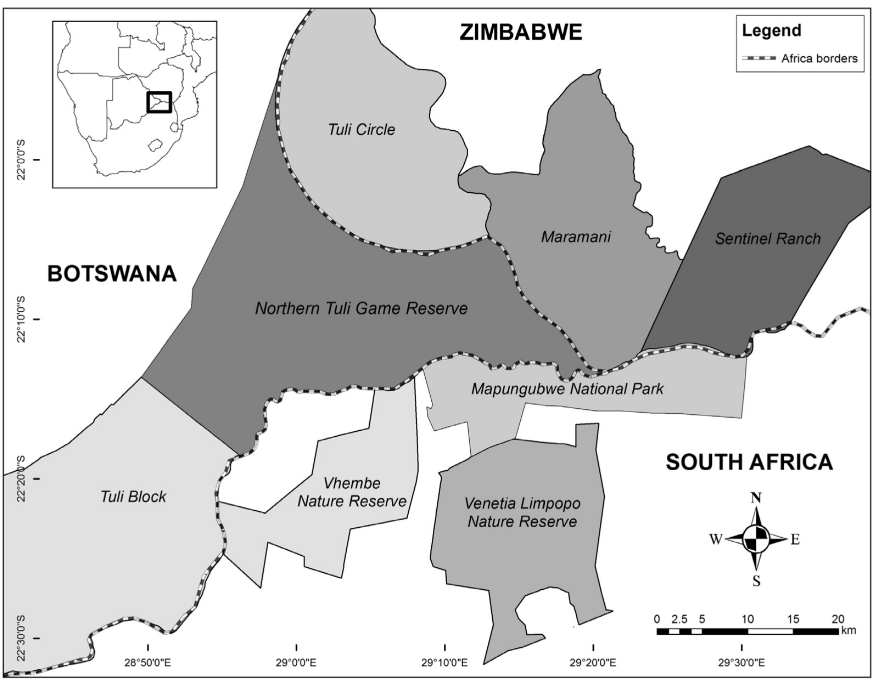

Fig. 1. The Greater Mapungubwe Transfrontier Conservation Area bordering Botswana, South Africa and Zimbabwe in Southern Africa. Image from Peace Parks Foundation.

Table 1. Summary of the listed properties, their size, and potential impact on wildlife in the Greater Mapungubwe Transfrontier Conservation Area at the time of the study (2007–2015).

Name	Country	Size (km²)	Photographic tourism	Safari hunting	Lion hunting
Northern Tuli Game Reserve	Bots	720	X		
Mapungubwe National Park	RSA	210	X		
Vhembe Private Nature Reserve	RSA	230	X	X	X
Tuli Circle	Zim	390		X	X
Sentinel Ranch	Zim	330	X	X	
Venetia Limpopo Nature Reserve	RSA	330	X	X	X

280 km^2), Vhembe Private Nature Reserve (VPNR, 307 km^2), Venetia Limpopo Nature Reserve (VLNR, 330 km^2); and in Zimbabwe, Sentinel Ranch (SR, 320 km^2) and the Tuli Circle (TC, 416 km^2) (Fig. 1, Table 1).

Between May 2007 and October 2015 we captured and fitted GPS collars to a total of nine adult (4+ years) lions (7 males, 2 females) (Africa Wildlife Tracking, Pretoria, South Africa) throughout our study area. Based on an average collar life of 2 years, and re-collars of some animals, this represented a total of 26 lion-years' of movement data. GPS collar readings ranged between 4 and 8 hourly readings per day. Lions were captured using standard lion capture techniques (Smuts *et al.*, 1977). Lions were immobilized with a combination of 0.03–0.05 mg/kg medetomidine 20 mg/ml (Kyron Laboratories, South Africa) and 0.5–1.0 mg/kg Zoletil 100 (tiletamine-zolazepam) (Virbac, South Africa) based on estimated weight by dart injection by a Botswana registered wildlife veterinarian. Medetomidine was reversed with 0.2 mg/kg atipamezole 5 mg/ml (Pfizer, South Africa) administered intramuscularly.

We calculated lion home range size in ArcGIS (ESRI, Redlands, California) extension software ArcMET (Wall, 2014) by using a 95% kernel density estimate (KDE) isopleth. Kernel bandwidth also called a smoothing parameter, reference ($^{h}{}_{REF}$) (Worton, 1989) was used for the calculations, due to its objectivity and computational simplicity. KDE spatial resolution was set at 30 × 30 m in keeping consistency with all other spatial data used for this study. The average height of each utilization distribution (UD, Van Winkle, 1975) was calculated using Focal Statistics on a 3 × 3 cell basis. After UDs were converted from raster to point format types, the Extract Multi Values to Points feature in ArcGIS was used to assign values to each location from the covariates in this study. To provide a normal distribution, the natural log (100-UD) was used as the response variable whereby higher values indicate higher levels of utilization. We square root-transformed elevation (m), distance to rivers (m) and settlements (m), and used the log of terrain ruggedness index before RUF analysis. Variance Inflation Factor (VIF) in software R (R Development Core Team, 2014) was used to determine multicollinearity between our set of variables (package 'usdm' (Naimi, 2015). Any variable with a VIF larger than 10 was excluded from that particular individual's model (Dormann *et al.*, 2013).

Utilization distributions and resource utilization functions

We created UDs to investigate how environmental and anthropogenic factors affected lion space use in the study area by quantifying third-order selection, which is the differential space use patterns of an individual within its home range (Johnson, 1980). RUFs are considered a continual probabilistic density function (Silverman, 1986) that calculate an individual's space use where the height of a UD at each location represents the level of utilization relative to the rest of the locations while accounting for spatial autocorrelation (Van Winkel, 1975; Kernohan *et al.*, 2001; Hepinstall *et al.*, 2005). A particular strength of using the UD approach is estimating a UD for each study animal, which treats the animal as a primary sampling unit (Otis & White, 1999; Erikson *et al.*, 2001).

The landscape features that drive variation between the UD values of each location can be determined using multiple linear regression. Positive (+) and negative (–) signs indicate whether use increases or decreases with variation in the quantity of that resource (Marzluff *et al.*, 2004). Standardized coefficients allow for comparisons between variables, determines the statistical significance of each variable using 95% CIs, ranks relative importance of variables by their absolute value, and determines the positive or negative influence of each variable on animal space use, whereas unstandardized coefficients are used for predictive mapping occurrence (Marzluff *et al.*, 2004). In this study, we focus on the standardized coefficients given their statistical relevance for testing our hypotheses: relative preference for riparian areas and avoidance of human settlements.

Spatial autocorrelation, often evident in ecological studies (Schiegg, 2003), was accounted for by the RUF using maximum likelihood procedure with a Matern correlation function (Marzluff *et al.*, 2004). For each predictor variable, the mean standardized β coefficient and associated variance were calculated using the Delta method (Powell, 2007). The standardized partial regression coefficients from each variable were estimated by

$$\beta j = \hat{\beta} j \frac{s_{xj}}{S_{\mathrm{RUF}}}$$

where $\hat{\beta} j$ is the maximum likelihood estimate of the partial regression coefficient from the multiple regression estimates (unstandardized β), S_{xj} is the standard deviation of the resource value *j*, and S_{RUF} is the estimate of the standard deviation of the UD values (Marzluff *et al.*, 2004). As each lion was taken to be independent from year to year (Kertson *et al.*, 2011), population-level estimates were calculated by averaging the RUFs across all lions with variance calculated to include both between and within lion variance (Marzluff *et al.*, 2004). Significant predictors of space use were identified by not having 95% confidence intervals that overlapped with zero (Marzluff *et al.*, 2004). All means are given ± S.E. All statistical analysis was done using R (version 2.13, R Core Development Team, 2014). RUF analyses were performed using the package ruf.fit (http://csde.washington.edu/~handcock/ruf/).

An overall mean from the population level is useful to evaluate what the lion population is responding to overall, whereas the inter-individual level results are useful to tease apart what factors could have attributed to each specific lion's space use for that particular year (Kertson *et al.*, 2011).

Covariates

We identified environmental and anthropogenic features of the landscape that were hypothesized *a priori* to be good predictors of lion space use. Covariates included: land cover (Funston *et al.*, 2001; Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Davies *et al.*, 2016), land use (Woodroffe, 2000; Woodroffe, 2001), elevation, terrain ruggedness (Hopcraft *et al.*, 2005; van Dyk & Slotow, 2003), distance to human settlements (Valeix *et al.*, 2012; Elliot *et al.*, 2014; Cotteril *et al.*, 2015), and distance to rivers (Hopcraft *et al.*, 2005; Balme *et al.*, 2007; Mosser *et al.*, 2009).

Inferences from standardized coefficients with 95% confidence intervals that did not overlap with zero were considered significant predictors of a particular resource (Marzluff *et al.*, 2004). For example, for distance metrics, positive values mean an avoidance of that landscape feature whereas negative values would indicate selection. For terrain ruggedness and elevation, positive standardized β coefficients indicate selection of rugged terrain or elevation, whereas the opposite is true for negative values. The relative importance of landscape metrics was ranked using the magnitude of the mean standardized β coefficients. Wet and dry seasons were defined as ranging from November to March and April to October, respectively.

RESULTS

Lions were tracked on average 808 (S.E. = 272) days resulting in a total of 26 345 GPS fixes with an average of 2927 fixes per lion (S.D. = 2131, ranging from 900 to 8137). Lions moved on average 1477 m (S.E. = 409, *n* = 9) between 6-hr fixes. Furthermore, only nocturnal GPS readings were used in the analysis, providing insight into lion spatial ecology during the period when they are most active (Hayward & Slotow, 2009)

Resource selection

Due to multicollinearity, the weighted importance of land use to lions was excluded from the RUF model and instead calculated by using the percentage of GPS locations that fell within four land-use zones: protected, semi-protected, unsafe and hostile. Factors considered to influence lion survival and safety included: human tolerance towards lions (measured by interviews and interactions with the landowners), the risk of being shot, the presence of livestock and whether lions were known to have been shot and killed in each zone (Table 2). Protected and semi-protected areas categorized in this study made up 42% of the total study area and contained 95% of all recorded lion GPS locations (Table 2). It is worth noting that 73% of lion locations were recorded in only 14% of the study area (Table 2).

Population-level

We estimated population level RUFs for lions in the GM-TFCA during the dry and wet seasons between 2008 and 2015, with an average of 183 locations per individual for each 6-month season. Mean standardized $\hat{\beta}$ coefficients at the population level across seasons provided little evidence for landscape-level influences on lion resource utilization as all landscape composition variables overlapped zero (Table 3). Mean standardized $\hat{\beta}$ coefficients for elevation ($\hat{\beta}$ ± S.E., 95% CI's) (–0.190 ± 0.108, CI = –0.401, 0.021) and distance to human settlements (0.173 ± 0.105, CI = –0.034, 0.379) provided some evidence for low elevation and avoidance of human settlements driving space use (Fig. 2, Table 3). When we evaluated data by season, we found that strong evidence for avoidance of elevation (–0.278 ± 0.107, CI = –0.4881, –0.0676) on space use during the dry season, which suggests that lions at the population level are selecting lower-lying areas in the study area (Fig. 2). We found little evidence for landscape feature effects on space use during the wet season, although there was some evidence that low elevation may have driven space use during wet months (Fig. 2).

Individual-level – Combined season

We found no evidence that land cover affected resource selection within home ranges at the individual level across seasons (Table 3). However, the geographic and topographic features of the study area were significant drivers of space use. We found strong support for effects of elevation, distance to rivers and settlements, and to a lesser degree terrain ruggedness, as predictors of space use (Table 3). Eighty-three per cent of lions (15/18) showed effects of elevation on space use, and 77% of our study individuals (14/18) preferred lowlands within their home ranges. Lions showed a strong avoidance of proximity to human settlements; 66% (12/18; Table 3) of individuals in our sample selected for areas within their home range that were farther from human settlements ($\bar{x}$ (range): 3925.3 m (30.3–10457.5; Table 4). The directionality of space use as regards distance to rivers was mixed; 44% (8/18) of lions selected areas closer to rivers, and nearly 17% (3/18) strongly selected for regions farther from rivers (1774.1 m (0–4449.0; Table 4). Space use of the

Table 2. Land-use summary of the Greater Mapungubwe Transfrontier Conservation Area incorporating Botswana, South Africa and Zimbabwe at the time of the study (2007–2015).

Class	Size (km²)	% of GM-TFCA	% of lion GPS locations	Human tolerance towards lions	Risk of lions being shot/hunted	Livestock	Lions known to have been shot and killed
Protected	926	14	73	High	None	None	No
Semi-protected	1 916	28	22	High	Moderate	None	Yes
Unsafe	234 909	35	4	Low	Moderate	High	Yes
Hostile	1 586	23	1	None	High	High	Yes

Table 3. Mean estimates of standardized RUF coefficients (β), standard error, 95% lower- and upper confidence intervals and inter-lion resource selection of resources where the 95% C.I did not include zero, for nine lions (up to n = 22 lion years' of data) in the Greater Mapungubwe Transfrontier Conservation Area during the study (2008–2015). Signs (±) indicate whether the use of resource increases or decreases with increasing quantity of that resource. TRI = Terrain Ruggedness Index, Inter-lion resource selection is based on the number of lions with use significantly associated with the resource. Positive (+), negative (−) or 'ns' (Not significant).

	Combined seasons					Wet season					Dry season				
	β	S.E.	L95CI	U95CI	+/−/ns	β	S.E.	L95CI	U95CI	+/−/ns	β	S.E.	L95CI	U95CI	+/−/ns
Dense Veg	0.038	0.156	−0.269	0.345	**0,0,18**	0.055	0.142	−0.223	0.333	**0,0,22**	0.072	0.154	−0.230	0.374	**0,0,18**
Woody/Grass	0.044	0.165	−0.279	0.366	**0,0,18**	0.058	0.151	−0.238	0.353	**0,0,22**	0.083	0.162	−0.235	0.401	**0,0,18**
Woody No Grass	0.028	0.165	−0.294	0.350	**0,0,18**	0.044	0.151	−0.252	0.339	**0,0,22**	0.086	0.162	−0.232	0.403	**0,0,18**
Open Ground	−0.007	0.154	−0.309	0.296	**0,0,18**	0.022	0.154	−0.280	0.324	**0,0,20**	0.056	0.167	−0.273	0.384	**0,0,16**
Settlements distance	0.173	0.105	−0.034	0.379	**12,1,5**	0.073	0.096	−0.115	0.262	**10,7,5**	0.121	0.105	−0.086	0.327	**9,4,5**
River distance	−0.034	0.104	−0.237	0.169	**3,8,7**	0.008	0.095	−0.178	0.193	**6,8,8**	0.007	0.104	−0.196	0.211	**6,5,7**
Elevation	−0.190	0.108	−0.401	0.021	**1,14,3**	−0.185	0.098	−0.378	0.007	**1,16,5**	−0.278	0.107	−0.488	−0.068	**0,15,3**
TRI	−0.004	0.093	−0.185	0.178	**0,2,16**	−0.011	0.086	−0.180	0.159	**2,4,16**	0.033	0.097	−0.157	0.222	**5,2,11**

majority of lions (89%, n = 16/18) was not affected by terrain ruggedness, only 11% (2/18) showed avoidance of rough terrain 3.5 m (1.6–9.0; Table 4).

Inter-individual level – Dry season

The mean standardized $\hat{\beta}$ coefficients for the four vegetation classes provided no evidence of an effect of vegetation type on space use (Table 3, Fig. 2). However, we did find that geographic and topographic variables were important factors underlying lion distribution (Table 3). The majority, 83% (15/18), of lions showed a significant preference within their home range for lower-lying areas (Table 3) with three having no preference. Avoidance of human settlements in the dry season decreased slightly from the combined season; 50% (9/18) of lions avoided areas close to human settlement 4988.8 m (42.8–17083.9) and four lions (22%) selected areas closer to people 2595.2 m (30.3–10457.5, Table 4). Thirty-three per cent (6/18) of lions selected areas away from rivers 1373 m (0.0–4449.0), while five lions (25%) selected areas closer to rivers 25.95.2 m (30.3–10457.5, Table 4). Sixty-one per cent (11/18) of lions did not show any evidence of preference related to terrain ruggedness, while five lions (27%) indicated selection for rougher terrain 5.4 (1.6–17.2); two lions (11%) showed a selection of smoother terrain 3.9 (1.6–16.9).

Inter-individual level – Wet season

Vegetation type was not a driver of space use during the rainy season (Fig. 2). However, we detected substantial variability among lions in their response to elevation, distance to rivers and human settlements, and terrain ruggedness (Table 3, Fig. 2). Sixteen of 22 (73%) lions showed some evidence for the high use of lower-lying areas 558.8 m (484.0–715.0, Table 4), yet only one lion selecting low-lying areas (Table 3, Fig. 2). Forty-five per cent (10/22) of lions used areas farther away from people 4335.7 m (30.3–16714.2) and 31% (7/22) selected regions closer to human habitation 3029.3 m (30.3–14596.0). Thirty-six per cent (8/22) of lions preferred areas closer to rivers 975.4 m (0.0–4426.0), whereas 27% (6/22) lived in areas farther away from river systems 1474.9 m (0.0–4520.9). Seventy-two per cent of lions (16/22) showed no evidence of effects of terrain ruggedness within their home range; four lions (18%) selected areas with lower ruggedness 3.6 (1.6–16.9), and one lion selected areas that were rugged.

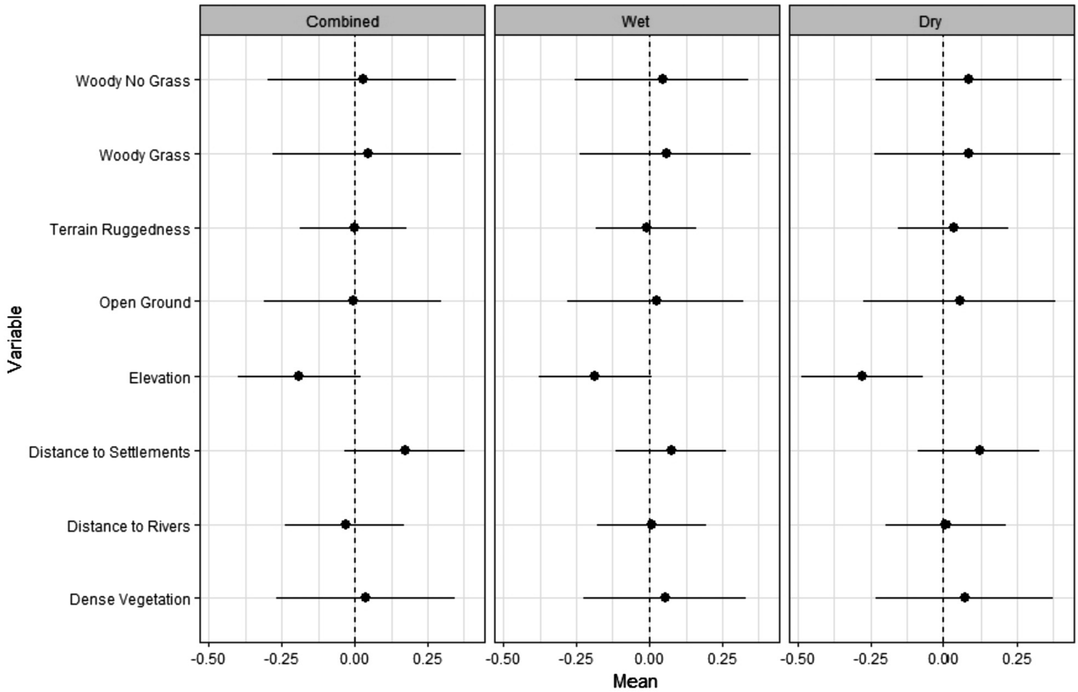

Fig. 2. Mean standardized β coefficients (95% CI) for lion resource utilization at the population level for combined, wet (Nov–Mar) and dry (Apr–Oct) seasons in the Greater Mapungubwe Transfrontier Conservation Area during the study period (2007–2015). Signs (+/–) indicate whether the use of the specific resource increases or decreases with increasing quantity of that resource.

Table 4. Mean (range) values of environmental and anthropogenic features of the landscape used by African lions (*Panthera leo*) in the Greater Mapungubwe Transfrontier Conservation Area during the study (2008–2015). TRI = Terrain Ruggedness Index. Positive (+), negative (–) or 'ns' (not significant).

Landscape features		**Combined season**	
	+	**–**	**NS**
Settlement distance (m)	3925.3 (30.3–10457.5)	2381.7 (95.7–9249.1)	2451 (30.3–10457.5)
River distance (m)	1774.1 (0.0–4449.0)	747.7 (0.0–4155.6)	1434.5 (0.0–4449.0)
Elevation (m)	584.4 (512.0–644.0)	553.6 (0.0–721.0)	570.4 (492.0–617.0)
TRI	na*	3.5 (1.6–9.0)	4.2 (0.0–17.6)
		Wet season	
	+	**–**	**NS**
Settlement distance	4335.7 (30.3–16714.2)	3029.3 (30.3–14596.0)	3058.8 (67.7–11647.9)
River distance	975.4 (0.0–4426.0)	975.4 (0.0–4426.0)	927.4 (0.0–4121.9)
Elevation	574.4 (492.0–617.0)	558.8 (484.0–715.0)	562.6 (505.0–660.0)
TRI	4.6 (1.8–13.3)	3.6 (1.4–18.5)	3.9 (1.4–17.6)
		Dry season	
	+	**–**	**NS**
Settlement distance	4988.8 (42.8–17083.9)	2595.2 (30.3–10457.5)	2706.9 (90.8–16160.3)
River distance	1373.0 (0.0–4449.0)	677.9 (0.0–3878.8)	1294.2 (0.0–4424.3)
Elevation	na	na	na
TRI	5.4 (1.6–17.2)	3.9 (1.6–16.9)	3.7 (0.0–17.3)

*na = not available.

DISCUSSION

Large carnivores are a critical component of any ecosystem, and their extirpation has impacts that may reverberate throughout ecosystems (Estes *et al.*, 2011, Ripple *et al.*, 2010, 2014). Thus, understanding how they utilize their landscape is becoming increasingly important given their global population declines (Packer *et al.*, 2013, Ripple *et al.*, 2010, 2014, Bauer *et al.*, 2015). Lion populations in modern Africa can accurately be described as fragmented and scattered across the continent (IUCN, 2013; Bauer *et al.*, 2015). Conservation of smaller, isolated lion populations has become essential in the quest to curb the current decline (Riggio *et al.*, 2016). Understanding what factors drive lion space use that underlies landscape-level distribution is essential for their conservation efforts.

Vegetation

In this study, none of the four vegetation classifications (dense vegetation, woody-grass, woody-no-grass, and open ground) showed any notable selection by lions at both the population and individual levels, which implies that lions were not selecting any particular type of land cover in the study periods investigated here. With the majority (95%) of lion GPS locations within less than half (42%) of the total study area (Table 2), the contrast from our findings to that of Hopcraft *et al.* (2016) and Davies *et al.* (2016) could be because lions are forced to utilize all available habitat within the protected and semi-protected classified landscapes.

Distance to rivers

Proximity to riverbeds is an important factor underlying lion space use as these areas provide dense cover for both hunting and shade. The linear features also offer greater opportunities for encountering prey seeking water and suitable food resources (Hopcraft *et al.*, 2005; Mosser & Packer, 2009; De Boer *et al.*, 2010). However, dry and wet seasonal differences in selection for riverbeds might be observed as illustrated by Lehmann *et al.* (2008). Due to a wider abundance and distribution of water sources during the wet season, prey tends to be widely distributed. Thus, prey density is often less dense in high-risk areas such as riverbeds during the wet season. In contrast, prey animals are forced to enter high-risk zones to gain access to water and food in the dry season (Lehmann *et al.*, 2008; De Boer *et al.*, 2010). We found that proximity to rivers had little influence on space use at the population level during the wet, dry and combined seasons. Even at the inter-individual level, our analyses found no clear indication that lions selected areas closer to rivers during the dry season or further away in the wet season. During both the wet and dry season, approximately one-third of our sample of lions showed selection for areas of their home range that were close to river systems, one-third showed selection for areas farthest from rivers, and one-third showed no selection with regard to distance from rivers. We believe that these results can be explained by a combination of both the size of the study area and the distribution of rivers and drainage lines classified in this study. Drainage lines and major rivers, such as the Limpopo, Shashe, and Motloutse River were all categorized as ‘rivers’ collectively, not primary or secondary river systems. Whether these rivers were flowing or not during our study would have also influenced prey distribution (Polis *et al.*, 1997; Gaylard *et al.*, 2003) and, by extension, lion space use.

Elevation

Elevation in the dry season was the only significant predictor of lion space use in our pooled analyses (population level). In addition, more than three-quarters of the individuals in our sample showed selection for lowland areas in the wet and dry seasons. Elevation has not, to our knowledge, been recorded as a major driver of African lion space use previously. Hopcraft *et al.* (2005) found that lions living on the plains of the Serengeti used view-sheds from rocky outcrops as a means to increase their view range. This effect, however, was not detected for lions living in the woodlands of the Serengeti (Hopcraft *et al.*, 2005), which implies that lions in flatter geographic landscapes might use higher elevated vantage points as a fine-scale hunting tactic when they scan during hunting. We did not use a fine-scale approach in our study with specific viewsheds; rather, elevations were relative to the extent of the study area. One plausible argument for this finding is that lions from the GM-TFCA predominantly occupy territories that are situated in protected and semi-protected areas, and these protected areas are located in the lowlands of the study area.

Distance to human settlements

Lions are vulnerable to direct persecution by humans, and as with most large carnivores, their presence or absence in an area could be an ecosystem indicator to the degree of human impact on that region (Woodroffe, 2001). Oriol-Cotterill *et al.* (2015) found that lions showed behavioural changes in response to human-caused mortality risk that ultimately depended on environmental factors such as rainfall and moon phase. Their study also revealed that lion movements within a 1.5 km radius were affected by human presence. More importantly, Oriol-Cotteril *et al.* (2015) found that lions showed significantly, but not total, avoidance of pastoral lands.

Our results demonstrated that at the population level, pooling across all seasonal categories, lion space use within their home range did not appear to be influenced by the proximity to human settlements. However, at the inter-individual level, 67% (n = 12) of lions utilized areas within their home range further away from human settlements across both seasons. During the dry and wet seasons, lions at the individual level showed less clear preference to human-dominated areas with 45% (n = 10) and 50% (n = 9) utilizing areas further from human proximity, respectively. Our study used human presence/absence as a covariate and not human density, which may have shed further light on the subject.

We suggest that lions might have different avoidance tendencies for remote cattle posts, which are defined as small settlements, lived in by the people looking after their cattle that graze in the surrounding region, than for larger villages. Lions will move near cattle posts (A. Snyman, unpubl. data; Oriol-Cotterill *et al.*, 2015), but these movements are typically on dimly lit nights and at higher speeds (Valeix *et al.*, 2012). In contrast, areas with human densities above 25 people/km^2 are believed to be highly unsuitable for lions and are avoided at all times (Woodroffe, 2000; Riggio *et al.*, 2013), even though livestock associated with the villages are largely unattended. Therefore, avoidance patterns may be an example of fine-scale spatiotemporal adjustments, where larger villages were predominantly avoided (A. Snyman, unpubl. data). Our data on distance to settlements suggest that lions selected areas that were generally far from settlements for their home range, and this initial level of selection appears to have importance. Once established in a home range, our data suggest that lions were not as selective of where they moved within the home range, and this may have been due to a dependence on their initial choice of the boundaries of their home range to minimize disturbance from humans, which is similar to the findings of Kuiper *et al.* (2015). Furthermore, less than 5% of all reported cases of livestock depredation (31 cases from 702) over an 18-month period were attributed to lions (Brassine, 2014) in this study area; most depredation was caused by spotted hyaena (*Crocuta crocuta*) (>33%). Brassine (2014) also found that over 47% of respondents to a questionnaire claimed that lions were completely absent from communal farmlands.

Terrain ruggedness

At both the population and individual levels, lions did not show any preference, or avoidance, for terrain ruggedness within their home ranges during any season. Unlike African wild dogs (*Lycaon pictus*) that prefer rugged terrain as a survival mechanism when choosing a denning site (Mills and Gorman, 1997; Van Dyk & Slotow, 2003; Jackson *et al.*, 2014), lions generally do not prefer rugged, mountainous terrain. The GM-TFCA has a wide variety of landscapes ranging from open plains to woodland thickets and wetlands, to cliffs and rugged sandstone ridges. Prey abundances are higher in lower-lying areas with nutrient-rich soils that support a diverse flora community (Polis *et al.*, 1997). Water sources are also predominantly found in riverbeds and human-made features such as dams and weirs, which are typically not found on ridges and rough mountainous terrain.

CONCLUSION

Our analyses showed that lions in the GM-TFCA did not respond to vegetation type, distance to rivers and terrain ruggedness within their home ranges. Rather, lions showed a preference for low-lying areas and utilized areas within their home range that were farther away from human settlements. Lions avoided areas that were classified as hostile and unsafe, with approximately three-quarters of locations in protected areas and a quarter of locations in semi-protected areas.

Our results inform conservation efforts for lions that typically exist in isolated populations. We suggest that conservation efforts to create corridors to improve lion movement and reduce mortality to increase population viability should focus on areas in the lower-lying regions of the GM-TFCA as well as areas away from human settlements. The wide-ranging nature of lions and the danger they pose to both livestock and human life makes conserving and protecting them a challenging and complex task. For example, the lack of avoidance of settlements by some lions in our study exemplifies the problems of trying to find a 'one-size-fits-all' solution for lion conservation. Indeed, individual variation among lions can result in a range of potential for human–wildlife conflicts. Perhaps the most critical observation from our study is that individual lions acted very differently as they used the landscape, which suggests the need for management plans that are landscape- and case-specific.

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