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Cats, connectivity and conservation: incorporating data sets and integrating scales for wildlife management

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Summary

1. Understanding resource selection and quantifying habitat connectivity are fundamental to conservation planning for both land-use and species management plans. However, data sets available to management authorities for resource selection and connectivity analyses are often highly limited and fragmentary. As a result, measuring connectivity is challenging, and often poorly integrated within conservation planning and wildlife management. To exacerbate the challenge, scale-dependent resource use makes inference across scales problematic, resource use is often modelled in areas where the species is not present, and connectivity is typically measured using a source-to-sink approach, erroneously assuming animals possess predefined destinations.

2. Here, we used a large carnivore, the leopard *Panthera pardus*, to characterise resource use and landscape connectivity across a vast, biodiverse region of southern Africa. Using a range of data sets to counter data deficiencies inherent in carnivore management, we overcame methodological limitations by employing occupancy modelling and resource selection functions across three orders of selection, and estimated landscape-scale habitat connectivity – independent of *a priori* source and sink locations – using circuit theory. We evaluated whether occupancy modelling on its own was capable of accurately informing habitat connectivity, and identified conservation priorities necessary for applied management.

3. We detected markedly different scale-dependent relationships across all selection orders. Our multi-data, multi-scale approach accurately predicted resource use across multiple scales and demonstrates how management authorities can more suitably utilise fragmentary data sets. We further developed an unbiased landscape-scale depiction of habitat connectivity, and identified key linkages in need of targeted management. We did not find support for the use of occupancy modelling as a proxy for landscape-scale habitat connectivity and further caution its use within a management context.

4. *Synthesis and applications*. Maintaining habitat connectivity remains a fundamental component of wildlife management and conservation, yet data to inform these biological and ecological processes are often scarce. We present a robust approach that incorporates multi-scale fragmentary data sets (e.g. mortality data, permit data, sightings data), routinely collected by management authorities, to inform wildlife management and land-use planning.

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We recommend that management authorities employ a multi-data, multi-scale connectivity approach – as we present here – to identify management units at risk of low connectivity.

Key-words: circuit theory, conductance, fragmentation, landscape resistance, land-use planning, leopard, occupancy modelling, *Panthera pardus*, permeability, resource selection functions

Introduction

Habitat loss, fragmentation and degradation are primary causes of global biodiversity loss (Fahrig 2003). Habitat connectivity confers ecosystems with greater resilience towards disturbance (Olds *et al.* 2012), and ultimately facilitates species persistence (Doerr, Barrett & Doerr 2010). Conservation of connectivity has thus become a well-established concept (Zeller, McGarigal & Whiteley 2012), which seeks to maintain or restore genetic exchange between populations (Stockwell, Hendry & Kinnison 2003), thus reducing levels of inbreeding and genetic drift (Soulè & Mills 1998), and provides opportunities for mitigating the negative effects of environmental and demographic stochasticity in a changing world (Hodgson *et al.* 2009). Although globally recognised, connectivity is often poorly considered, or simply does not feature, within wildlife management. As a fundamental component of connectivity conservation, practitioners must identify resources within habitats that facilitate species movement and persistence. Several methods are available to model resource selection and connectivity (Zeller, McGarigal & Whiteley 2012); however, none are without limitations. First, resource selection is scale-dependent, such that inference at one scale may not adequately explain resource use at another (Boyce 2006). Second, resource selection within a used-available design is constrained by an ‘asymmetry of errors’ (Boyce 2006), where presence data are observed and known with certainty, but absence data are less certain and often randomly assumed (MacKenzie *et al.* 2006). Third, connectivity is often modelled using a source-to-sink approach (McRae *et al.* 2008), which assumes that animals have a predefined destination (Koen *et al.* 2014). To overcome the constraints of scale dependency, resource selection can be integrated across multiple scales (DeCesare *et al.* 2012; Martin *et al.* 2012); while occupancy modelling may be used to account for imperfect detection and more accurately capture resource use at appropriate scales (Gu & Swihart 2004). Similarly, to overcome source-to-sink limitations, connectivity can be mapped across the landscape – irrespective of predefined destination locations – using unbiased spatial techniques (Koen *et al.* 2014).

Here, we use a wide-ranging large carnivore, the leopard *Panthera pardus*, as a model species to estimate resource use and landscape connectivity across leopard range in Limpopo Province, South Africa (hereafter ‘Limpopo’). Leopards are long distance dispersers (Fattebert *et al.* 2015). Their high vagility, and ecological and economic significance (Dalerum *et al.* 2008; Lindsey *et al.* 2012; Maciejewski & Kerley 2014) make leopards an ideal candidate species to identify landscape-scale conservation priorities. Using a range of techniques that overcome the limitations mentioned above, we estimated leopard resource selection across three orders of scale (Meyer & Thuiller 2006): S_1, first-order population-level selection across the study area; S_2, second-order landscape-level selection across key leopard areas; and S_3, third-order individual-level selection across individual home ranges. Specifically, by using occupancy modelling to infer probable locations that are available to leopards across the broader landscape (S_1), and resource selection functions (RSFs) to link finer-scaled habitat relationships (S_2 and S_3), we produce a scale-integrated description of leopard resource use. We use this to develop an unbiased landscape-scale representation of leopard habitat connectivity using circuit theory to identify critical movement pathways across the region (McRae *et al.* 2008). Since broad-scale occupancy data can be conveniently and cheaply collected using questionnaire surveys (Zeller *et al.* 2011), we evaluate whether occupancy modelling on its own is capable of accurately informing habitat connectivity (as derived from circuit theory); with the intention of providing a simple method of incorporating both occupancy and connectivity analyses under a single framework. Finally, we show how our multi-scale approach can be used to identify conservation priorities. Our results provide an unbiased landscape-scale depiction of leopard resource use and connectivity optimised for both finer- and coarser-scaled management objectives applicable for large carnivore conservation and land-use planning more generally.

Materials and methods

STUDY AREA

Limpopo (c. 125 977 km^2; Fig. 1) is rich in biodiversity and comprises the largest proportion of suitable leopard habitat in South Africa (Swanepoel *et al.* 2013). A number of formally protected areas occur throughout Limpopo, the most significant being the Kruger National Park (KNP). KNP represents an important source population for leopards within the study area, and is largely unaffected by human-mediated disturbance (Bailey 2005). Outside of KNP, leopards in Limpopo – and South Africa more generally – are managed within geographical catchments representing leopard management units (LMUs). The primary

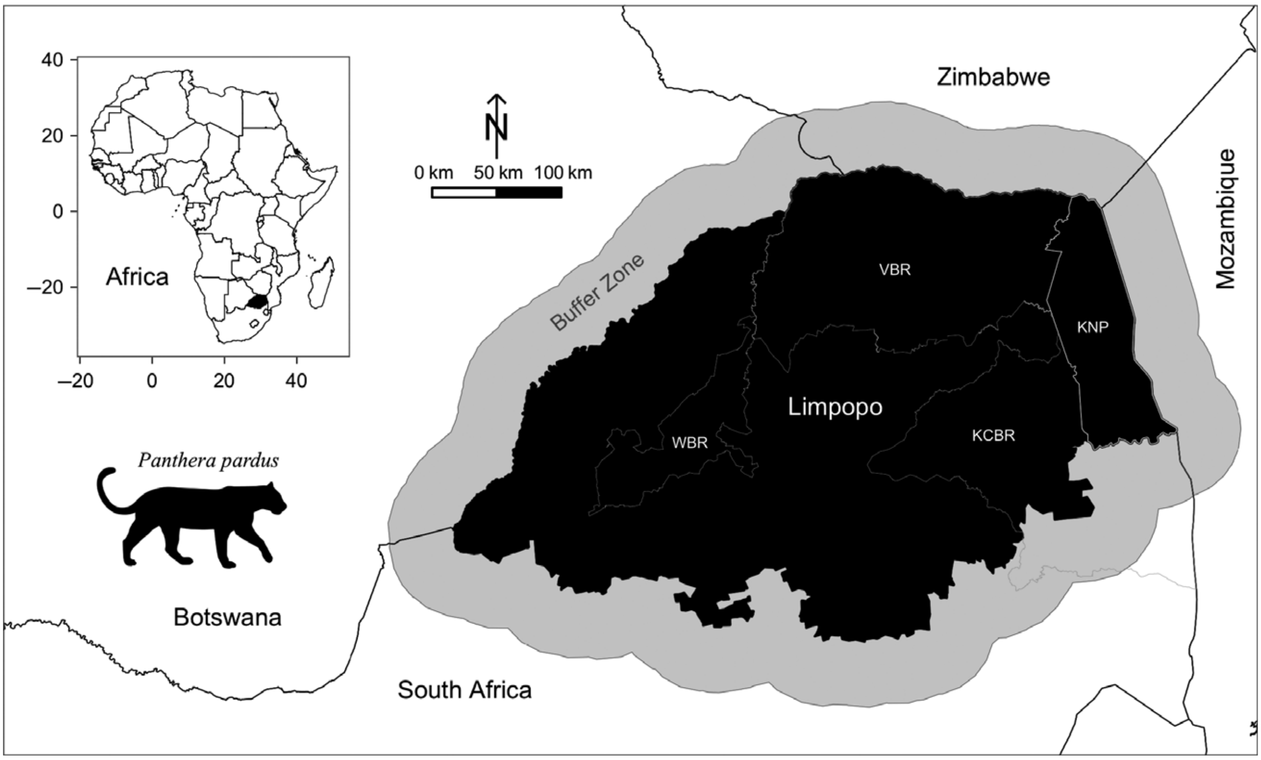

Fig. 1. Location of the study area situated between northern South Africa, Botswana, Zimbabwe and Mozambique. The grey region around Limpopo Province, South Africa ('Limpopo'; black polygon) represents the 50 km buffer used to develop an unbiased landscape permeability map. Limpopo represents a highly biodiverse region of southern Africa, comprising three UNESCO Biosphere Reserves: Waterberg Biosphere Reserve (WBR), Vhembe Biosphere Reserve (VBR) and Kruger to Canyons Biosphere Reserve (KCBR). Kruger National Park (KNP) lies adjacent to Limpopo's eastern boundary. Inset represents the location of the study area within Africa.

carnivore management practices in Limpopo (i.e. trophy hunting and problem animal control) are strictly designated within LMUs (Pitman *et al.* 2015).

FIRST-ORDER (S_1) SCALE OF SELECTION

In order to delineate leopard distribution at the broadest scale, we developed a multi-season occupancy model using questionnaire surveys (Zeller *et al.* 2011). The study area (Limpopo and buffer zone; Fig. 1) was divided into 596 sampling cells (20 × 20 km). A random stratified sampling approach was used to select a subset of sampling cells to conduct interviews with local inhabitants across Limpopo (Fig. S1, Supporting Information). Respondents acted as surveyors within their 'area of knowledge' defined by a single or group of sampling cells, where each interview from the same sampling cell was considered a separate replicate (Zeller *et al.* 2011). To avoid including residents that spent very little time on their properties, interviews specifically targeted individuals who were resident within their 'area of knowledge' at least twice per month for a minimum of 1 year. Detections comprised a direct sighting of a leopard or direct observation of sign (e.g. tracks, scat, vocalisations or cached kill). To assess the credibility of each respondent, we asked them to identify photographs of four local species and the tracks of five local species (Fig. S1). If a respondent was considered non-credible by failing to correctly identify leopard during the vetting process, their data were excluded from all analyses. Surveys were conducted within 98 sampling cells during November 2013 ($n = 1024$ respondents). In November 2014 ($n = 736$) and November 2015 ($n = 560$), the same respondents were contacted via telephone to conduct the questionnaire verbally. Respondent attrition across years was due to death, change of contact details or residency. A further ground survey was conducted during November 2015 to increase respondent sample size ($n = 599$ additional respondents) across a randomly stratified subset of sampling cells ($n = 55$). The distribution of S_1 data can be visualised in Fig. S2.

For multi-season occupancy analyses, we used the package *unmarked* (Fiske & Chandler 2011) within the R statistical environment (R Core Team 2015). Interview responses resulted in detection/non-detection matrices, with a maximum of 40 replicates per sampling cell. Due to potential fluxes in leopard occupancy over the sampling intervals, the assumption of population closure was violated (MacKenzie *et al.* 2006), which changed the occupancy parameter (ψ) from 'proportion of area occupied' to 'proportion of area used'. This new interpretation was sufficient to meet our goals, since we were interested in the use of sampling cells, rather than occupation of them (Zeller *et al.* 2011). We used a suite of standardised (mean = 0; standard deviation = 1) resource variables expected to influence leopard distribution (Table S1), and extracted mean values for each resource variable across each sampling cell. Multi-season occupancy modelling seeks to estimate probabilities of occupancy, detection (P), colonisation (γ) and extinction (ϵ). We modelled each component (i.e. ψ, P, γ, ϵ) as functions of resource variables using logit link functions (MacKenzie *et al.* 2006) by employing a sampling design whereby surveyors (i.e. respondents) visit a sample of M sampling cells and record the binary response Y_{ij} of species detection ($Y = 1$) or non-detection

($Y = 0$) during $j = 1,\ldots, J_i$ visits to the ith site during a season (MacKenzie *et al.* 2002). We fitted models with increasing complexity and used Akaike's information criterion (AIC) for model selection (Burnham & Anderson 2002). Within each model component, we introduced resource variables in a fixed sequence. On identifying a preferred model, and using a backwards stepwise approach, we tried all possible single-term deletions and retained the most parsimonious models (Kéry, Guillera-Arroita & Lahoz-Monfort 2013). We retained non-significant variables within candidate models if they increased parsimony and were ecologically justified. Model-averaging was applied to the most supported models (ΔAIC $\leq$2). The final averaged model was used to predict ψ for each sampling cell across the study area, and was used to delineate available habitat in our S_2 RSF.

SECOND- (S_2) AND THIRD-ORDER (S_3) SCALE OF SELECTION

In order to assess leopard resource use at an intermediate scale, S_2 data sets were collected from 2000 to 2015 and comprised published ($n = 580$ locations) (Swanepoel, Somers & Dalerum 2015) and unpublished camera-trapping studies ($n = 1745$ locations; R. Pitman/Panthera, unpublished data), expert sightings data ($n = 1384$ locations) (Pitman *et al.* 2013) and leopard mortality data ($n = 1176$ locations) (Pitman *et al.* 2015). We randomly distributed an equal number of available locations across the study area, but excluded any areas where ψ was within the lower 25th percentile, as described by our occupancy model. Excluding regions within the lower 25th percentile effectively refined our approach at the landscape-level (S_2), and allowed for the exclusion of areas mostly unoccupied by leopards. Although a 25th percentile threshold could be considered arbitrary, this cut-off adequately depicted leopard exclusion areas suggested by previous research (Swanepoel *et al.* 2013).

Leopard resource use at the finest scale (i.e. home ranges) was assessed by collating a range of S_3 data sets comprising global positioning system (GPS) collar data and expert long-term sightings data of known individuals from 2004 to 2015. GPS collar data from 18 adult leopards were obtained from provincial research surveys ($n = 2$ leopards; North West Parks and Tourism Board), published studies ($n = 8$ leopards) (Swanepoel, Dalerum & van Hoven 2010; Pitman, Swanepoel & Ramsay 2012; Pitman *et al.* 2013; Swanepoel *et al.* 2014) and unpublished research ($n = 8$ leopards; R.A. Hill). GPS location accuracy metrics (e.g. dilution of precision) were not recorded. All collars acquired a GPS location fix $\geq$4 times per day over the duration of each collar's life span ($n = 24\,027$ locations). The GPS collar data set was filtered by removing any erroneous locations that were beyond the possible range of the study animals (D'Eon *et al.* 2002). Long-term sightings data of known adult individuals were compiled from the Sabi Sands Game Reserve (SSGR; $n = 17\,942$ locations; 62 individuals). While traversing all habitat types within SSGR, field guides are required to record daily leopard sightings, resulting in comprehensive data sets for each known individual (Balme *et al.* 2012). We generated 95% fixed-kernel home ranges for both GPS collared and resighted individuals (using the reference bandwidth) (Worton 1989). Within each home range, we generated an equal number of randomly distributed locations representing available locations.

Using the same resource variables as S_1 (Table S1), we extracted mean values for each resource variable using varying buffer radii (m) for each leopard location. This approach was taken as large carnivore resource use is scale-dependent and suggests that an optimum predictive radius exists at each order of selection (DeCesare *et al.* 2012; Martin *et al.* 2012). Buffer radii for S_2 models comprised 250–1000 m (at 250 m increments), 1000–3000 m (at 500 m increments) and 3000–7000 (at 1000 m increments). Buffer radii for S_3 models comprised 50–200 m (at 50 m increments) and 300 m. Buffer radii for S_2 and S_3 models were determined after accounting for computational efficiency and preliminary assessments. We used fixed-effects logistic regression to compare resource values of used and available locations for S_2 scale of selection (i.e. modelling across populations), and mixed-effects logistic regression for S_3 scale of selection (fitting leopard individual identities as a random intercept for S_3, and thus accounting for correlation and unequal sample sizes) (Gillies *et al.* 2006; Fieberg *et al.* 2010). Correlated resource variables ($|r| > 0{\cdot}7$) were removed, while retaining resource variables that produced the lowest AIC values. S_2 and S_3 data sets were randomly subset into 80% training and 20% testing data sets to enable internal and external model validation (Boyce *et al.* 2002). Using the training data set, we ran a suite of models for each order of selection, using resource variables at varying radii. We employed an exhaustive screening approach and ranked candidate models according to AIC. We selected the most parsimonious models, using a single optimum radius for each order of selection, and if necessary, applied model-averaging to the most supported models (ΔAIC $\leq$2) using R package *glmulti* (Calcagno & de Mazancourt 2010). The distribution of S_2 and S_3 data sets can be visualised in Fig. S2.

SCALE-INTEGRATED HABITAT MAPPING

The used-available designs of S_2 and S_3 models generated RSFs that are proportional to the probability of use (Manly *et al.* 2002; DeCesare *et al.* 2012). Using a 30 × 30 m resolution, per pixel predicted values (w_{js}) were spatially mapped across the study area. We estimated S_2 and S_3 RSF predicted values (Manly *et al.* 2002), as

$$w_{\mathrm{js}}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k) \qquad \text{eqn 1}$$

We applied a linear stretch to rescale S_2 and S_3 RSF predicted values between 0 and 1 (Johnson, Seip & Boyce 2004), as

$$\hat{w}_{\mathrm{js}} = \left(\frac{w_{\mathrm{js}}(x) - w_{\min}}{w_{\max} - w_{\min}}\right). \qquad \text{eqn 2}$$

To develop a scale-integrated RSF (SRSF) across the study area representing relative probability of use for a given pixel (w_{SRSF}), we multiplied each scale's probabilities (P) (Johnson, Seip & Boyce 2004; DeCesare *et al.* 2012), as

$$w_{\mathrm{SRSF}} = P(S_2) \times P(S_3) \qquad \text{eqn 3}$$

Finally, we applied a linear stretch to rescale the resulting SRSF between 0 and 1 using eqn (2).

MULTI-SCALE MODEL VALIDATION

We used model validation procedures to examine the predictive capacity of single scale RSFs (S_2 and S_3) and scale-integrated

(SRSF) models. We reclassified models into 10 equal area bins using percentile breaks at 10% intervals (Boyce *et al.* 2002). Withheld testing data sets were used as validation points for each scale separately (i.e. independent and partially dependent validation). We then projected validation points across the landscape, and assigned each a bin value according to the underlying reclassified landscape. We used Spearman's rank correlation to compare the frequencies of validation points in each bin to each RSF's bin rank (Boyce *et al.* 2002). A strongly predictive model will have a high positive correlation, indicating a greater number of locations in probability bins that approach 1 (Johnson, Seip & Boyce 2004).

CONNECTIVITY MAPPING

We combined our SRSF with circuit theory to explore habitat connectivity using Circuitscape v.4.0.5 (McRae *et al.* 2008). We chose circuit theory over other commonly used connectivity methods (e.g. least-cost path) since circuit theory models movement ecology via random walk pathways across all available movement possibilities (McRae *et al.* 2008). The SRSF was used as an index of conductance, where all cells are defined by networks of electrical nodes connected by resistors (see McRae *et al.* 2008 for a review). Random walk conductance modelling is analogous to habitat permeability (i.e. movement potential of an organism across the landscape), and is directly related to the likelihood of a 'walker' choosing to move through a cell, relative to other cells available to it (McRae *et al.* 2008). By predicting net movement probabilities through electrical nodes, current flow (i.e. permeability) can be used to identify core use areas, habitat connectivity and key movement pathways (McRae *et al.* 2008). Connectivity modelling is typically conducted between habitat patches, or between *a priori* source and sink locations. However, this is a key limitation, as animals often lack a predefined destination (Koen *et al.* 2014). To overcome this constraint, we developed a landscape-scale permeability map that is independent of *a priori* source or destination locations by randomly placing regularly distanced nodes (hereafter 'random nodes') around the 50 km buffer perimeter (Koen *et al.* 2014). Connectivity was then measured across the landscape, from one random node to another, in a pairwise fashion. To identify the optimum number of random nodes required to generate an unbiased landscape-scale permeability map, we conducted a sensitivity analysis using 10–300 random nodes at intervals of 10. Current flow was modelled across all random nodes to generate 30 permeability maps. If our estimates of permeability were independent of node placement and quantity, we should expect little variation in the spatial distribution of current flow as the number of random nodes increases (Koen *et al.* 2014). To test this prediction, we removed the buffer region and distributed 100 000 random locations across Limpopo. The buffer region was removed prior to testing because its inclusion would result in a biased estimate resulting from overestimated landscape conductivity at the periphery (Koen *et al.* 2010). We compared estimates extracted from each permeability map (i.e. 10–290 node maps) against estimates from the full permeability map (developed with 300 random nodes) by evaluating Pearson correlation coefficients. An optimum number of random nodes is only deemed suitable once an asymptote in correlation coefficients is reached (Koen *et al.* 2014). We applied a linear stretch to rescale the final permeability map between 0 and 1 using eqn (2).

MANAGEMENT IMPLICATIONS

To assess habitat permeability within LMUs (n = 207), we compared LMU current density estimates (i.e. flow of current km^{-2}; $\frac{\text{total current flow}_{\text{LMU}_i}}{\text{total area}_{\text{LMU}_i}}$) across Limpopo (excluding KNP; n = 180) against current density estimates from LMUs across KNP (n = 27) using a two-sampled t-test. Using the mean current density of LMUs within KNP as an optimum baseline (KNP$_{\text{base}}$), we categorised the permeability potential for LMUs across Limpopo as either below-optimum (<KNP$_{\text{base}}$) or above-optimum (>KNP$_{\text{base}}$). Given the size, low degree of human disturbance and optimal habitat (Swanepoel *et al.* 2013), KNP represents an ideal baseline on which to gauge the permeability potential of LMUs across Limpopo. Capacity for species and environmental monitoring is often a limiting factor; therefore, to test whether broad-scale occupancy modelling (S$_1$) could be used as a proxy for landscape permeability, we ranked ψ estimates and compared them against mean current density estimates within each S$_1$ sampling cell using Spearman's rank correlation.

Results

MODELLING RESOURCE USE AT S$_1$

We recorded 312, 150 and 138 leopard detections during 2013, 2014 and 2015 respectively. Four top models qualified for model-averaging (Table 1), while four resource variables were removed due to collinearity (EVI, NDVI, NPP and terrain ruggedness). Leopards selected, and were more likely detected, in drier regions further from major road networks. Although the parameters were likely non-informative (95% CI overlapped with zero), leopards appeared to avoid areas with denser vegetation, but selected areas with more people. We assumed these two variables were more likely associated with detection probability – particularly selection for areas closer to people, since this might represent a bias in our survey approach. However, we found this not to be the case as these models were outperformed by more parsimonious models (Table 1). Both γ and ϵ were held constant, as candidate models did not improve when resource variables were included. The resulting predictive map (ψ, Fig. 2a) agreed with previously published research (Swanepoel *et al.* 2013).

MODELLING RESOURCE USE AT S$_2$ AND S$_3$

Two vegetative resource variables (NPP and NDVI) were removed due to collinearity at both orders. Leopard selection response to features was strongest when resource variables were measured at radii of 7000 m (Fig. 3a) and 100 m (Fig. 3b) for S$_2$ and S$_3$ scales of selection respectively. S$_2$ scale of selection, model-averaging comprised two top models. Leopards favoured areas close to riverine and protected areas that were less rugged and at higher elevations, but further from major road networks. Tree canopy cover and EVI were all positively selected for,

Table 1. Top multi-season occupancy models for predicting leopard *Panthera pardus* habitat use (ψ; 'proportion of area used') from 2013 to 2015

						Coefficients of resource variables									
						ψ**					γ[††]	ϵ[‡‡]	P[§§]		
Models*	ΔAIC[†]	AIC[‡]	AIC$_w$	CW[§]	K[¶]	Intercept	D.Road	Precip[¶¶]	Canopy[¶¶]	Human[¶¶]	Intercept	Intercept	Intercept	D.Road	Precip
ψ(D.Road + Precip) γ(.) ϵ(.) *P*(D.Road + Precip)	0·0	2198	0·34	0·34	8	−3·4 (1·7)***	0·005 (0·001)	−0·002 (0·002)	–	–	−0·598 (0·340)	−0·437 (0·209)	−0·015 (0·280)	8·0E-04 (9·9E-05)	−0·004 (4·6E-04)
ψ(D.Road) γ (.) ϵ(.) *P* (D.Road + Precip)	0·3	2199	0·63	0·63	7	−5·0 (1·4)	0·005 (0·001)	–	–	–	−0·067 (0·354)	−0·514 (0·213)	−0·039 (0·275)	8·0E-04 (9·8E-05)	−0·004 (4·6E-04)
ψ (D.Road + Canopy) γ(.) ϵ(.) *P* (D.Road + Precip)	0·7	2199	0·87	0·87	8	−4·3 (1·3)	0·005 (0·001)	–	−0·065 (0·061)	–	−0·650 (0·346)	−0·472 (0·211)	−0·116 (0·275)	8·0E-04 (9·8E-05)	−0·003 (4·5E-04)
ψ(D.Road + Precip + Human) γ (.) ϵ (.) *P* (D.Road + Precip)	2·0	2200	1·00	1·00	9	−3·4 (1·7)	0·005 (0·001)	−0·002 (0·002)	–	0·015 (9·179)	−0·598 (0·340)	−0·437 (0·209)	−0·015 (0·281)	8·0E-04 (9·9E-05)	−0·004 (4·6E-04)

*Top models were averaged using R package *unmarked* (Fiske & Chandler 2011).

[†] Delta AIC.

[‡] Akaike's information criterion (Burnham & Anderson 2002).

[§] Cumulative AIC weights.

[¶] Number of parameters in each model.

**Probability of occupancy, interpreted in this study as 'probability of habitat use'.

[††] Probability of colonisation.

[‡‡] Probability of extinction.

[§§] Probability of detection.

[¶¶] Non-informative parameters (95% CI overlapping with zero).

***Standard error given in parentheses.

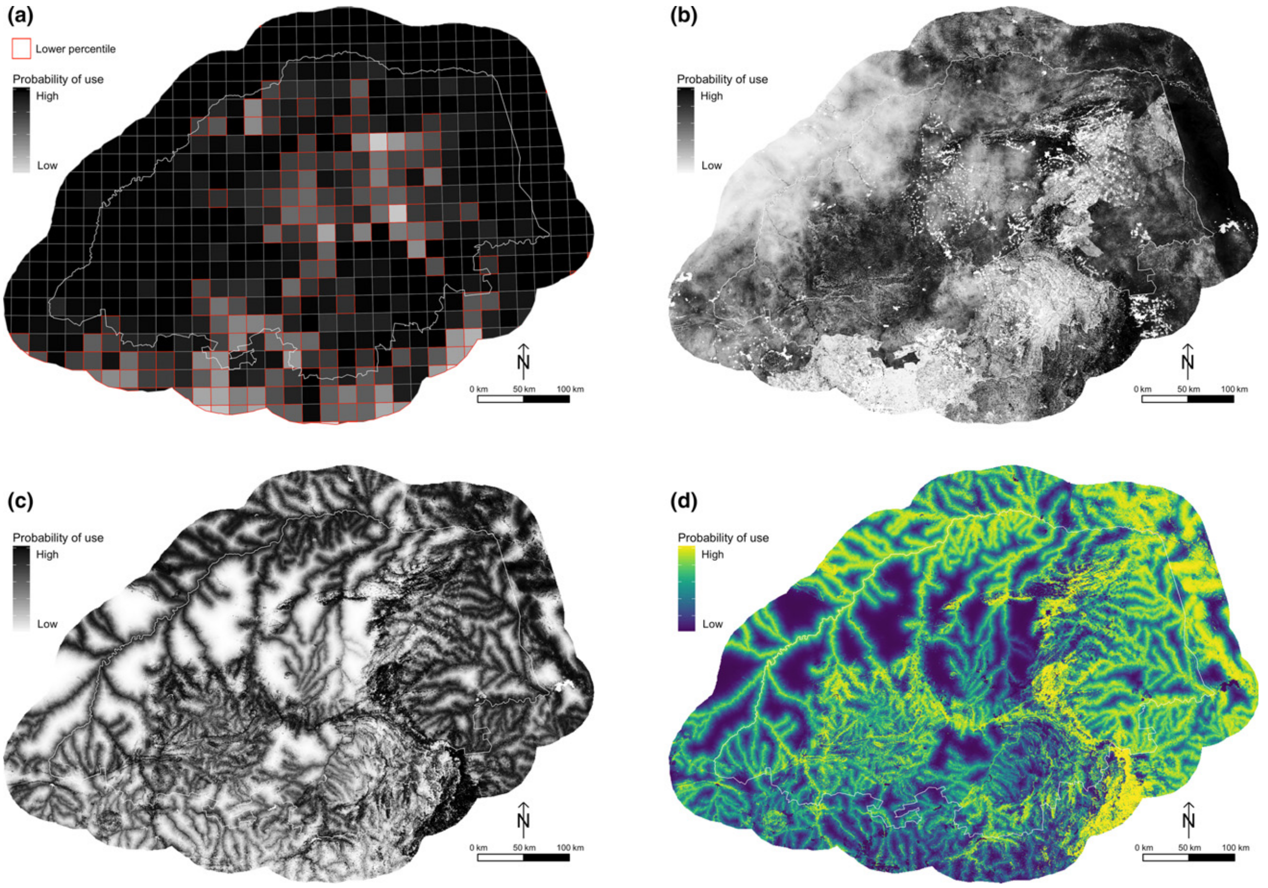

Fig. 2. (a) Predictive map (ψ) depicting leopard *Panthera pardus* habitat use across the study area. Sampling cells outlined in red represent those that were omitted from the S_2 analysis (i.e. <25th percentile). (b) RSF map at S_2 scale of selection. (c) RSF map at S_3 scale of selection. (d) Scale-integrated resource selection function (SRSF). White overlay represents the administrative boundary of Limpopo Province, South Africa. Units represent values from low (0) to high (1).

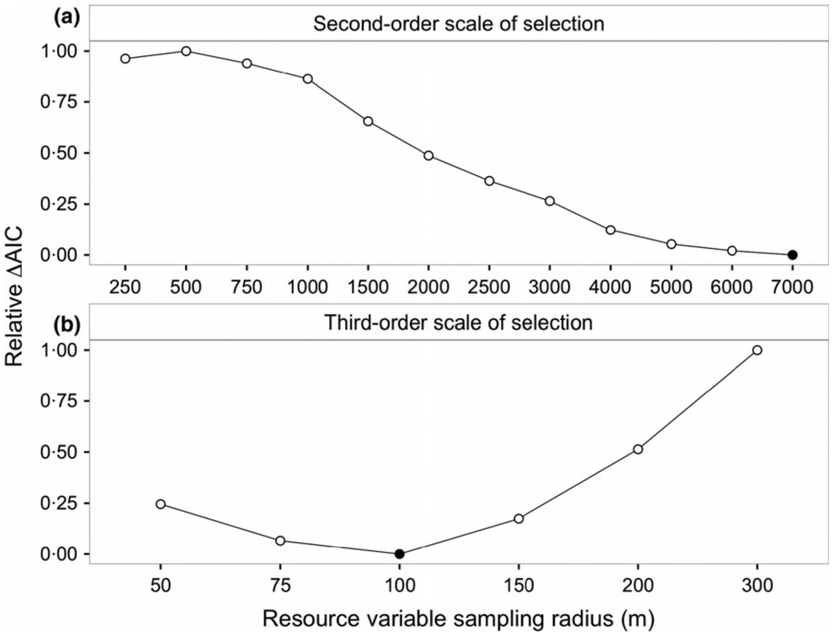

Fig. 3. Relative ΔAIC ($\Delta\mathrm{AIC}/\Delta\mathrm{AIC}_{\mathrm{max}}$) of (a) fixed- and (b) mixed-effect logistic regression models for S_2 and S_3 scales of selection respectively. Black points represent optimum resource variable sampling radii.

whereas human population density was negatively selected for (Table 2). S_3 scale of selection comprised two top models. Leopards favoured riverine areas of high vegetative productivity (EVI and tree canopy cover) and ruggedness, but in regions of lower precipitation (Table 2). Model validation at S_2 (partially dependent testing data set: $r_s = 0{\cdot}99$, $P < 0{\cdot}001$; independent testing data set: $r_s = 0{\cdot}92$, $P < 0{\cdot}001$) and S_3 (partially dependent testing data set: $r_s = 1$, $P < 0{\cdot}001$; independent testing data set: $r_s = 0{\cdot}92$, $P < 0{\cdot}001$) scales of selection performed well, and similarly for the final SRSF (partially dependent testing data set: $r_s = 1$, $P < 0{\cdot}001$), suggesting the predictive capacity of all models was very high (Fig. 2b–d).

MODELLING LANDSCAPE-SCALE HABITAT PERMEABILITY

Using the final SRSF as an index of conductance (Fig. 2d), we developed an unbiased landscape-scale permeability map using ≥200 random nodes (Pearson mean $r_{200\text{–}290\ \text{nodes}} = 0{\cdot}89$) – note an asymptote is reached by 200 random nodes (Fig. 4). As there is no penalty to including too many random nodes (Koen *et al.* 2014), we chose to use the full map for further connectivity assessments (Fig. 5a). Leopard habitat permeability was moderate across Limpopo (mean current flow = 0·5 ± 0·001 SE; range: 0–1). Three distinct regions exhibited markedly low habitat permeability (Fig. 5a). Current density of LMUs within KNP were significantly higher (mean = 1·7 ± 0·1 km^{-2} SE; KNP$_{\text{base}}$) than LMUs outside of KNP (1·3 ± 0·06 km^{-2} SE; two-sample *t*-test: $t_{(46)} = 3{\cdot}6$, $P < 0{\cdot}001$). Using KNP$_{\text{base}}$ as an optimum baseline, a total of 51 LMUs (25%; 18 198 km^2) were characterised with above-optimal permeability (Fig. 5b), while the remaining 156 LMUs (75%; 108 983 km^2) were characterised with below-optimal permeability (Fig. 5b). We detected a weak relationship between ranked ψ estimates and mean current density estimates across S_1 sampling cells ($r_s = 0{\cdot}31$, $P < 0{\cdot}001$), suggesting occupancy modelling was a poor predictor of landscape permeability.

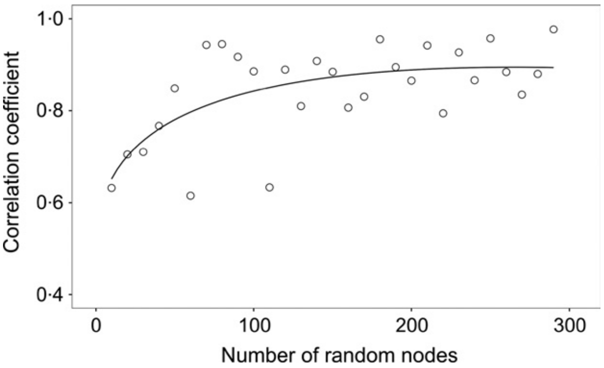

Fig. 4. Pearson correlation coefficients of extracted values (n = 100 000) from a full permeability map developed using 300 random nodes compared to extracted values from permeability maps developed using fewer random nodes (i.e. 10–290).

Table 2. Fixed-(S_2) and mixed-effects (S_3) logistic regression coefficients from averaged models (ΔAIC ≤2)

Coefficient*	β	SE	*z*	*P*	RI†
S$_2$					
Intercept	−1·68	0·09	19·78	<0·001	1·00
d.water.7000	−0·63	0·08	7·61	<0·001	1·00
d.roads.7000	0·59	0·12	5·11	<0·001	1·00
human.7000	−6·50	0·28	23·03	<0·001	1·00
evi.7000	1·27	0·08	15·65	<0·001	1·00
elevation.7000	0·22	0·05	5·01	<0·001	1·00
t.rugged.7000	−0·52	0·06	8·38	<0·001	1·00
t.canopy.7000	0·19	0·08	2·38	0·02	1·00
d.PA.7000	−1·82	0·13	13·73	<0·001	1·00
precip.7000	0·01	0·04	0·21	0·84	0·28
S$_3$					
Intercept	−0·57	0·08	6·81	<0·001	1·00
d.water.100	−0·62	0·04	16·61	<0·001	1·00
precip.100	−0·22	0·02	9·05	<0·001	1·00
evi.100	0·17	0·02	9·95	<0·001	1·00
t.rugged.100	0·12	0·01	14·72	<0·001	1·00
t.canopy.100	0·15	0·02	10·11	<0·001	1·00
dpa.100	0·12	0·14	0·84	0·40	0·57

*Resource variable prefixes: d.water – distance to water; d.roads – distance to roads; human – human population density; evi – environmental vegetation index; elevation – altitude; t.rugged – terrain ruggedness; t.canopy – tree canopy cover; d.PA – distance to protected area; precip – precipitation.

†AIC weights of relative variable importance.

Discussion

We integrated across multiple scales of resource selection and generated an unbiased landscape-scale permeability map that was independent of *a priori* source or sink locations. We demonstrated a scale-integration method capable of overcoming scale-dependent limitations to accurately predict resource use for an elusive, large carnivore. We compiled a range of data sets to counter the dearth of information often attributed to large carnivore research, which enabled the delineation of broad-scale (S_1) leopard distribution, and finer-scaled resource selection (S_2 and S_3), and identified key variables influencing different scales. Given the wide-ranging dispersal capabilities of leopards, and to facilitate a more informed used-available design, we used occupancy modelling (S_1) to delineate areas available to leopards at the intermediate (S_2) scale. Occupancy modelling is being increasingly adopted at broad-scales to address species distributions and habitat linkages (Zeller *et al.* 2011; Koen *et al.* 2014); however, although we produced a ψ map that was consistent with previous research from the same region (Swanepoel *et al.* 2013), we did not find support for the use of broad-scale occupancy modelling as a proxy for landscape permeability. This finding suggests that management authorities should exercise caution when attempting to use broad-scale occupancy modelling to infer landscape-scale linkages (Zeller *et al.* 2011). More specifically, we found that leopard habitat permeability across Limpopo is moderate, and identify three key regions that exhibit markedly low permeability. Importantly, the permeability of LMUs across Limpopo is largely below-optimal when compared to prime leopard

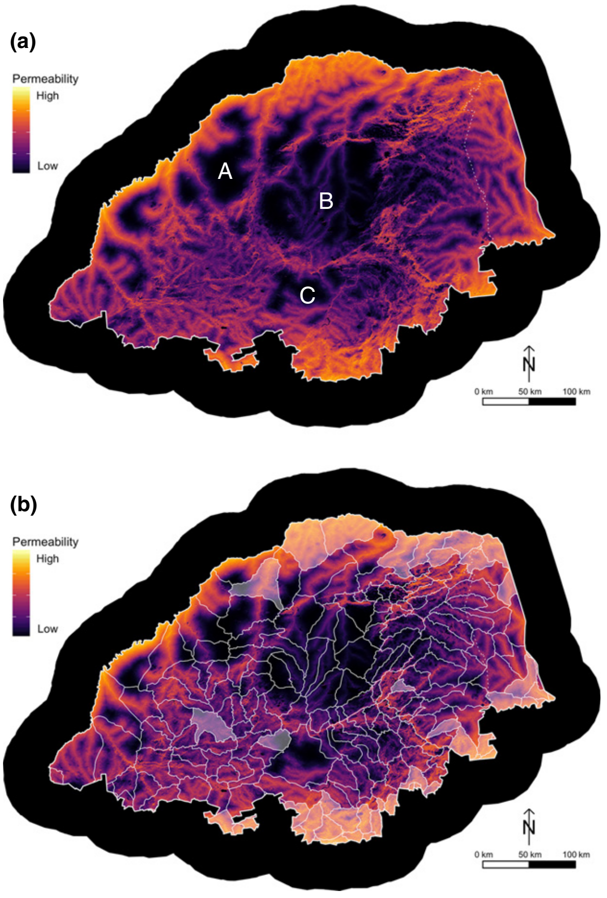

Fig. 5. (a) Full permeability map developed using 300 regularly distanced random nodes around the buffer periphery. Three key regions (A, B and C) are characterised by markedly low habitat permeability. Clear habitat linkages are visible between regions A–B and B–C, which likely require focussed conservation effort. (b) Full permeability map overlaid with above- (opaque polygons) and below-optimal (transparent polygons) leopard management units (LMUs). The SRSF, used to develop the permeability maps, was resampled to 500 m × 500 m for computational efficiency. Units represent values from low (0) to high (1). Kruger National Park is depicted by the dotted polygon.

habitat, which warrants further conservation attention and management intervention.

Obtaining data for the management of elusive animals is challenging and often results in fragmentary data sets (Martin *et al.* 2012). By incorporating multiple data sets across multiple scales, resource selection models can be developed that infer fine-scale spatial relationships represented by the larger population, but which are less prone to spatial bias in resource use typically caused by limited data sets (Martin *et al.* 2012; Elliot *et al.* 2014). Elliot *et al.* (2014) demonstrated the importance of using a range of data sets (i.e. demographic categories) when parameterising resistance surfaces for connectivity modelling, so as not to produce erroneous conclusions. We too advocate the use of a range of data sets in situations where broad-scale ecological and management questions are being posed for elusive species that cover vast areas (i.e. leopards); particularly since the management of these species are largely characterised by data deficiencies. Our study produced robust estimates of leopard distribution (ψ) at the broadest scale, which informed finer scale RSF analyses (i.e. by excluding areas mostly unoccupied by leopards). Fine-scale resource use is governed by fine-scale resource availability, which is itself governed by broad-scale resource selection (DeCesare *et al.* 2012). This hierarchically nested relationship has previously been exploited for other large mammals, such as woodland caribou *Rangifer tarandus caribou* (DeCesare *et al.* 2012) and brown bear *Ursus arctos* (DeCesare *et al.* 2012; Martin *et al.* 2012). However, earlier studies relied on limited data sets to delineate population distribution at the broadest scale. This potentially limits the robustness of a used-available study design, as available locations at finer scales might be randomly placed within areas unoccupied by the study species. The elusive nature and low detection rates of large carnivores calls for a more robust framework (Ripple *et al.* 2014), which occupancy modelling may provide.

Patterns of resource use involve balancing the trade-off between the costs of resource acquisition against the benefits of resource use (Brown, Laundré & Gurung 1999). For large carnivores such as the leopard, selection trade-offs exist between prey abundance and catchability (Balme, Hunter & Slotow 2007), and avoidance of intraspecific and interspecific threats (Vanak *et al.* 2013). Depending on the scale, selection trade-offs can act at differing intensities, which can render wildlife–habitat relationships non-informative, resulting in skewed connectivity metrics (Boyce 2006). Here, we demonstrated markedly different scale dependencies for a highly adaptive large carnivore (Hayward *et al.* 2006). Leopard distribution patterns at the broadest scale of selection (S_1) were primarily driven by a lack of major road networks. At finer scales (S_2 and S_3), leopard resource use was governed by three factors; avoidance of anthropogenic disturbance (road networks and people), selection of prey-rich areas (riverine features, proximity to protected areas, high EVI and high precipitation) and selection of rugged areas with sufficient vegetative cover likely to maximise hunting success and minimise kleptoparasitism (Balme, Hunter & Slotow 2007). By integrating across multiple scales of resource selection, we accommodated complex leopard–habitat relationships within a single framework capable of generating accurate predictions of resource use necessary for applied large carnivore management.

Free-ranging wildlife is under significant anthropogenic pressure (Ripple *et al.* 2014, 2015). Land-use practices, in particular, have led to increased fragmentation and human–wildlife conflict (Pitman *et al.* 2016a). Habitat connectivity is not only essential to maintain genetic variability (Broquet *et al.* 2010), trophic diversity and ecosystem functions (Olds *et al.* 2012) but also ensures the persistence of free-ranging charismatic species that play an important economic role (Lindsey, Roulet & Romanach 2007). Wildlife management is increasingly focused at the landscape-scale, where connectivity conservation across vast regions are superseding those at smaller scales (Koen *et al.* 2014). Although connectivity is typically modelled using a source-to-sink approach (Zeller, McGarigal & Whiteley 2012), we stress the importance of methodologies that do not rely on *a priori* destination locations. The distribution of wildlife in human-dominated landscapes is poorly understood (Koen *et al.* 2014), particularly at finer scales (Boyce 2006). Moreover, knowledge of definitive source and sink locations is severely lacking, even for a large, charismatic species such as the leopard (Pitman *et al.* 2015). Using random nodes placed around the perimeter of the buffered study area, we modelled connectivity across the entire landscape independent of *a priori* source or sink locations. This broader applicability results in landscape permeability maps relevant not only to leopard ecology and management but also to species at comparable or lower trophic levels reliant on similar habitat types.

Large carnivores have undergone significant range contractions (Ray, Hunter & Zigouris 2005), leading to increased calls for improved management and conservation (Ripple *et al.* 2014). As with wildlife management more generally, large carnivore management is often implemented across discrete geographical units (e.g. wildlife management units, hunting concessions, administrative zones) (Messmer *et al.* 1998). For instance, lions *Panthera leo* are typically managed within hunting concessions (Lindsey, Roulet & Romanach 2007), while cougar *Puma concolor* hunting in Utah, USA is managed within geographical watersheds (Stoner *et al.* 2013). Although connectivity is a fundamental component of successful conservation (Zeller, McGarigal & Whiteley 2012), connectivity metrics are infrequently considered within the regulatory processes of many range states. This exclusionary approach is largely down to the difficulty, and high cost, of collecting data of sufficient quality and quantity for connectivity analyses; and often prevents management authorities from incorporating connectivity metrics within wildlife management. Management authorities, however, frequently collect fragmentary, opportunistic data sets such as mortality records, permit records and sightings data (Pitman *et al.* 2015, 2016a,b). As our approach clearly demonstrates, data from these multiple sources (and scales) can be efficiently incorporated into connectivity analyses and applied within a management context. Moreover, since carnivore management is often focused within geographical units (e.g. LMUs), management authorities could efficiently address regions of low connectivity by selectively modifying management practices (e.g. reducing trophy hunting quotas and problem animal control within management units) to mitigate human-mediated pressures. In our case study, we show that three regions in Limpopo exhibit markedly low habitat permeability and warrant urgent conservation attention. For instance, the establishment of conservancies can greatly increase wildlife persistence by linking suitable habitat (Lindsey, Romanach & Davies-Mostert 2009); therefore, as an alternative to modifying management practices within management units, management authorities could incentivise conservancy establishment across units requiring targeted management. Similarly, community engagement can play an important role in improving perceptions and tolerance of carnivores (Dickman 2010). Community outreach projects could thus be more effectively implemented if management authorities employ a multi-data, multi-scale connectivity approach – as we present here – to identify management units at risk of low permeability. Lastly, environmental impact assessments, which are routinely conducted in the region, could draw on the findings presented in this study; particularly with regard to game ranching practices, which are leading to increased landscape fragmentation through the adoption of heavily fortified predator-proof fencing (Pitman *et al.* 2016a). Although our findings focus on a large carnivore across a biodiverse region of southern Africa, they remain easily transferable for the management of other ecologically important species exhibiting wide-ranging dispersal capabilities and diverse habitat requirements.

Authors' contributions

S.T.W., K.S.W., R.A.H., J.P., L.S. provided data and valuable comments on the manuscript. J.F., H.R. assisted with analyses and provided valuable comments on the manuscript. L.T.B.H., R.S. and G.A.B. assisted with design and provided valuable comments on the manuscript. R.T.P. provided data, analysed and wrote the manuscript.

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Data accessibility

RData files comprising first-, second- and third-order data sets: Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.h4tn7 (Pitman *et al.* 2016b).

Conflict of interest

The authors declare no conflicts of interest.

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Structured questionnaire survey.

Fig. S2. (a) Distribution of data sets across three orders of selection. S_1 scale of selection depicted by 400 km^2 red sampling cells, (b) S_2 scale of selection depicted by red point locations, and (c) S_3 scale of selection depicted by red point locations used to develop individual leopard home ranges.

Table S1. Description of resource variables used to model leopard *Panthera pardus* resource selection at first- (S_1), second- (S_2) and third-order (S_3) scales of selection.