Extent and fragmentation of suitable leopard habitat in South Africa

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Abstract

Large mammalian carnivores are threatened by anthropogenic environmental impacts, particularly through habitat loss which often cause population declines. Understanding the extent of suitable habitat is therefore of great importance for carnivore conservation. The leopard (*Panthera pardus*) is a widespread and relatively common large carnivore, but the species is declining in large parts of its range. Using maximum entropy-based habitat models, we estimated the extent of suitable leopard habitat in South Africa, what variables that are associated with suitable leopard habitats, the extent of habitat that has been negatively impacted by human activity and the effectiveness of protected areas to capture suitable habitat. Suitable leopard habitat was highly fragmented. Although vegetation and physical variables were the most influential variables for habitat suitability, livestock farming primarily seem to underlie fragmentation. We suggest that the sustainability of the South African leopard population depends on maintaining dispersal routes between areas with suitable habitat. This will require mitigation of human–carnivore conflict in habitat corridors, particularly mitigation strategies targeting conflict between carnivores and livestock farmers. Because most suitable habitat occurred outside of protected areas, we also recommend that leopard conservation efforts should focus on areas that are not legally protected.

Introduction

Large mammalian carnivores play a key role in regulating terrestrial ecosystems (Terborgh *et al*., 1999). For example, apex predators can maintain species diversity by preventing mesopredator release, by preventing competitive exclusion or through indirect habitat effects (Crooks & Soule, 1999; Ripple & Beschta, 2006). Despite their important ecological role, the geographical range of many large carnivores has drastically declined during the last century. In Africa, the ranges of some of the most wide-ranging carnivores have declined by more than 76% (Ray, Hunter & Zirgouris, 2005), and similar-range contractions have been observed in Asia and South America (Sanderson *et al*., 2002, 2006). Effective conservation of carnivores is therefore dependent on the identification and maintenance of suitable carnivore habitat (Ray *et al*., 2005; Rabinowitz & Zeller, 2010).

The leopard *Panthera pardus* is a large carnivore with a wide geographic distribution in Africa and tropical Asia (Henschel *et al*., 2008). Despite its adaptability, the African range of leopards has declined by 37% during the past 100 years (Ray *et al*., 2005). Habitat loss (Ray *et al*., 2005), declining prey populations (Henschel *et al*., 2011), human persecution (Balme, Slotow & Hunter, 2010) and unsustainable harvest levels (Packer *et al*., 2011) are thought to be the main drivers of leopard range declines. Range contraction of leopards has been especially prominent in South Africa, where, for example, leopards on unprotected lands have been restricted to isolated areas that are inaccessible to daily human activities (Norton, 1986; Skead, 2007). It is therefore important to identify potentially suitable leopard habitats as a basis for successful conservation and sustainable management of South African leopards (Gavashelishvili & Lukarevskiy, 2008).

A variety of statistical methods are available to construct species distribution models (Guisan & Thuiller, 2005). When reliable absence data are lacking, techniques are primarily restricted to rule-based models using the software Garp (Stockwell & Peters, 1999), ecological-niche factor analysis (Hirzel *et al*., 2002) and maximum entropy modelling using the software MaxEnt (Phillips, Anderson & Schapire, 2006). Of these options, MaxEnt has been the most extensively used and is advantageous compared with other techniques because it is robust against correlated environmental variables (Phillips *et al*., 2006; Elith *et al*., 2010), less sensitive to the number of occurrence points (Elith *et al*., 2006), and it is not strongly effected by spatial error (Graham *et al*., 2008).

In this study, we combined maximum entropy-based habitat models implemented in the software MaxEnt with information-theoretic model selection to identify suitable leopard habitat in South Africa, to evaluate what variables affect habitat suitability, to evaluate the spatial extent of negative human impact on suitable leopard habitat and to evaluate the extent of suitable leopard habitat that is currently harboured inside conservation areas. We used this novel combination of algorithmic and data modelling techniques because it has been suggested to perform better than model selection methods traditionally associated with maximum entropy models, and because selecting an appropriate level of model complexity has been shown to be critically important for the performance of such models (Warren & Seifert, 2011).

Methods

Occurrence data

We used 1826 presence points from 2000 until 2010, except for Kgalagadi and Orange River Basin, where data ranged from 1988 to 2010 (Supporting Information Fig. S1). We obtained leopard occurrence data from the following sources: (1) provincial nature conservation offices; (2) provincial biodiversity databases; (3) field studies; (4) questionnaire data; (5) leopard sighting data from national parks. Each presence point included a date, a spatial coordinate and a measure of precision. Because 3.16 km approximates the diameter of the smallest recorded leopard home ranges in South Africa (Bailey, 2005), we only included presence records with at least this spatial accuracy. Data sources are given as supporting information (Supporting Information Table S1).

Environmental data

We used 11 uncorrelated environmental variables as predictors (Supporting Information Table S2). These were selected from a set of 14 variables identified as important for leopard habitat selection and distribution (Nowell & Jackson, 1996; Gavashelishvili & Lukarevskiy, 2008; Supporting Information Table S3). We only included variables with pairwise correlation coefficients of less than 0.7 to reduce multicollinearity (Mateo-Tomás & Olea, 2010). Among correlated variables, we selected the variable that had the highest significance to leopard biology (Austin, 2002). All spatial data were converted to a cell size of 10 km^2 to correspond with the resolution of the leopard presence data.

We grouped environmental variables into the following three broad themes: (1) vegetation; (2) physical attributes (i.e. topography and drainage); (3) human impact (Supporting Information Table S2). The vegetation theme consisted of land cover, a normalized difference vegetation index (NDVI) and grazing capacity. Land cover was derived from high-resolution satellite imagery from 2001/2002 (Van den Berg *et al.*, 2008). We favoured this data set over a more recent one from 2005, because the latter was too coarsely classed for our analysis. Moreover, land cover at a spatial scale relevant to our analyses seem to have changed little between 2001 and 2005 (Schoeman *et al.*, 2010). The NDVI is a measure of photosynthetically active biomass and reflects vegetation productivity and related bioclimatic variables (Tucker & Sellers, 1986; Chamaille-Jammes, Fritz & Murindagomo, 2006). Grazing capacity is a measure of the available biomass for grazing animals and was estimated from vegetation biomass, while incorporating NDVI and tree density (Morgental *et al.*, 2005). The physical attribute themes included a digital elevation model, surface ruggedness and distance to nearest river. The digital elevation model was created from elevation data taken from the Shuttle Radar Topography Mission (90-m resolution), and is a digital representation of altitude. Surface ruggedness was created with digital elevation model surface tools for ArcGIS 9.3 (Jenness, 2010), and was included because it has been found to affect the distribution of large generalist felids (Hatten, Averill-Murray & van Pelt, 2005), including leopards (Gavashelishvili & Lukarevskiy, 2008). Distance to rivers was estimated as the Euclidian distance to perennial and non-perennial rivers (Spatial analyst ArcGIS 9.3; ESRI, Redlands, CA, USA). The human impact theme consisted of human density, distance to roads, distance to villages, cattle density and small ruminant density. Human density (individuals km^{-2}) was estimated by rasterizing the enumeration area polygons from the 2001 census data of South Africa (http://www.statssa.gov.za). Distance to roads (primary and secondary) and villages (rural settlement with more than 10 inhabitants) were calculated as Euclidean distances. We divided livestock into cattle and small ruminants because leopards are a threat to small ruminants through their entire lifespan whereas leopard predation on cattle is limited to the calving season (Ogada *et al.*, 2003). Data sources for all environmental layers are given as supporting information (Supporting Information Table S2). We acknowledge that predator distribution and densities are affected by the distribution and density of prey and other carnivores (Creel, Spong & Creel, 2001; Carbone & Gittleman, 2002). However, such data does not exist for South Africa on a national level and could therefore not be incorporated into our models.

To account for potential spatial bias arising from grid cells with varying sizes because of the extended latitude range (Elith *et al.*, 2010), we projected the grids onto an equal area projection (Africa Albers Equal Area Conic). While the extent of the subsampled background region can affect the MaxEnt solution (VanDerWal *et al.*, 2009), we did not restrict the background region in our analyses because leopards occur widely throughout South Africa (Dalerum *et al.*, 2008).

Model selection

The software MaxEnt implements a maximum entropy approach to habitat modelling that estimates an unknown density distribution over a finite set of spatial units by maximizing the entropy subject to unit-specific constraints. These are implemented as environmental data associated with species occurrences (Phillips *et al.*, 2006).

For each theme of predictors (vegetation, physical attributes and human impact), we ran models for all possible predictor and feature type combinations. We used sample size-corrected Akaike's information criterion (AIC_c; Akaike, 1974; Burnham & Anderson, 2002) to identify the most parsimonious set of predictors and feature type combinations within each theme. To calculate the AIC_c values, we used the sum of the natural logarithm of the standardized raw probabilities of all cells containing a presence as the model log-likelihood (Warren & Seifert, 2011), which were penalized by the number of parameters according to Akaike (1974). The most parsimonious set of variables in each theme was combined to construct two different models, one including all variables (full model) and one including only variables from the vegetation and physical attributes themes (restricted model). We used this nested model selection approach to avoid the very large number of candidate models associated with many independent predictor variables and feature types.

We used default values for convergence threshold (10^{-5}), maximum iterations (500) and a regularization multiplier of 1 because these settings have been found to achieve good performance (Phillips & Dudík, 2008). We followed a cross-validation method where 10 random partitions of the occurrence localities were made (Phillips *et al.*, 2006). In each partition, 70% of the presence localities were used for training and 30% set aside for testing the final model. We used more than one metric to evaluate the models (Elith & Graham, 2009). Firstly, we used regularized model gain, which is a measure of the likelihood of the samples given the model compared with random background pixels (Phillips *et al.*, 2006). Secondly, we used the area under the receiver operating characteristic curve (AUC) as a measure of how well the model predictions discriminated between locations where observations were present and absent (Phillips *et al.*, 2006). We tested if the AUC was significantly different from that of a random model (AUC = 0.5) using a Mann–Whitney test based on 10 sensitivity values (one test omission) at each of the fractional 0.1 intervals of the predicted area from the MaxEnt omission output (Phillips *et al.*, 2006). Thirdly, we evaluated model performance by reclassifying our models into binary presence/absence maps. However, for brevity, the results from these binary tests are reported as supplementary materials (Supporting Information Appendix S1), together with a more thorough description and additional results related to model evaluation. We used MaxEnt's jacknife and heuristic test to evaluate importance of each predictor in the final MaxEnt models. Percent contribution of each predictor was calculated as the proportional contribution by each predictor to the model training gain (Phillips *et al.*, 2006). In the jacknife tests, firstly, we calculated the loss in regularized training gain of models with each predictor sequentially omitted. A consistent low loss of gain compared with the complete model suggests that none of the predictors contain information that is contained in any other predictor. Secondly, we calculated the gain for models containing each predictor separately. A large difference between the gain of these and the complete model supports that none of the predictors had sufficient explanatory power on their own. All of the tests were implemented in the software MaxEnt. We used MaxEnt software version 3.3.3e (http://www.cs.princeton.edu/~schapire/maxent/) and the user-contributed package 'dismo' to port MaxEnt into the statistical package R version 2.12.1 (Hijmans *et al.*, 2011; R Development Core Team, 2011).

Quantifying extent of suitable habitat, extent of human impact and effectiveness of conservation areas

We graphically visualized the output from our models using a logistic score for each pixel representing spatially explicit probabilities of species presence (Phillips & Dudík, 2008). We also used these logistic scores to calculate the spatial extent of human impact on habitat suitability as described later. To classify our model predictions into suitable and unsuitable habitat, we assumed that at least 10% of the presence points suffered from spatial error (Raes *et al.*, 2009). Therefore, we used the minimum logistic score of the presence points after the lowest 10% had been omitted as a threshold for defining suitable leopard habitat, which corresponded to a logistic score of 0.22. We therefore classified pixels with logistic scores below 0.22 to contain unsuitable leopard habitat and pixels with a score equal to or higher than 0.22 as suitable habitat.

We identified areas impacted by human activities by superimposing the full model over that of the model excluding all human variables, and extracted the difference in logistic pixel probabilities. Negative pixel values will therefore denote areas where humans have negatively influenced the probability of leopard presence and positive values areas where human activities have had a positive influence. We used the proportion of pixels with negative values in each province as a measure of negative human impact on leopard habitat. In contrast to evaluate human impact directly from the parameter estimates in the full model, this approach had the advantage of allowing for spatially explicit estimates of human impact. Moreover, the level of complexity favoured by MaxEnt models generally makes interpretations directly from parameter values difficult (Warren & Seifert, 2011).

Finally, we also investigated the extent of suitable leopard habitat that exists inside of conservation and formally protected areas by counting pixels classed as suitable habitat within these areas. Protected areas were taken from the 2009 World database of protected areas (http://www.wdpa.org), while conservation areas were taken from data supplied by the Department of Land Affairs of South Africa (http://www.ngi.gov.za). Conservation areas were defined as areas managed for biological conservation, but are not formally protected by law. Conservation areas do not include game ranches managed for biological conservation because such areas are still classed as commercial farming.

Results

Both the full and the restricted models performed significantly better than random predictions [full model: W(1) = 51 265.45, $P = 4.65E\text{-}03$; restricted model: W(1) = 48 971.1 $P < 8.93E\text{-}03$; Supporting Information Table S4]. However, the full model generally performed better in predicting leopard habitat than the restricted model (Full model: AUC = 0.89, Restricted model: AUC = 0.85; Supporting Information Table S4). The full model classed 20% (248 770 km^2) of South Africa as suitable leopard habitat (Table 1). Suitable habitat was fragmented and clustered into four general regions: one stretching along the south-east coast, one occurring in the interior of KwaZulu-Natal province, one encompassing Kruger National Park and the interior of the Limpopo province, and one in the northern region containing the Kgalagadi Transfrontier National Park (Fig. 1a). This fragmentation was greatly reduced by the restricted model, which excluded human impact variables (Fig. 1b). Three provinces had more than 30% of the land area classed as suitable (Limpopo 63%, Western Cape 38% and Mpumalanga 33%), and three provinces had less than 10% of the land area classed as suitable habitat (Gauteng 8%, Northern Cape 5%, Free State 0.10%; Table 1). The contribution of provinces to the total area of suitable habitat in South Africa varied with six provinces contributing to less than 10% of the total area of suitable habitat (Fig. 1a, Table 1). The three highest contributors to suitable habitat were Limpopo (31%), Western Cape (20%) and Eastern Cape (15%; Table 1).

Our information-theoretic approach to model selection suggested that the inclusion of all predictors consistently produced the most parsimonious models for each theme, but not the inclusion of a full set of feature types (Table 2). In the full model, NDVI, surface ruggedness and small ruminant density had a combined contribution of 57% (Fig. 2a). Conversely, human-related factors other than small ruminant density made relatively minor contributions to the models. The highest contributor to the restricted model was NDVI (Fig. 2b). There was no redundancy in information contained in predictors for either the full or the restricted model, and no single predictor seemed to provide good model predictions on their own (Fig. 2c,d). Within each theme of environmental variables, NDVI was the most influential predictor among the vegetation predictors (Supporting Information Fig. S2a), surface ruggedness the most influential of the physical predictors (Supporting Information Fig. S2b), and small ruminant density the most influential of the human impact predictors (Supporting Information Fig. S2e).

A total of 28% (343 288 km^2) of South Africa was negatively affected by predictors related to human impact (Fig. 1c). The spatial extent of human impact was highest in the Eastern Cape (47% of provincial area negatively

Table 1 Estimates of areas of suitable leopard habitat, areas of suitable leopard habitat predicted without human variables, and areas negatively impacted by human activities in South Africa

		Suitable habitat[a]			Suitable habitat[a] modelled without human variables			Human impact		
	Area (1000 km^2)	Area (1000 km^2)	Proportion of province[b]	Proportion of SA[c]	Area (1000 km^2)	Proportion of province[b]	Proportion of SA[c]	Area (1000 km^2)	Proportion of province[d]	Proportion of SA[e]
South Africa	1220.81	248.77		0.20	429.75		0.35	343.29		0.28
Province										
Limpopo	125.75	79.21	0.63	0.32	102.11	0.81	0.24	50.31	0.40	0.15
Western Cape	129.46	49.85	0.38	0.20	70.76	0.55	0.16	37.54	0.29	0.11
Mpumalanga	76.49	25.70	0.34	0.10	30.54	0.40	0.07	10.28	0.13	0.03
Eastern Cape	168.97	38.67	0.23	0.15	75.27	0.44	0.17	79.41	0.47	0.23
KwaZulu-Natal	94.36	21.11	0.22	0.08	50.15	0.53	0.12	41.77	0.44	0.12
North West	104.88	12.87	0.12	0.05	32.42	0.31	0.07	29.98	0.29	0.09
Gauteng	18.18	1.47	0.08	0.01	2.78	0.15	0.01	2.48	0.14	0.01
Northern Cape	372.89	19.78	0.05	0.08	64.56	0.17	0.15	88.90	0.24	0.26
Free State	192.83	0.11	0.00	0.00	1.15	0.01	0.00	2.61	0.01	0.01

[a]A logistic pixel probability of occurrence of 0.22 was used as a threshold to define suitable leopard habitat from the MaxEnt model.
[b]Proportion of suitable habitat in each province, calculated as the number of pixels with suitable habitat divided by the total number of pixels in each province.
[c]Contribution of each province to the area of suitable habitat within SA, calculated as the number of pixels with suitable habitat in each province divided by the total number of pixels in SA.
[d]Proportion of area in each province that has been negatively impacted by human activities in terms of habitat suitability, calculated as the number of pixels with a negative human impact divided by the total number of pixels in each province.
[e]Contribution of each province to the total area in South Africa that has been negatively impacted by human activities in terms of habitat suitability, calculated as the number of pixels with a negative human impact in each province divided by the total number of pixels in South Africa.
SA, South Africa.

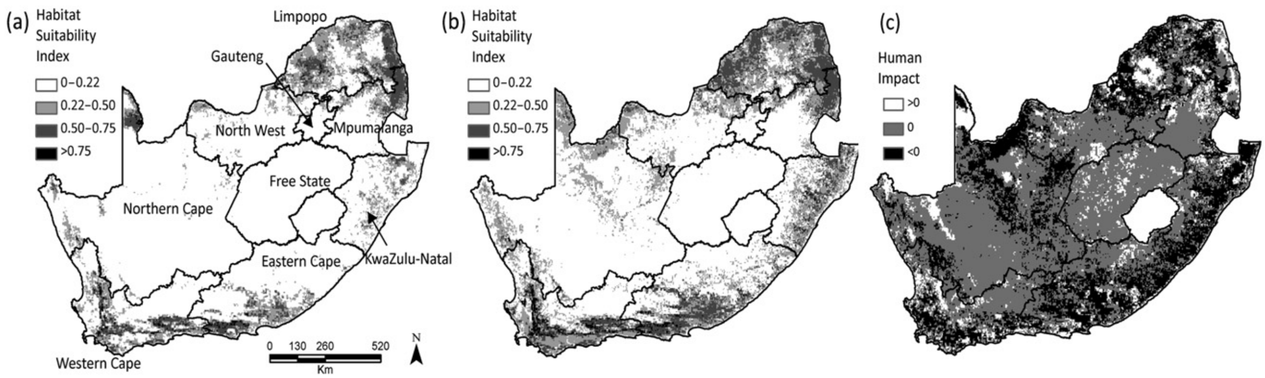

Figure 1 Suitable leopard habitat in South Africa predicted from a model containing the full set of environmental variables (a), from a model excluding human variables (b), and estimated human impact calculated as the difference in the model predictions from the model without and with human variables (c). The habitat suitability index represents logistic probabilities of occurrences. We regarded logistic probabilities of above to 0.22 indicate suitable leopard habitat, which corresponds to the 10th percentile training presence threshold. Human impact represents a binary coding of the differences in the logistic probabilities between the model without and with human impact variables. Negative values delineate areas where human variables had a negative human impact on leopard habitat suitability, and positive value areas where human variables had a positive impact and zero values areas where human variables did not influence habitat suitability.

impacted) followed by KwaZulu-Natal (44%), Limpopo (40%), Western Cape (29%) and North West (29%; Table 1). Three provinces had less than 20% of their area negatively impacted by humans (Mpumalanga 13%, Gauteng 14%, Free State 1%; Table 1).

Approximately, one-third (32%) of suitable leopard habitat was situated in conservation or protected areas. This compares with conservation or protected areas only constituting 9.30% of the total land area in South Africa. However, only 12% of the total suitable habitat was contained within national parks. The proportion of conservation areas that was classed as suitable habitat differed between the provinces (Table 3). However, even in the province with the highest proportion of protected areas classed as suitable, the largest proportion of suitable leopard habitat was still situated outside protected areas (Limpopo, 95%; Table 3).

Discussion

Our full model predicted that approximately 20% of South Africa presently is suitable leopard habitat, with an outline that closely resembles the current extent of the occurrence map (Henschel *et al*., 2008). However, our model indicated that suitable habitat is severely fragmented and largely restricted to four general areas. Such habitat fragmentation has frequently been found for other large carnivores [e.g. grizzly bears (*Ursus americanus*): Proctor, *et al*., 2005; tigers: Linkie, *et al*., 2006; jaguars (*Panthera onca*): Haag *et al*. 2010] and has been suggested as a serious cause for concern, because it may cause negative effects on populations both directly through demographic effects of isolation, but also through genetic dilution (Crooks, 2002; Haag *et al*., 2010).

Variables with the highest contribution to the most parsimonious habitat suitability model with all variable themes included NDVI, surface ruggedness and small ruminant density. The large contribution of NDVI and surface ruggedness agrees with habitat models for other large felids (Hatten *et al*., 2005; Linkie *et al*., 2006). The NDVI represents various factors that contribute to suitable leopard habitat including the abundance of prey, water and vegetation cover (Gould, 2000). The importance of surface ruggedness agrees with studies on cougars *Puma concolor* (Riley & Malecki, 2001), jaguars (Hatten *et al*., 2005) and leopards (Gavashelishvili & Lukarevskiy, 2008), which highlights the importance of rugged topography as suitable habitat. However, both in South Africa and elsewhere in Africa leopards also inhabit non-mountainous areas (e.g. Balme *et al*., 2010; Henschel *et al*., 2011). Therefore, we suggest that mountainous areas are heavily utilized because they offer more refugia from human persecution, as well as less direct competition for space caused by a lower amount of human activity compared with less rugged terrain (Norton, 1986; Gavashelishvili & Lukarevskiy, 2008).

The observed level of habitat fragmentation was reduced when human variables were excluded as predictors, which strongly suggests that human impact is contributing to habitat fragmentation. Small ruminant density and cattle density where found to be the most influential of the human predictors. We therefore suggest that livestock farming may be a possible cause for the fragmentation of leopard populations in South Africa. In particular, small ruminants are of a preferred prey size for leopards and are therefore heavily predated on (Ogada *et al*., 2003; Hayward *et al*., 2006). This has resulted in conflict where leopards have largely been eliminated from areas with small ruminant farming (Norton, 1986). Consequently, areas with high levels of small ruminant farming, primarily in the Eastern Cape, southern and north-east Free State, eastern parts of Northern Cape and central parts of Mpumalanga, coincide with the areas we identified as having high negative human impact and low amounts of suitable leopard habitat.

Table 2 AIC scores, AUC_{train} and AUC_{test} values for the most parsimonious MaxEnt models for each of the three broad themes of predictor variables: vegetation, physical attributes and human impact

Predictors	Feature types	Parameters[a]	Log-likelihood[b]	AIC_c[c]	Delta AIC_c[d]	AUC[e]
Vegetation						
Grazing capacity, NDVI SA land cover	Threshold, hinge, product	64	–18 351.59	36 835.90	0.00	0.84
Grazing capacity, NDVI SA land cover	Linear, threshold, hinge Product	65	–18 351.95	36 838.77	2.88	0.84
Grazing capacity, NDVI SA land cover	Quadratic, threshold, hinge Product	65	–18 352.12	36 389.12	3.23	0.84
Grazing capacity, NDVI SA land cover	Linear, quadratic, threshold Hinge, product	65	–18 352.12	36 389.12	3.23	0.84
Grazing capacity, NDVI SA land cover	Threshold, product	64	–18 353.56	36 389.56	3.95	0.84
Grazing capacity, NDVI	Linear, threshold, product	64	–18 353.56	36 389.56	3.95	0.84
Physical attributes						
Altitude, distance to rivers Surface ruggedness	Linear, threshold, hinge, Quadratic	46	–19 883.58	39 861.59	0.00	0.78
Altitude, distance to rivers Surface ruggedness	Linear, quadratic, threshold Hinge, product	46	–19 883.58	39 861.59	0.00	0.78
Altitude, distance to rivers Surface ruggedness	Quadratic, threshold, hinge	45	–19 885.04	39 862.40	0.82	0.78
Altitude, distance to rivers Surface ruggedness	Quadratic, threshold, product Hinge	45	–19 885.04	39 862.40	0.82	0.78
Altitude, distance to rivers Surface ruggedness	Threshold, hinge	52	–19 877.87	39 862.85	1.27	0.78
Altitude, distance to rivers Surface ruggedness	Linear, hinge, threshold, Product	49	–19 877.87	39 862.85	1.66	0.78
Human impact						
Cattle density, small ruminant Density, human density Distance to villages Distance to roads	Quadratic, threshold Product	99	–19 441.85	39 093.17	0.00	0.84
Cattle density, small ruminant Density, human density Distance to villages Distance to roads	Linear, quadratic Threshold, product	96	–19 445.69	39 094.16	0.99	0.84

Following Burnham, Anderson & Huyvaert (2011), we regarded models that fell within seven AIC unit of the most parsimonious model as having approximately equal support. These models were selected from a large set of possible candidate models which within each variable theme included all possible combinations of predictors and feature types for each predictor

[a]Parameters is the number of parameters in each model calculated by counting all parameters with a nonzero weight in the lambda file produced by Maxent (Warren & Seifert, 2011).

[b]Log-likelihood was calculated as the natural logarithm of the raw probabilities of all pixels containing a known leopard occurrence.

[c]AIC_c; sample size-corrected AIC, which was calculated by penalizing the log-likelihood by the number of parameters according to Akaike (1974) and Burnham & Anderson (2002).

[d]Delta AIC was calculated as the difference in AIC scores between the most parsimonious model and subsequent models.

[e]AUCs calculated as the AUC value for 30% of randomly selected locations that was withheld for model testing and for 70% of randomly selected locations that were used for model construction. Because the AUC values for the training and testing partitions were equal in all our models, we have only reported one AUC value.

AIC, Akaike's information criterion; AUC, area under the operating receiver characteristics curve; NDVI, normalized difference vegetation index.

However, we highlight that this negative impact of livestock farming could not only be mediated through direct persecution and competition for space between farmers and carnivores, but also through diminished populations of wild prey.

While one-third of suitable leopard habitat was found in protected areas, only 12% was found within areas completely protected according to the International Union for Conservation of Nature (IUCN) criteria (Dudley, 2008). This is because South Africa has a low number of national parks (IUCN category II areas), but a high number of private and provincial reserves. The effectiveness of conservation areas in capturing suitable leopard habitat also varied provincially, with some provinces having their protected areas in unsuitable leopard habitat. Combined,

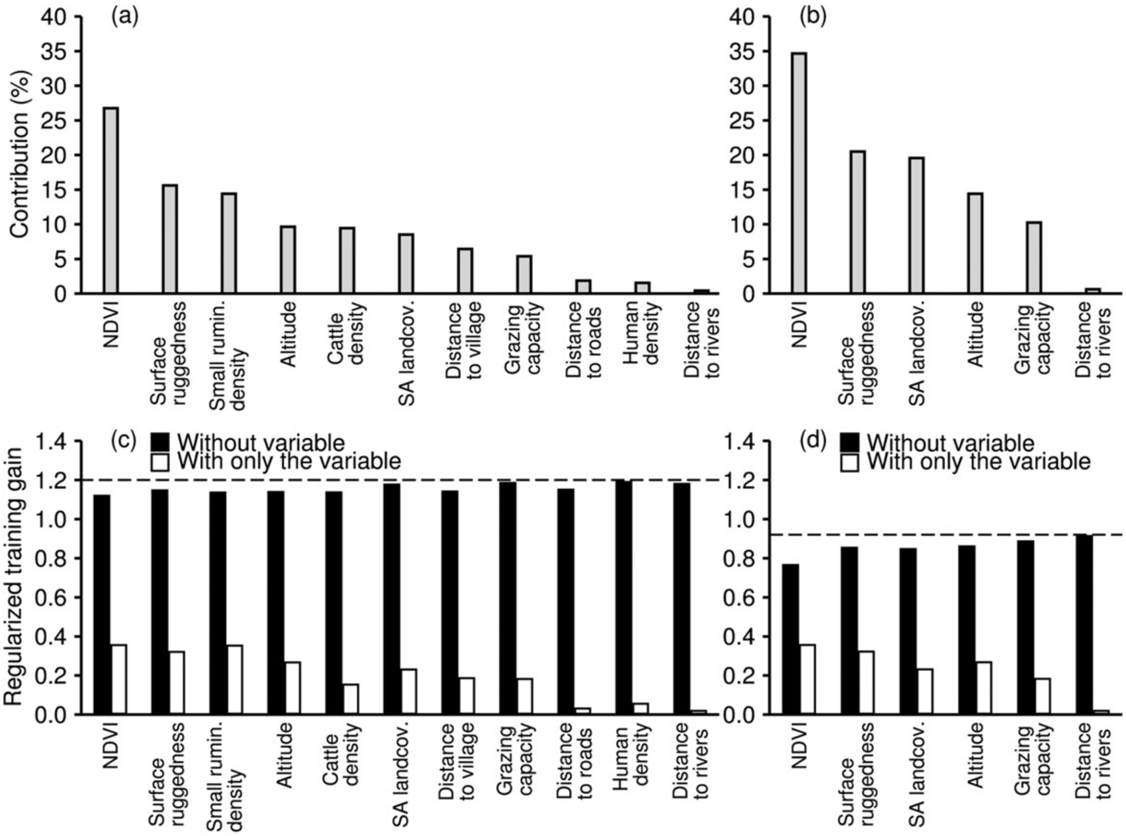

Figure 2 The relative model contributions of variables to the most parsimonious model including all predictor themes (full model: a) and the most parsimonious model excluding the human impact theme (restricted model: b) and importance of environmental variables to the regularized training gain (full model: c, restricted model: d), expressed as the regularized training gain for models with each variable omitted (black bars) and for models only containing each variable (white bars). These results are presented in relation to the regularized training gain of the full and restricted models, respectively (dashed line). A high loss of training gain when one variable is omitted compared with the complete model suggest that this variable contain information that is already provided by other variables. Conversely, a low training gain of models on individual variables suggest that no variable on its own was useful for estimating leopard habitat. NDVI, normalized difference vegetation index; SA, South Africa.

Table 3 Proportion of suitable leopard habitat harboured in conservation areas

Province	Proportion of Province/South Africa in conservation areas[a]	Area of suitable leopard habitat in conservation areas (1000 km^2)[b]	Proportion of conservation areas that contain suitable leopard habitat	Proportion of suitable leopard habitat in conservation areas
South Africa	0.08	70.46	0.68	0.25
Limpopo	0.19	22.02	0.92	0.28
Western Cape	0.15	15.01	0.79	0.30
Mpumalanga	0.15	9.82	0.87	0.38
Eastern Cape	0.08	9.14	0.71	0.24
KwaZulu-Natal	0.15	4.98	0.34	0.24
North West	0.05	2.04	0.38	0.16
Northern Cape	0.03	7.40	0.57	0.37
Gauteng	0.02	0.05	0.11	0.03
Free State	0.01	0	0	0

[a]Conservation areas include both nationally protected and private conservation areas.

[b]A threshold in pixel specific logistic probability of occurrence of 0.22 was used to define suitable leopard habitat.

these findings suggest that unprotected, mostly privately owned land is extremely important for South African leopard conservation. This concurs with other studies that have highlighted that private land in South Africa could be favourable for carnivore conservation (Friedmann *et al*., 2002; Lindsey, Du Toit & Mills, 2004). However, carnivore conflict and management efforts such as translocation and killing of problem animals are limiting carnivore persistence on private land (Lindsey *et al*., 2004). Conservation of carnivores could therefore be enhanced by focusing conservation effort on strategies to increase tolerance such as education, improving financial benefits from carnivores and mitigation strategies to reduce livestock predation.

Finally, our information-theoretic approach generally favoured models of intermediate complexity. The inclusion of all variables within respective subset of predictors consistently produced the most parsimonious models, and models with a low number of feature types associated with each predictor variable where generally less parsimonious than more complex models. However, models including all predictors with a full set of feature types were generally not the most favoured ones. This level of complexity suggest that although MaxEnt may be a useful tool for predicting suitable habitat, it may be less useful as a tool for evaluating the direct mechanisms in which how specific environmental variables are influencing habitat suitability.

Conclusions

Our models indicated that approximately 20% of South Africa is potentially suitable leopard habitat, but that these areas are severely fragmented. We suggest that long-term sustainability of the South African leopard population will depend on maintaining dispersal corridors among areas with suitable habitat. Moreover, because this fragmentation seems to be negatively influenced by human activities, particularly small livestock farming, corridor maintenance may require mitigation of human conflict, including strategies mitigating conflict with livestock farmers. The small amount of suitable leopard habitat in fully protected areas suggests that private land plays an important role for the South African leopard population. Leopard conservation efforts should therefore focus strongly on areas not formally protected under conservation laws. Finally, on a technical level, our information-theoretic approach supported previous studies showing that although the software MaxEnt can produce models that accurately predict species presence, it favours a level of complexity that makes it less useful to elucidate how specific environmental variables is influencing the distribution of species across landscapes.

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Supporting information

Appendix 1. Model evaluation

We used three separate methods of model evaluation (Elith & Graham, 2009). First we used model gain which is a measure of the likelihood of the samples given the model compared to random background pixels. The uniform distribution has a gain of 0, so the model gain can be thought of as a measure of how much better the model fits the sample points than the uniform distribution does. Gain is closely related to deviance in generalised linear models (Phillips, *et al.,* 2006). Secondly, we used the Area Under the Receiver Operating Characteristic Curve (AUC) as a measure of how well the model predictions discriminated between locations where observations were present and absent (Phillips, *et al.,* 2006). We tested if the AUC was statistically different from that of a random model (AUC=0.5) using a Mann-Whitney test based on 10 sensitivity values (1-test omission) at each of the fractional 0.1 intervals of the predicted area from the MaxEnt omission output (Phillips, *et al.,* 2006). Thirdly, we evaluated model performance by reclassifying our models into binary presence/absence maps. There are no defined criteria for defining thresholds in presence only modelling (Jiménez-Valverde & Lobo, 2007). We chose the 10^{th} percentile training presence threshold to reclassify our models. The 10th percent percentile threshold value predicts the 10% presence observations with the lowest predicted model values as absent as they may suffer from spatial errors because our data spanned over a 10 year period and came from various sources (Raes, *et al*., 2009). The 10th percent percentile corresponded to a logistic probability of 0.22; we therefore coded pixels with logistic probabilities of occurrences as suitable habitat if it fell above 0.22 and as unsuitable if it fell below 0.22. The binary maps were used to calculate a series of threshold dependant statistics. A Kappa value is an index of model accuracy which is used to measure the agreement between the model predictions and known occurrences, while correcting for change agreements. Kappa ranges from -1 to +1, with +1 indicating maximum accuracy (agreement) while 0 indicates an agreement no better than random (Allouche, Tsoar & Kadmon, 2006). True Skills Statistics (TSS) is similar to the Kappa but is not affected by prevalence, which has been noted as a shortcoming of Kappa (Allouche, *et al.*, 2006). Percent Correctly Classified (PCC) is a measure of the proportion of correctly classified presences and absences, given the threshold. Finally, we calculated sensitivity and specificity, which estimate how well the model categorized presences and absences respectively. All data were analysed in R version 2.12.1 (R Development Core Team, 2011), using functions in the user contributed package 'PresenceAbsence' (Freeman, 2007) to calculate threshold dependant statistics.

The full model had high discriminatory power, indicated by a high model gain and AUC values significantly deviating from that of a random model. The good performance of the full model was further indicated by the results from the threshold dependent tests, which indicated good model predictions except for the Kappa statistic (Table S4). The low Kappa values indicate that there was only a fair agreement between predicted and observed presence. However, the TSS suggested a good agreement between predicted and observed values.

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Table S1. Sources for leopard occurrence data collected from the different provinces in South Africa used to model suitable leopard habitat with MaxEnt

Province	Size ($100km^2$)	Nr of points	Type of data	Source
Limpopo	125.75	1010	Farm names of translocated, hunted, or problem leopards	Provincial nature conservation office
		422	Camera trapping field data	L H Swanepoel, unpublished 2008-2010
				I Gaigher, unpublished data 2008
		104	Sightings data	South African National Parks
Mpumalanga	76.49	69	Farms names of translocated, hunted, or problem leopards	Provincial nature conservation office
		80	Sightings data	South African National Parks
KwaZulu-Natal	94.36	62	Farms names of translocated,	Ezemvelo KZN Wildlife biodiversity database

			hunted, or problem leopards	
		437	Sightings data	Ezemvelo KwaZulu Natal Wildlife biodiversity database
Eastern Cape	168.97	279	Field study	McManus, 2009
Western Cape	129.46	600	Sightings data	Cape Nature biodiversity database
Northern Cape	372.89	9	Farms names of translocated, hunted, or problem leopards	Provincial nature conservation office
		143	Field study	Bothma, Knight, Le Riche et al., 1997
		17	Field study	C.T Stuart & T. Stuart, unpublished report, 1988
North West	104.88	97	Farms names of translocated, hunted, or problem leopards	Provincial nature conservation office
		39	Questionnaire data	M Thorn, unpublished data 2008

		40	Sighting data	L. H. Swanepoel, unpublished data
Gauteng	18.18	6	Farms names of translocated, hunted, or problem leopards	Provincial nature conservation office

Table S2. Environmental predictors used to generate habitat suitability map models for leopards in South Africa

Theme	Variable	Description	Units and classes	Source
Vegetation	South Africa land cover	Land use classes	Categorical in 18 classes	South Africa land cover database (2001), http://www.arc.agric.za/ accessed 2011/12/15
	Normalized Difference Vegetation Index (NDVI)	Vegetation productivity and cover	Continuous ranging from -1 to +1	Moderate Resolution Imaging Spectroradiometer , http://modis-atmos.gsfc.nasa.gov/NDVI/ index.html, accessed 2011/12/15
	Grazing capacity	Potential grazing	Continuous describing hectare per animal unit ranging from 0 – 100 ha AU^{-1}	Institute for soil, water and climate. National Agricultural Research Council, Republic of South Africa.
Physical attributes	Digital elevation model	Altitude	Continuous ranging from 0 - 3322 m	Shuttle Radar Topography Mission, http://www2.jpl.nasa.gov/srtm/africa_radar_images.htm, accessed 2011/08/03
	Surface ruggedness	Measure of topographic ruggedness	Continuous ranging from 1 (level) to 2 (extremely	Created with Surface Tools (Jenness 2010) Using Digital elevation model data

			rugged)	
	Distance to river/streams	Euclidian distance from primary rivers	Continuous ranging from 0 to 69 km	Drainage data taken from Department of Land Affairs and Department of Water Affairs and Forestry, Republic of South Africa
Human impact	Human density	Nr of people per unit of area	Continuous ranging from 0 to 9950 persons/km²	Statistics South Africa (2001), www.statssa.gov.za, accessed 2011/08/02
	Distance to roads	Euclidian distance from primary/secondary roads	Continuous ranging from 0 to 118 km	Department of Land Affairs, Republic of South Africa.
	Distance to villages	Euclidian distance from village	Continuous ranging from 0 to 295 km	Department of Water Affairs and Forestry (2006), Republic of South Africa.
	Cattle density	Nr of cattle per unit of area	Continuous ranging from 0 to 701 cattle/ km²	Food and Agriculture Organisation of the United Nations (2005). http://www.fao.org, accessed 2011/08/02
	Small ruminant density	Nr of sheep and goats per km²	Continuous ranging from 0 to 3613 animals/ km²	Food and Agriculture Organisation of the United Nations (2005), http://www.fao.org, accessed 2011/08/02

Table S3. Spearman correlation coefficients for all pairwise correlations between different environmental variables identified as candidates for modelling habitat suitability for leopards in South Africa. Variables in bold represented correlated variables at an alpha level of 0.05.

	Cattle density	Altitude	Grazing capacity	Human density	Primary production	Distance to rivers	SA Land cover	Small ruminant density	Tree density	Distance to villages	Topographic roughness	Distance to roads	Precipi-tation
Cattle density	1.00	0.24	-0.25	0.63	**0.77**	-0.11	0.32	0.25	0.56	-0.62	0.19	-0.20	**0.73**
Altitude	0.24	1.00	-0.12	0.13	0.33	0.05	0.29	0.23	0.08	-0.01	0.01	-0.15	0.30
Grazing capacity	-0.25	-0.12	1.00	-0.16	-0.33	0.03	0.16	0.00	-0.37	0.18	-0.18	-0.02	-0.33
Human density	0.63	0.13	-0.16	1.00	**0.73**	-0.17	0.32	0.01	0.58	-0.61	0.27	-0.32	**0.72**
Primary production	**0.77**	0.33	-0.33	0.73	1.00	-0.19	0.28	0.06	**0.76**	-0.69	0.32	-0.22	0.96
Distance to rivers	-0.11	0.05	0.03	-0.17	-0.19	1.00	-0.12	-0.04	-0.20	0.22	-0.35	0.13	-0.20
SA Land cover	0.32	0.29	0.16	0.32	0.28	-0.12	1.00	0.25	0.04	-0.25	0.10	-0.21	0.28

Small ruminant density	0.25	0.23	0.00	0.01	0.06	-0.04	0.25	1.00	-0.07	-0.00	0.07	-0.08	0.06
Tree density	0.56	0.08	-0.37	0.58	**0.76**	-0.20	0.04	-0.07	1.00	-0.56	0.41	-0.14	0.78
Distance to villages	-0.62	-0.01	0.18	-0.61	-0.69	0.22	-0.25	-0.00	-0.56	1.00	-0.29	0.22	-0.69
Topographic roughness	0.19	0.01	-0.18	0.27	0.32	-0.35	0.10	0.07	0.41	-0.29	1.00	-0.11	0.40
Distance to roads	-0.20	-0.15	-0.02	-0.32	-0.22	0.13	-0.21	-0.08	-0.14	0.22	-0.11	1.00	-0.22
Precipitation	**0.73**	0.30	-0.33	0.72	0.96	-0.20	0.28	0.06	**0.78**	-0.70	0.40	-0.22	1.00
NDVI	0.64	-0.02	-0.36	0.68	**0.82**	-0.23	0.11	-0.05	0.84	-0.68	0.46	-0.18	**0.86**

Table S4. Performance of the full and restricted Maxent model fitted to leopard presence as evaluated by threshold independent and threshold dependent tests.

	Threshold independent tests				Threshold dependent tests					
	Gain[a]	Training AUC[b]	Test AUC	Average Test AUC *p* value[c]	Threshold[d]	PCC[e]	Sensitivity[f]	Specificity[g]	Kappa[h]	TSS[i]
Full model	1.19	0.91	0.89	4.65E-03	0.22	0.83	0.90	0.82	0.37	0.72
Restricted model	0.92	0.89	0.85	8.93E-03	0.22	0.72	0.89	0.71	0.24	0.60

[a] Gain is a measure of the likelihood of the locations given the current model compared to random background probabilities of occurrences. The model gain can be thought of as a measure of how much better the model fits the sample points than the uniform distribution (with gain of 0) does.

[b] Area Under Receiver Operator Curve (AUC) which is a measure of how well the model predictions discriminated between locations where observations were present and absent.

[d] Average AUC *p*-values from the Mann-Whitney test to test model AUC values against random AUC.

[d] Logistic threshold value at the 10th percentile training presence.

[e] Percent Correctly Classified is a measure of the proportion of correctly classified presences and absences, given the threshold.

[f] Sensitivity estimate how well the model categorized presences.

[g] Specificity estimate how well the model categorized absences.

[h] Kappa is a measure of the agreement between the model predictions and known occurrences, while correcting for change agreements. It ranges from -1 to +1, with +1 indicating maximum accuracy (agreement) while 0 indicates an agreement no better than random.

[i] True Skill Statistic is a measure of the agreement between the model predictions and known occurrences, while correcting for change agreements and it not affected by prevalence. It ranges from -1 to +1, with +1 indicating maximum accuracy (agreement) while 0 indicates an agreement no better than random.

Figure S1. Map containing raw location points as well as delineation of conservation areas within South Africa.

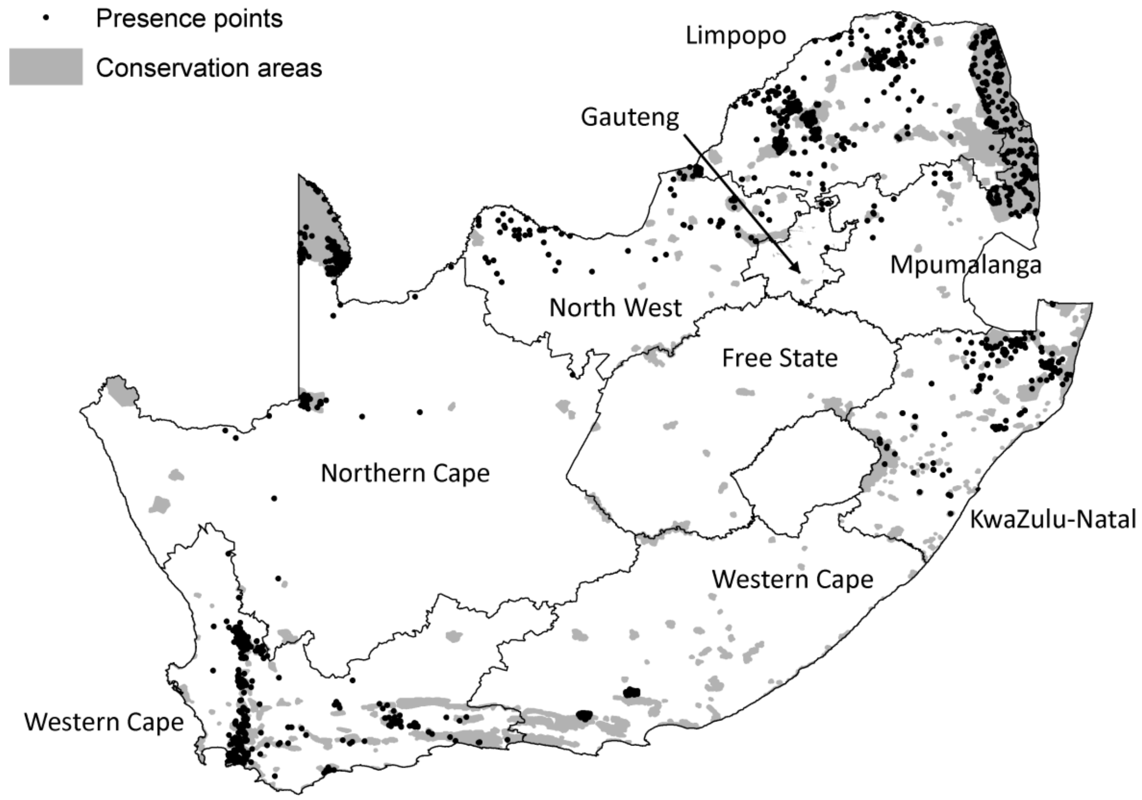

Figure 3S. The relative model contributions of variables assessed by heuristic tests to the most parsimonious model of each variable theme (physical: a; vegetation: b; human impact: c), and importance of environmental variables to the regularized training gain assessed by jacknife analysis (physical: d; vegetation: e; human impact: f), expressed as the regularized training gain for models with each variable omitted (black bars) and for models only containing each variable (white bars). The results from these jacknife tests are presented in relation to the regularized training gain of the complete full and restricted models, respectively (dashed line). A high loss of training gain when one variable is omitted compared to the complete model suggest that this variable contain information that is already provided by other variables. Conversely, a low training gain of models on individual variables suggest that no variable on its own was useful for estimating leopard habitat.