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Modelling the habitat requirements of leopard *Panthera pardus* in west and central Asia

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Summary

1. Top predators are seen as keystone species of ecosystems. Knowledge of their habitat requirements is important for their conservation and the stability of the wildlife communities that depend on them. The goal of our study was to model the habitat of leopard *Panthera pardus* in west and central Asia, where it is endangered, and analyse the connectivity between different known populations in the Caucasus to enable more effective conservation management strategies to be implemented.

2. Presence and absence data for the species were evaluated from the Caucasus, Middle East and central Asia. Habitat variables related to climate, terrain, land cover and human disturbance were used to construct a predictive model of leopard habitat selection by employing a geographic information system (GIS) and logistic regression.

3. Our model suggested that leopards in west and central Asia avoid deserts, areas with long-duration snow cover and areas that are near urban development. Our research also provides an algorithm for sample data management, which could be used in modelling habitats for similar species.

4. *Synthesis and applications*. This model provides a tool to improve search effectiveness for leopard in the Caucasus, Middle East and central Asia as well as for the conservation and management of the species. The model can predict the probable distribution of leopards and the corridors between various known populations. Connectivity patterns can be used to facilitate corridor planning for leopard conservation, especially in the Caucasus, where the leopard is a top priority conservation species. Also, as top predators are often associated with high biodiversity, the leopard habitat model could help to identify biodiversity hotspots. The protection of biodiversity hotspots is seen as the most effective way to conserve biodiversity globally.

Key-words: Caucasus, connectivity, conservation, GIS, habitat, leopard, logistic regression, west and central Asia

Introduction

Conservationists recognize that the best way to save threatened species is to protect the places where they live. Identifying and protecting irreplaceable habitats in the context of local politics, economic stability and human needs is a key conservation objective in managing the species that these habitats support. In efforts to protect or restore wildlife communities, top predators are seen as keystone species and indicators of the species richness of these communities (Meffe & Carroll 1997; Berger *et al*. 2001; Hebblewhite *et al*. 2005; Soulé *et al*. 2005). Focusing on the protection of high biodiversity sites is believed to be the most effective way to conserve biodiversity globally (Myers *et al*. 2000). One method of identifying high biodiversity areas is to model the habitats of top predators because these sites are often biodiversity hotspots (Schmitz 2003; Sergio, Newton & Marchesi 2005).

The leopard *Panthera pardus* is a top predator and the most adaptable, and hence the most widespread, wild representative of the family Felidae (Nowell & Jackson 1996). Its range spreads from South Africa through the countries of subSaharan Africa, across the Middle East to south-east Asia and Java, and northwards to the Russian Far East (Nowell & Jackson 1996). Leopards are found in a variety of habitats, from desert to rainforest and high mountains. Leopards are most common and best known in east, central and southern Africa. North of the Sahara and in Asia Minor, their distribution is poorly known. In spite of this, because they are nocturnal and secretive, they often survive in close proximity to humans. However, a reduced prey base, poisoned baits for carnivore control, the fur trade and direct conflicts with people over

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livestock predation have dramatically reduced leopard populations (Nowell & Jackson 1996; Nowak 1999).

In west and central Asia, seven leopard subspecies are described. These are the South Arabian leopard *Panthera pardus nimr* Ehrenberg & Hemprich 1833, the Asia Minor leopard *Panthera pardus tulliana* Valenciennes 1856, the Caucasus leopard *Panthera pardus ciscaucasicus* Satunini 1914, the North Persian leopard *Panthera pardus saxicolor* Pocock 1927, the Baluchistan leopard *Panthera pardus sindica* Pocock 1930, the Sinai leopard *Panthera pardus jarvisi* Pocock 1932 and the Central Persian leopard *Panthera pardus dathei* Zukowsky 1964. IUCN lists *P. p. nimr*, *P. p. tulliana* and *P. p. ciscaucasicus* as critically endangered, and *P. p. saxicolor* as endangered. However, based on analyses of molecular and morphological data, Miththapala, Seidensticker & O'Brien (1996) recommended the unification of these seven subspecies into one, *P. p. saxicolor*, although the most recent phylogenetic research on leopards (Uphyrkina *et al.* 2001) distinguishes *P. p. nimr* from *P. p. saxicolor* (hereafter we use leopard as a group name for these subspecies).

The unfavourable conservation status of the leopard, the recent discovery of leopards in areas where decades ago it had been considered extirpated or had never been documented (Nowell & Jackson 1996; Nowak 1999; Antelava 2004; Butkhuzi 2004; Lukarevsky *et al.* 2007) and its status as a flagship species for all six Caucasus countries (Zazanashvili *et al.* 2007), were the reasons for this study. Our aim was to examine closely the habitat selection by leopards in west and central Asia, and analyse the connectivity between different known populations in the Caucasus. Our objective was to identify those factors essential for the survival of the leopard and generate a model with good predictive power over large areas outside the sampling areas. Sustainable conservation of species is possible in broader scale habitats but it is important to identify corridors for movements between different areas (McCullough 1996; Dobson *et al.* 1999; Margules & Pressey 2000; Mech & Hallett 2001; Chetkiewicz, Clair & Boyce 2006). The model developed was used to identify leopard corridors in the Caucasus, set as one of the top priorities by WWF and the Ecoregional Conservation Plan (Zazanashvili *et al.* 2007). It will also facilitate planning, zoning and reintroduction efforts for leopard in the national park systems in west and central Asia.

Materials and methods

STUDY AREA AND SAMPLING

In 2001–05 we recorded presence/absence locations of leopard in Armenia, Azerbaijan, Georgia, Iran, Russian Federation, Turkey and Turkmenistan (Fig. 1) using a Garmin Etrex 12 Channel Global Positioning System (GPS) unit (Garmin Corp., Olathe, KA). We sampled *c.* 4000 km of ridgelines, trails and roadsides by car, on foot and on horseback. Data were mapped using ArcView v.3·3 GIS software (ESRI Inc., Redlands, CA). We sampled areas where leopard had been reported in the literature (Satunin 1905, 1915; Dinnik 1914; Nasimovich 1941; Vereschagin 1942; Bogdanov 1952; Geptner & Sludsky 1972; Lukarevskiy 2001; Kiabi *et al.* 2002) and by local people. Selection of presence points was based on observation of signs (footprints, scat, spoor, scrapes and kills) and sightings. Records of leopards poached during our study were also used to locate presence points. Signs of adult leopards were easily distinguished from those of any other animals occurring in the survey areas (Lukarevskiy 2001; Lukarevsky *et al.* 2007). To avoid the repeated sampling of habitat variables (see Table S1 in the supplementary

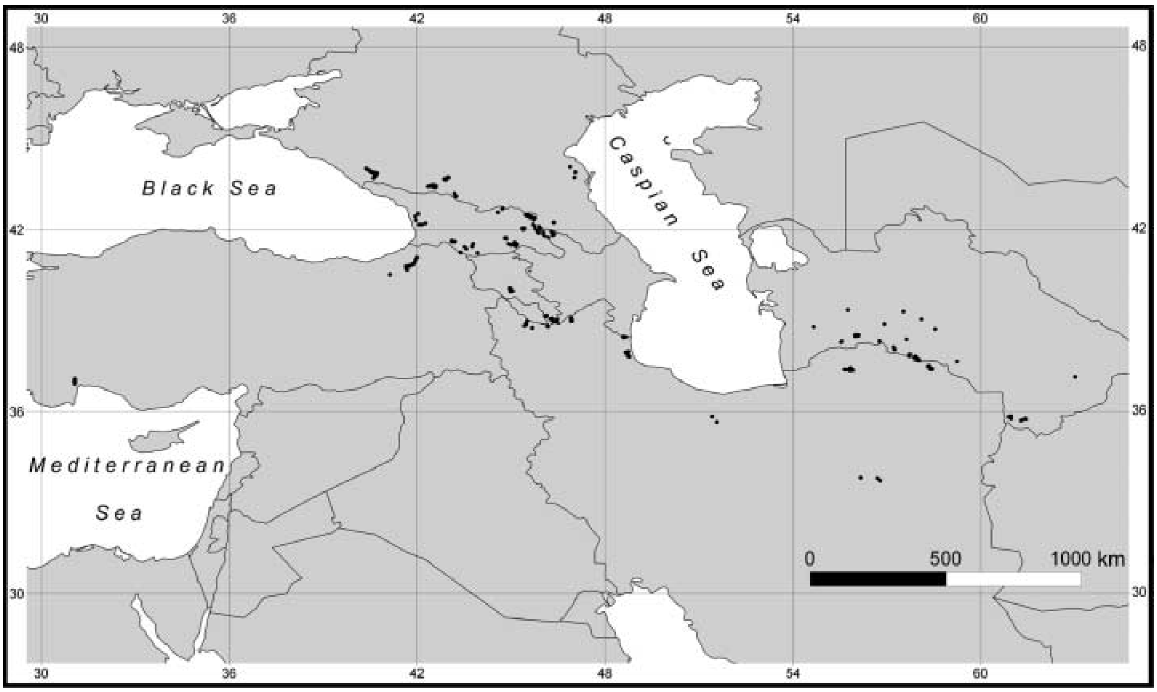

Fig. 1. The distribution of GPS locations of leopard presence/absence used for habitat modelling in west and central Asia.

material), we used presence points that were > 130 m from neighbouring points and our analyses were performed on a habitat variable grids of 90 × 90-m cells. We obtained 500 presence points for our analyses.

We obtained leopard absence points from areas of potential leopard habitat where leopard did not occur. We used ranges of the habitat variables (see Table S2 in the Supplementary material) measured at all 500 presence points to identify areas similar to those where leopard presence was confirmed. We generated 500 random points within the identified patches where our repeated surveys revealed no signs of leopard presence. These patches were surveyed in the same way as the areas with leopard presence.

HABITAT CHARACTERISTICS

We considered habitat variables related to climate, terrain, land cover and human disturbance (see Table S1 in the supplementary material). Extracting terrain, anthropogenic and land cover data from topographic maps and atlases of large areas is time-consuming and expensive. Instead we downloaded free on-line digitalized data and managed them using ArcView v.3·3 GIS software. The variables used were based on documented species–habitat associations (Jenny 1996; Nowell & Jackson 1996; Nowak 1999; Khorozyan 2003; Lukarevsky, Malkhasyan & Askerov 2007), our field experience and studies and models developed for similar species (Jackson & Ahlborn 1984; Ortega-Huerta & Medley 1999; Hatten, Averill-Murray & Van Pelt 2005; Mccarthy, Fuller & Munkhtsog 2005), with regard to their availability.

Terrain data were measured from the Shuttle Radar Topography Mission (SRTM) elevation data in the Universal Transverse Mercator (UTM) projection (data set from the Global Land Cover Facility, GLCF; http://www.landcover.org, accessed in 2005) at a resolution of 90-m pixels. These data were also used to calculate potential annual direct incident radiation (Megajoule (mj) cm^{-2} $year^{-1}$) from the following equation (McCune & Keon 2002):

$$[(0{\cdot}808 \times \cos(L) \times \cos(S)] - [0{\cdot}196 \times \sin(L) \times \sin(S)] - [0{\cdot}482 \times \cos(180 - |A - 180|) \times \sin(S)] + 0{\cdot}339$$

where L is latitude, S slope and A aspect.

We indexed climate using the equation [(0·0075 × elevation) + latitude] based on the observed relationship that an increase in elevation of 100 m is roughly equivalent to moving 80 km (45′ or 0·75° of latitude) towards the pole (UNEP-WCMC 2002). Higher values of the index correspond to harsher climate. Vegetation cover productivity was measured from 1000-m normalized difference vegetation index (NDVI) time–series maps and snow cover from status maps, both provided by the VEGETATION Program (SpotImage/VITO; http://www.vgt.vito.be, accessed in 2005). We used 2001–05 VGT-S10 data for both variables. Tree cover was taken from 500-m Moderate Resolution Imaging Spectroradiometer (MODIS) Tree Cover Continuous Field (Hansen *et al*. 2003), which estimates percentage tree canopy cover per 500-m MODIS pixel. Both VEGETATION and MODIS data were reprojected into a UTM projection using ArcView GIS Grid and Theme Projector v·2 (Jenness 2004) and resampled to a 90-m pixel size.

To identify urban areas, we first acquired human populated points accurate to a scale of 1 : 50 000 (GIS-Lab Ltd, Tbilisi, Georgia) and then derived polygons of urban areas at each of these points. We identified urban areas as polygons of compact networks of intersecting straight lines extracted from Landsat imagery (Heikkonen & Varfis 1998; Sengupta *et al*. 2003). Linear features were extracted using four detectors (Chittineni 1983), which enhances the high-frequency components of an image in four directions (east to west, north to south, north-west to south-east, and north-east to south-west). We used the near-infrared image of Landsat Enhanced Thematic Mapper (ETM) data at a pixel resolution of 28·5 m in a UTM projection. The source for this data set was GLCF (http://www.landcover.org). We chose the near-infrared band because this band visualizes the largest contrast along spatial structures such as roads, paths, streets, alleys and the edges of crop field areas. We detected line patterns using the ArcView GIS Convolution Filter Tool (Thorsten 2001). To classify the line pattern grid into straight-line and non-straight line classes, we defined cut-off values using the Receiver Operating Characteristic (ROC) curve (Hanley & McNeil 1982; Zweig & Campbell 1993) and linear and non-linear training pixels selected visually from the near-infrared image of Landsat ETM. The ROC curve analysis was performed with SPSS v.11 for Windows (SPSS Inc., Chicago, IL). As surrogates for human disturbance and development, we derived Euclidian and least-cost distances from polygons of urban areas (see Table S1 in the supplementary material). The computation of least-cost distances was based on the cost–distance algorithm implemented in the ArcView module Spatial Analyst. This algorithm considers a friction grid that is a raster map where each cell indicates the relative difficulty (or cost) of moving through that cell. A least-cost path minimizes the sum of frictions of all cells along the path, and this sum is the least-cost distance (Adriaensen *et al*. 2003). In the calculation of cost distances we incorporated information about the terrain to provide more realistic terrain-adjusted distances for human movement than the straight-line Euclidian distances that are often used in present-day modelling.

MODEL DEVELOPMENT AND VALIDATION

For habitat modelling, we used binomial logistic regression (LR; Hosmer & Lemeshow 1989; Menard 2002). Before running regression analyses, the multicollinearity of variables was diagnosed by checking a variance inflation factor (VIF). Variables with a VIF value > 10 were removed from subsequent analyses (Bowerman & O'Connell 1990). Each initial model was improved by removing influential points and transforming variables through residual analysis (Draper & Smith 1981; Weisberg 1985). Quadratic, cubic, square root, logarithmic and inverse transformations were tested to eliminate non-linearity. The classification cut-off values that equally balanced sensitivity and specificity were defined using the ROC curve (Hanley & McNeil 1982; Zweig & Campbell 1993). Model predictive accuracy was validated using a test presence/absence data set based on the kappa statistic (Fielding & Bell 1997; Scott *et al*. 2002). Model development was carried out using SPSS v.11 for Windows.

The best model was selected from two approaches. In one approach (hereafter the conventional approach), we randomly selected 80% of presence/absence pairs from a leopard sample data set and performed LR on them. The remaining 20% of the data set was used for model validation. In the other approach (hereafter the model multiplication approach; Fig. 2), we analysed the relationship of leopard presence separately with climate, vegetation productivity and human disturbance. To do so, we first hypothesized that leopards were more likely to occur in areas with milder climate, higher vegetation productivity and greater distance from urban areas. If this were true, then in our presence/absence data set: (i) climatic variables would account for leopard presence in areas with near-maximum values of vegetation productivity and distances from urban areas; (ii) vegetation cover variables would best explain leopard presence in areas with near-minimum values of climatic index and snow cover duration and near-maximum values of distances from

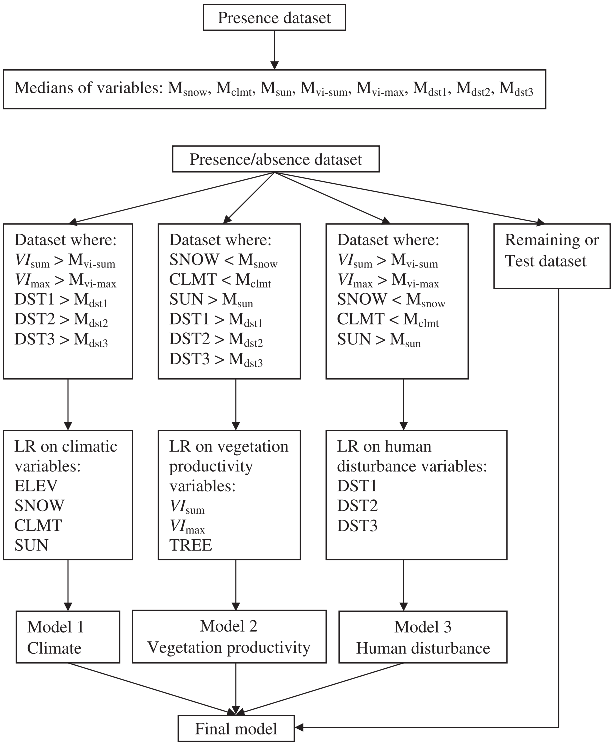

Fig. 2. Flow chart of major steps in generation of leopard habitat model using logistic regression (LR) and the model multiplication approach (see the text for details).

urban areas; and (iii) human disturbance variables would be more important in areas with near-minimum values of climatic index and snow cover duration and near-maximum values of vegetation productivity. We selected three subsets from leopard presence/absence points using median values calculated from the leopard presence data set (Fig. 2). The subsets included 105 presence/75 absence points for the climate model, 131 presence/91 absence points for the vegetation productivity model and 100 presence/60 absence points for the human disturbance model. The remaining 245 presence/295 absence points were used to test the final model. For each of the three subsets, we performed LR analyses, thus deriving three independent probability models. The product of these initial models produced the final model. We applied the best-fit models to the entire Caucasus and Middle East to generate a predictive map of leopard distribution. The resultant probability map was converted into a presence/absence map using a classification cut-off value that equally balanced sensitivity and specificity in the best-fit model.

EVALUATING HABITAT CONNECTIVITY IN THE CAUCASUS

Upon obtaining the model that had the best predictive power, we asked whether the model could be used to identify conservation corridors for leopards in west and central Asia. In this respect, we checked to see whether the recent discovery of the regular presence of leopard in Vashlovani Nature Reserve (Butkhuzi 2004) was a chance incident or evidence of a totally isolated population. The nearest known leopard populations occurred in the Greater Caucasus to the north (i.e. transboundary areas of Georgia and Russian Federation) and the Lesser Caucasus and Talish to the south (i.e. transboundary areas of Armenia, Azerbaijan and Iran) (Fig. 4). The narrowest gap (> 100 km) between Vashlovani Nature Reserve and the closest leopard population is heavily populated by humans. Before the recent discovery, leopards had never been recorded or even allegedly reported in the vast semi-arid area that includes Vashlovani Nature Reserve (28·5 km^2). Using the PATHMATRIX ArcView extension (Ray 2005), we defined least-cost paths among the known leopard populations in the Caucasus to see how the Vashlovani Nature Reserve related to the species connectivity between these populations. To calculate least-cost paths we used the following friction variable: $1/((P \times 100) + 1)$, where P is the probability of leopard presence calculated from the most accurate of our models. Therefore the least-cost path algorithm sought to link these populations by routes that followed higher probability values of leopard habitat.

Results

In general, leopards were found in or near relatively dry rugged terrain. Our analyses suggested that leopards in west and central Asia avoided areas with long-duration snow cover, low productivity (e.g. deserts) and areas that were easily accessed from urban development (Tables 1 and 2). The results of both modelling approaches demonstrated a negative response to the number of snow days per year and a positive response to the sum of differences in elevation along the least-cost path from urban areas. The conventional model was positively correlated with maximum vegetation productivity per year, while overall annual vegetation productivity was more important for the model multiplication approach. In addition, the model multiplication approach showed a positive response to actual length of the least-cost path from urban areas. However, it was more sensitive to the sum of differences in elevation along the least-cost path from urban areas.

The kappa statistic suggested that the model multiplication approach performed slightly better than the conventional model (Table 3). However, it should be noted that the model

Table 1. The best-fit model for leopard habitat, estimated from the conventional model approach, using binomial logistic regression

Model	Parameter estimate	SE	Wald	P
SNOW	–0·069	0·006	148·906	< 0·001
$\ln(VI_{max} + 1)$	0·729	0·221	10·895	0·001
DST3	0·003	0·0002	110·984	< 0·001
Constant	–3·640	1·082	11·326	0·001
2 log likelihood	–690·816			
Nagelkerke R^2	0·543			
d.f.	1			
Optimal cut-off	0·57			
Area under the curve (AUC)	0·836	0·015		< 0·001

Definition of the variable acronyms (see the text and Table S1 in the supplementary material for details): SNOW, days of snow cover per year maximized from 2001–05 time series; VI_{max}, maximum value of vegetation index (VI) over a year averaged from 2001–05 time series, where $VI = (\text{NDVI} + 0{\cdot}1)/0{\cdot}004$; DST3, sum of differences in elevation along the least-cost path from urban areas (m).

Table 2. Models for leopard habitat, estimated from the model multiplication approach, using binomial logistic regression

Model	Parameter estimate	SE	Wald	*P*
Climate				
SNOW	–0·099	0·016	38·414	< 0·001
Constant	4·999	0·695	51·687	< 0·001
2 log likelihood	–104·016			
Nagelkerke R^2	0·729			
d.f.	1			
Optimal cut-off	0·5			
AUC	0·929	0·024		< 0·001
Vegetation productivity				
$\ln(VI_{sum})$	8·029	1·074	55·814	< 0·001
Constant	–60·622	8·136	55·506	< 0·001
2 log likelihood	–155·450			
Nagelkerke R^2	0·647			
d.f.	1			
Optimal cut-off	0·5			
AUC	0·923	0·02		< 0·001
Human disturbance				
ln(DST2 + 1)	0·225	0·045	24·867	< 0·001
ln(DST3 + 1)	0·7	0·224	9·688	0·002
Constant	–6	1·141	27·635	< 0·001
2 log likelihood	–77·460			
Nagelkerke R^2	0·727			
d.f.	1			
Optimal cut-off	0·5			
AUC	0·941	0·029		< 0·001
The product of the above models				
Optimal cut-off	0·5			
AUC	0·939	0·014		< 0·001

Definition of the variable acronyms (see the text and Table S1 in the supplementary material for details): SNOW, days of snow cover per year maximized from 2001–05 time series; VI_{sum}, sum of vegetation index (VI) values per year averaged from 2001–05 time series, where VI = (NDVI + 0·1)/0·004 and NDVI is positive; DST2, actual length of the least-cost path from urban areas (m); DST3, sum of differences in elevation along the least-cost path from urban areas (m).

multiplication approach did so on a much larger test data set (refitting the conventional model by randomly increasing the size of test data set at the expense of that of training data set resulted in poorer results). In addition, the conventional model proved to be overly optimistic, widely misclassifying leopard presence (Fig. 3). For example, the conventional model predicted leopard presence deep in nearly lifeless deserts or inside heavily urbanized areas that showed high vegetation indices thanks to recreation parks or orchards. In contrast, the model multiplication approach was more consistent with current known distribution maps (Fig. 3) and did not predict presence in areas obviously unfavourable for leopard. The model multiplication approach also predicted correctly the recent findings of leopard in the Vashlovani Nature Reserve, Georgia (Butkhuzi 2004), Khevsureti, Georgia and Chechnia, Russian Federation (Lukarevsky *et al*. 2007), Meghri, Armenia (Khorozyan & Malkhasyan 2005), and the Sarigol National Park, north-eastern Iran (Iranian Cheetah Society (ICS); http://www.iraniancheetah.org/main.htm, accessed in 2005).

Connectivity analysis in relation to the recent discovery of leopard presence in Vashlovani Nature Reserve resulted in a number of least-cost paths that channelled into two major paths connecting the Greater Caucasus with Karabagh Mountains, which is part of the Lesser Caucasus. One of these two major paths ran exactly through the Vashlovani Nature Reserve (Fig. 4). The probability of leopard presence in Vashlovani Nature Reserve varied between 0·35 and 0·56, suggesting marginal or near marginal habitat.

Discussion

The identification and protection of core areas is an insufficient strategy to ensure long-term species conservation. Studies have shown that long-term survival of populations of large vertebrates is achieved by protecting source populations (core areas) and at the same time providing dispersal opportunities by linking these populations (Hanski 1994; McCullough 1996; Noss *et al*. 1996; Margules & Pressey 2000; Mech & Hallett 2001). Connectivity between core areas ensures species survival through maintaining genetic variability and

Table 3. Measures of predictive accuracy calculated for the best-fit models of leopard presence using test data sets

Measure	Calculation	Conventional approach	Model multiplication approach
Overall accuracy	$(a + d)/N$	0·88	0·89
Sensitivity	$a/(a + c)$	0·88	0·97
Specificity	$d/(b + d)$	0·88	0·85
Positive predictive power	$a/(a + b)$	0·88	0·79
Negative predictive power	$d/(c + d)$	0·88	0·98
Misclassification rate	$(b + c)/N$	0·12	0·11
Kappa statistic	$[N(a + d) - [(a + b)(a + c) + (c + d)(d + b)]]/[N^2 - (a + b)(a + c) + (c + d)(d + b)]$	0·76	0·78

$N = (a + b + c + d)$ where: a, number of presence cases correctly predicted by the model; b, number of absence cases where the model predicted presence; c, number of presence cases where the model predicted absence; d, number of absence cases correctly predicted by the model.

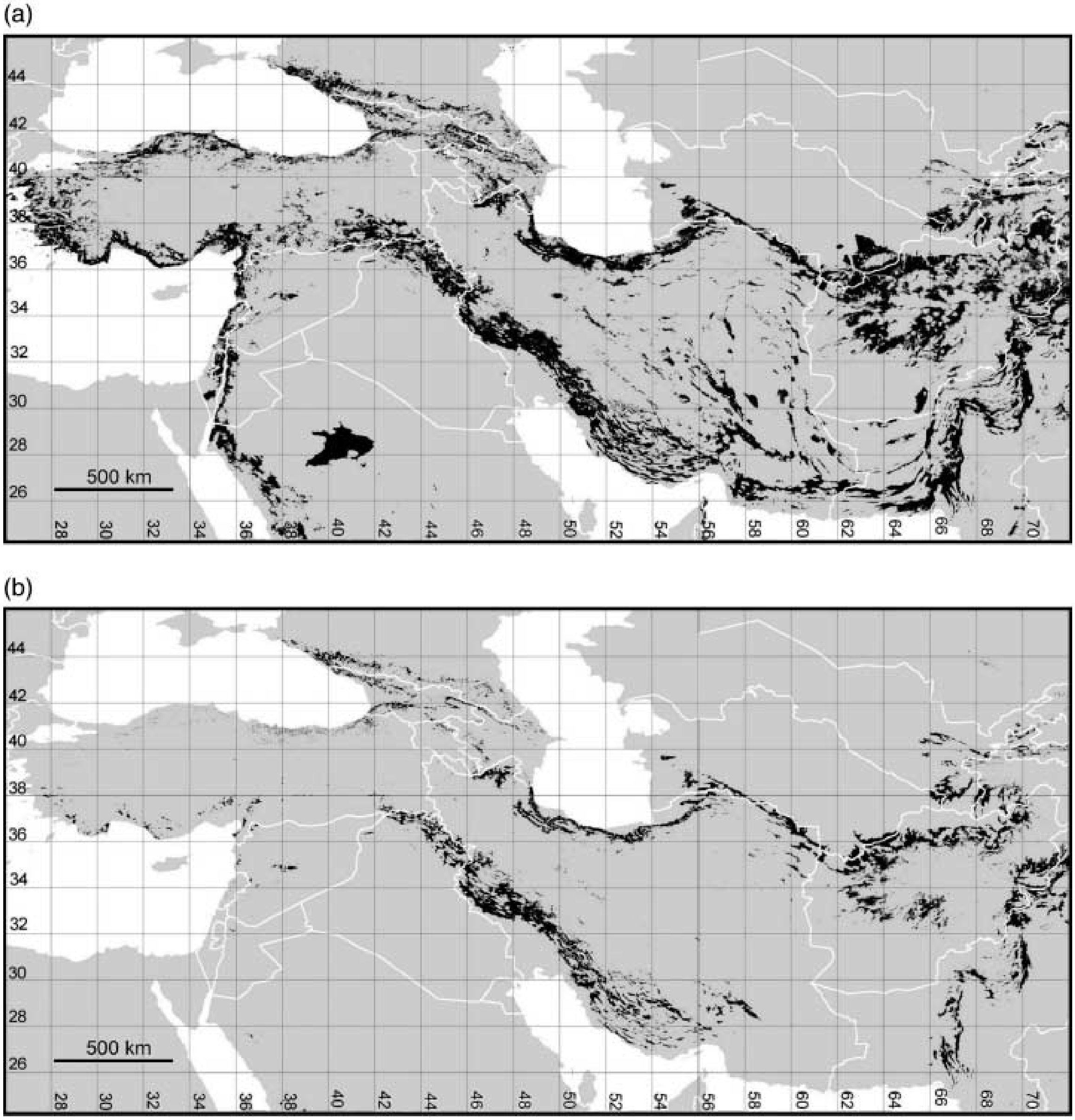

Fig. 3. Predicted distribution of leopard in west and central Asia, derived from (a) the conventional approach and (b) the model multiplication approach.

providing a source of individuals to offset losses caused by poaching, predation and accidents. Studies on big cats also emphasize the importance of connectivity (Ortega-Huerta & Medley 1999; Wikramanayake *et al*. 2004; Hatten, Averill-Murray & Van Pelt 2005; Carroll & Miquelle 2006; Linkie *et al*. 2006). Our study quantifies leopard habitat suitability and uses the habitat model to identify probable corridors between source populations.

Our objective was to provide an accurate approach to quantifying habitat requirements for leopard in west and central Asia, and to identify corridors among different leopard populations. To our knowledge this is the first attempt to model leopard habitat and connectivity over an area this large. Zimmermann *et al*. (2007) developed a habitat model for leopard in the Caucasus based on limited data (e.g. snow cover was not considered). We designed two approaches, of which the model multiplication method performed better.

The algorithm of our model multiplication approach differs from those used in other large-scale studies on big cats (Jackson & Ahlborn 1984; Ortega-Huerta & Medley 1999; Wikramanayake *et al*. 2004; Hatten, Averill-Murray & Van Pelt 2005; Carroll & Miquelle 2006; Linkie *et al*. 2006) and has a number of advantages over the conventional method. First, the reduction of independent variables per LR analysis improves model accuracy because the number of independent variables in relation to a sample size increases the likelihood of multicollinearity and the possibility that some variables would be significant just by chance. Secondly, in this approach predictive accuracy is less restricted to variable ranges within which models are developed. For example, in

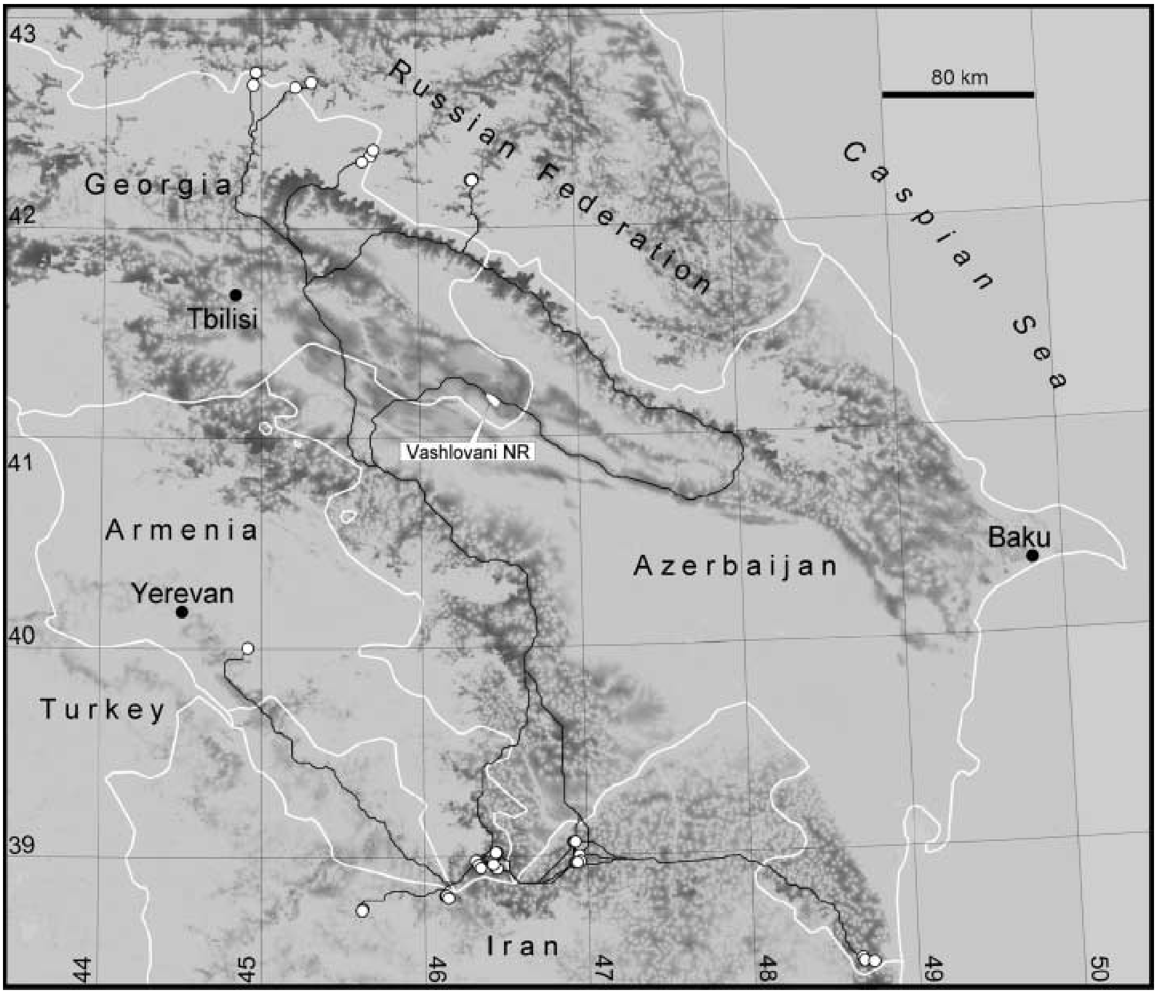

Fig. 4. Map showing least-cost paths (black lines) computed between known leopard populations (hollow points) in the Caucasus. The paths follow higher probability values of leopard habitat (darker areas).

the conventional approach the impact of variables that have negative correlation with species presence is offset by that of positively correlated variables. This might overpredict species presence even at high values of negative variables in areas where values of positive variables are much greater than their maximums in a training data set. In the model multiplication approach, important variables are split into a number of independent probability models, the product of which is to be a final model. As a result, overprediction is reduced by the multiplication effect of values ranging from 0 to 1. In other words, if the final probability P is the product of two probabilities, P_1 and P_2, and P_1 is $< 0{\cdot}5$, then P will not be $> 0{\cdot}5$ even at infinitely high values of positive variables included in P_2. Finally, our model multiplication approach tries to minimize errors that result from many or most cases sampled from unsuitable or marginal habitats where species presence is simply the result of proximity to suitable habitat. This is done by a priori assuming ideal conditions for a study species, estimating a model with those cases that match these conditions and using the remaining cases for final model validation. To reduce the error caused from sampling unsuitable or marginal habitats that are near suitable areas, researchers use neighbourhood statistics measured, for example, within search circles or rectangles around sampled points. However, the calculation of neighbourhood statistics over large areas may require a long computational time and could still be inaccurate, particularly as the result of an increase in the number of independent variables relative to a sample size.

Habitat models of ‘generalist’ big cats demonstrate associations with certain elevations, aspects, ruggedness and vegetation types, and negative correlations with proximity to roads and human density (Ortega-Huerta & Medley 1999; Hatten, Averill-Murray & Van Pelt 2005; Carroll & Miquelle 2006; Linkie *et al.* 2006). In comparison with these models, our model is applicable to generalist species (such as leopard) on a broader scale because the sample for model development was obtained from a larger area with a broader spectrum of landscape types. Broader sampling generated a model that includes more comprehensive variables, such as snow cover, vegetation productivity and terrain-adjusted proximity to urban areas.

The positive response of leopard presence to short-lived snow cover in our model might be linked to the negative impact of snow on movement and the food base, as occurs for other species. Also, analyses of the number of leopards shot suggest that, where snow cover lasts for more than 4 months, it is easier for hunters to track down and exterminate greater proportions of the leopard population (Lukarevskiy 2005). In the model, terrain-adjusted proximity to urban areas performed better than Euclidian distance. This may be because the terrain-adjusted distances between an urban area and a certain point account for not only straight-line distances but also the additional effort humans have to make to move through rugged terrain in order to reach the point. In mountaineering, the sum of differences in elevation along a certain path is known to better reflect the difficulty of a hike compared with the actual distance of the path. This explains the higher sensitivity of our model to the sum of differences in elevation along the least-cost path from urban areas, because this variable better reflects the expansion of human disturbance. Our model reveals a positive correlation of leopard presence with the annual sum of NDVI. Various studies have shown that NDVI integrates the influence of climatic variables (e.g. rainfall and evapotranspiration) and other environmental factors (Cihlar, St-Laurent & Dyer 1991) and is related to the distribution of both plant and animal species diversity (Walker *et al*. 1992). NDVI correlates directly with photosynthetically active biomass or vegetation productivity (Tucker & Sellers 1986; Reed *et al*. 1994), hence it accounts for biomass of wild ungulates and other herbivores in undeveloped and undisturbed areas (Andersen *et al*. 2004; Loe *et al*. 2005; Pettorelli *et al*. 2005a, b). Thus high annual values of NDVI indicate the presence of food (i.e. herbivores) and water for leopard, as well as cover (shrubs and trees) important for thermal protection, reproduction, escape and stalking prey.

Carnivore distribution and densities are clearly linked to prey distribution and abundance (Carbone & Gittleman 2002). In addition, the practice of laying non-species-specific poisoned bait for wolves and other carnivores is known to have inadvertently wiped out non-target animals, particularly rare and threatened ones (Sillero-Zubiri, Hoffmann & Macdonald 2004). Our failure to incorporate prey densities and the number of poisoned baits could lead to prediction errors. At present, these data are not available in adequate form or precision to be included in our habitat model. However, as prey distribution is also habitat dependent, we can assume that our model at least partly reflects prey availability. Assuming prey biomass to vary with habitat type, studies on carnivores demonstrate the potential for deriving accurate habitat and connectivity models (Wikramanayake *et al*. 2004; Carroll & Miquelle 2006; Linkie *et al*. 2006). Carroll & Miquelle (2006) suggest the superiority of non-prey-based models to prey-based ones if data on prey biomass or distribution are of poor quality.

Using our model in connectivity analysis in the Caucasus suggests that leopard is not present by chance in the Vashlovani Nature Reserve and that this reserve is part of one of the major corridors connecting the Greater and Lesser Caucasus. Interestingly, new signs of leopard presence were found right on this corridor, 55 km east of the reserve in Aharbahar Range, Azerbaijan (Lukarevsky *et al*. 2007). This provides further evidence of a high predictive accuracy and high conservation value of our model. This not only highlights the importance of the reserve, but also suggests that the establishment of protected areas outside the reserve (particularly a buffer zone around the reserve) and along the least-cost path is likely to increase the number of leopards, both within and outside the reserve, and will facilitate connectivity between distant leopard populations. As demonstrated here, our model could identify further conservation corridors among other important leopard populations in west and central Asia (e.g. the ranges of Zagros, Alborz and Kopetdagh).

The model we have constructed provides a tool for effective identification of potential leopard populations and habitats in the Caucasus, the Middle East and central Asia, as well as contributing to the successful conservation and management of the species. The model predicts the probable distribution of leopards and, when based on local knowledge of the territoriality of resident leopards, may enable more accurate estimation of population size. Searching for leopard and estimating numbers is difficult over vast and rugged areas; our model should facilitate improved detection and more accurate population estimates. Another practical use of the model will be predicting connectivity between different populations and therefore facilitating corridor planning for leopard conservation purposes. The identification of corridors will contribute to the WWF Caucasus-led campaign to ensure the long-term survival of leopard throughout the Caucasus Ecoregion. The research also provides an algorithm for sample data management that could be used in modelling habitats for similar species. Finally, as top predators are often associated with high biodiversity, the leopard habitat model could help to identify previously unknown biodiversity hotspots.

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Supplementary material

The following supplementary material is available for this article.

Table S1. Variables considered in modelling leopard habitat

Table S2. Variable statistics

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