

Predicting the potential distribution of the endangered Przewalski's gazelle

J. Hu^{1,2} & Z. Jiang¹

¹ Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

² Graduate School of Chinese Academy of Sciences, Beijing, China

Keywords

Maxent; *Procapra przewalskii*; scale effect; species distribution modelling; competing suitability models; threshold-determining approach.

Correspondence

Zhigang Jiang, Address: No. 1 Beichen West Road, Chaoyang District, Beijing 100101, China.

Email: jiangzg@ioz.ac.cn

Editor: Andrew Kitchener

Received 16 November 2009; revised 24 March 2010; accepted 26 March 2010

doi:10.1111/j.1469-7998.2010.00715.x

Abstract

Species distribution modelling can be a powerful tool in species conservation. Przewalski's gazelle *Procapra przewalskii* is an endangered ungulate and a conservation focus on the Qinghai–Tibetan Plateau. To identify the potential range and provide a conservation base for the species, we used the maximum entropy approach to build a habitat suitability map and took into account: (1) the comparison among three competing models (the full, uncorrelated and pruned models) with different sets of environmental predictors; and (2) scale effects on model spatial output and performance. Elevation, maximum temperature of the warmest month, mean temperature of the wettest and warmest quarter and isothermality were the five most effective predictors. The 11 threshold-determining approaches identified different thresholds. Spatial patterns of ranges predicted with the three models were similar, although the uncorrelated model was outperformed by the other two models. All three models identified regions in the eastern part of the Qinghai–Tibetan Plateau as the most suitable habitat for Przewalski's gazelle. Cross-validation area under the receiver operating characteristic curve (AUC) of the full model decreased slightly as the scale increased; spatial congruence AUC fluctuated with the small range, and the predicted range increased disproportionately. This study identifies areas to find new populations and representative habitats of a rare and endangered species.

Introduction

The Earth is currently undergoing a catastrophic loss of biodiversity (Lawton & May, 1995). An unknown but large number of species are already extinct while many others are at risk (Pimm & Raven, 2000; Primack, 2008) and monitoring populations of rare and endangered species is a priority for most conservation agencies and countries (Guisan *et al.*, 2006). Adequate conservation requires information on the geographical distribution (Pearce & Boyce, 2006) or the availability of a suitable habitat, which is invaluable to conservation planning and selecting an area for protection (Papeş & Gaubert, 2007). However, the distributions of many wild animals are extremely poorly known, even for some well-studied taxonomic groups (Anderson & Martinez-Meyer, 2004). Data on geographical range are therefore important to evaluate species conservation status and threat level (Thorn *et al.*, 2009).

Species distribution models (SDMs) are increasingly being used to address questions related to ecology, biogeography and species conservation (Engler, Guisan & Rechsteiner, 2004; Guisan & Thuiller, 2005; Guisan *et al.*, 2006; Carnaval & Moritz, 2008). Many techniques are now available and some methods that use presence-only (without absence) data have been shown to outperform others (Elith

et al., 2006; Hernandez *et al.*, 2006). For threatened species, due to the lack of appropriate presence data (Engler *et al.*, 2004), few predictive models have been applied (Godown & Peterson, 2000; Elith & Burgman, 2002). Furthermore, Guisan *et al.* (2007) showed that the operational scale (grid size) of SDMs affects model performance. However, these effects on the predicted range have seldom been evaluated. It is ideal to quantify the bias introduced by coarse-scale environmental predictors and identify the best scale (Meyer & Thuiller, 2006), as coarse-scale predictors may overpredict range even when performance metrics such as the area under the receiver operating characteristic (ROC) curve (AUC) are high (Seo *et al.*, 2009).

Przewalski's gazelle *Procapra przewalskii*, an endemic ungulate to China, occurs only over a small range (Jiang, 2004). Its previous distribution included parts of Qinghai, Ningxia, Inner Mongolia and Gansu Provinces. Increasing human activity since the beginning of the 20th century has resulted in the destruction of its habitat and range reduction (Jiang & Wang, 2001). During the 1990s, the species was only found around Qinghai Lake (about 300; Jiang *et al.*, 1995; Jiang, Feng & Wang, 1996); it was listed as Critically Endangered by the IUCN until 2008, when it was reclassified as Endangered, based on the most recently discovered populations (IUCN SSC Antelope Specialist Group, 2008).

Przewalski's gazelle is a Category I National Protected Wild Animal Species in China.

Although there are reports of new populations (Jiang, Li & Wang, 2000; Jiang, 2004; Ye *et al.*, 2006) and many studies on food competition, habitat selection, causes of decline, group size and composition, human–gazelle interactions, vigilance and sexual behaviour in Przewalski's gazelle (Jiang, 2004; Li, Jiang & Li, 2008; Hu *et al.*, 2009; Li *et al.*, 2009; Li, Jiang & Beauchamp, 2009), some questions remain unaddressed. For example, what environmental factors affect its potential distribution? Are there undetected populations? What areas is the species most likely to inhabit? Here, we predicted the potential distribution of the gazelle using the maximum entropy approach (Maxent). We generated a habitat suitability map, and also compared the predictive power of three competing models (the full, uncorrelated and pruned models) with different sets of predictors and tested the hypothesis that scale affects model spatial outputs and performance measures (Seo *et al.*, 2009). We hope this study will guide future field surveys and conservation programmes for Przewalski's gazelle and other rare and endangered species.

Methods

Species and eco-geographical data

The study area included historical and current ranges of Przewalski's gazelle. We took presence records, 3897 in total, from gazelle population censuses conducted in western China during 2002–2008 and the literature (Jiang, 2004) for model development.

We used 38 environmental predictors (Table 1) summarizing four types of data: (1) 19 bioclimatic data sources from WorldClim 1.4 (Hijmans *et al.*, 2005); (2) ecological variables, that is the normalized difference vegetation index (NDVI; <http://www.data.ac.cn/index.asp>) and land-cover (GLC, 2003); (3) human impact, including gross domestic product (GDP; <http://www.data.ac.cn/index.asp>) and human influence index (HII, incorporating four data types as proxies for human influence: human settlement, land transformation, accessibility and electrical power infrastructure; Last of the Wild Data Version 2, 2005); (4) topographical data from the United States Geological Survey's Hydro1K dataset (<http://edcdaac.usgs.gov/gtopo30/hydro/>). All initial predictors were at 1×1 km.

Model building with Maxent

Maxent is a recently developed general-purpose machine learning approach (Phillips, Anderson & Schapire, 2006; Phillips & Dudik, 2008). When estimating a target distribution, Maxent satisfies a set of constraints representing the incomplete information on the distribution and that, subject to those constraints, maximizes the entropy of the probability distribution (Phillips *et al.*, 2006). It uses presence-only occurrence data and has been shown consistently to outperform some other methods, including other presence-

only methods (Bioclim, Domain) and presence–absence methods (GAM, GLM and GARP), particularly for small sample sizes (Elith *et al.*, 2006; Hernandez *et al.*, 2006).

We implemented MAXENT 3.3.1 (Phillips *et al.*, 2006) and followed the default settings: regularization multiplier, 1; maximum iterations, 500; convergence threshold, 10^{-5} ; maximum number of background points, 10 000. Additionally, we selected the following: random test percentage, 20%; replicates, five; replicated run type, cross-validate. Selection of 'features' (predictors thereof) was carried out automatically, following the default rules dependent on the number of presence records. We selected the logistic output format, making the model easier to interpret (Phillips & Dudik, 2008), and carried out jackknife analyses of the regularized gain with training data to examine the importance of individual predictors.

Continuous model outputs were transformed into Boolean (presence/absence) maps by corresponding thresholds or 'cut-offs'. We estimated performances of the 11 threshold-determining approaches (1/2/3, fixed cumulative value 1/5/10; 4, minimum training presence; 5, 10 percentile training presence; 6/7/8/9, equal training/maximum training/equal test/maximum test sensitivity plus specificity; 10, balance training omission, predicted area and threshold value; 11, equate entropy of thresholded and original distributions).

Model comparison

We used a stepwise algorithm to compare the three competing models. First, we used all potentially useful predictors to build the full model, which may be oversized, overfitting or redundant (Parolo, Rossi & Ferrarini, 2008). We then implemented the uncorrelated model using a set of uncorrelated ($r < 0.8$) predictors. Finally, based on outcomes of jackknife analysis, we created the pruned model using the 10 most important predictors measured based on the regularized gain when predictors were used in isolation and on the decline of gain when predictors were omitted one at a time (Table 1).

We used two approaches to compare model outputs. First, we compared Boolean maps using the threshold indicating maximum training sensitivity plus specificity. Then, following Parolo *et al.* (2008), we conducted a comparison on a per-pixel basis with two formulas that yield the minimal and maximal divergence, respectively, namely $DIVERG_{\min} = (|a-b|, |a-c|, |b-c|)$ and $DIVERG_{\max} = (|a-b|, |a-c|, |b-c|)$ where: $||$ is the absolute value of the difference between two models; min and max operators are the minimum and maximum of differences among models; a , b and c represent the full, uncorrelated and pruned models in the order given.

Model evaluation and validation

We selected six scales (1×1 , 2×2 , 4×4 , 8×8 , 16×16 and 32×32 km) for the full model to explore the effect of scale and re-sampled initial presence records and predictors to

Table 1 Environmental predictor variables used to model the potential distribution of Przewalski's gazelle *Procapra przewalskii*

Code	Variable	Source	Used for model
bio01	Annual mean temperature	WorldClim 2004	Full, pruned
bio02	Mean diurnal range [mean of monthly (max temp–min temp)]	WorldClim 2004	Full, pruned
bio03	Isothermality (P2/P7) (× 100)	WorldClim 2004	Full, pruned
bio04	Temperature seasonality (standard deviation × 100)	WorldClim 2004	Full, pruned
bio05	Max temperature of the warmest month	WorldClim 2004	Full, uncorrelated, pruned
bio06	Min temperature of the coldest month	WorldClim 2004	Full, uncorrelated
bio07	Temperature annual range (P5–P6)	WorldClim 2004	Full
bio08	Mean temperature of the wettest quarter	WorldClim 2004	Full, pruned
bio09	Mean temperature of the driest quarter	WorldClim 2004	Full, uncorrelated
bio10	Mean temperature of the warmest quarter	WorldClim 2004	Full, pruned
bio11	Mean temperature of the coldest quarter	WorldClim 2004	Full, uncorrelated
bio12	Annual precipitation	WorldClim 2004	Full, pruned
bio13	Precipitation of the wettest month	WorldClim 2004	Full, pruned
bio14	Precipitation of the driest month	WorldClim 2004	Full, pruned
bio15	Precipitation seasonality (Coefficient of variation)	WorldClim 2004	Full
bio16	Precipitation of the wettest quarter	WorldClim 2004	Full, pruned
bio17	Precipitation of the driest quarter	WorldClim 2004	Full
bio18	Precipitation of the warmest quarter	WorldClim 2004	Full, pruned
bio19	Precipitation of the coldest quarter	WorldClim 2004	Full
ndvi01	Normalized difference vegetation index of January	CNRD	Full
ndvi02	Normalized difference vegetation index of February	CNRD	Full, uncorrelated
ndvi03	Normalized difference vegetation index of March	CNRD	Full
ndvi04	Normalized difference vegetation index of April	CNRD	Full, uncorrelated, pruned
ndvi05	Normalized difference vegetation index of May	CNRD	Full, pruned
ndvi06	Normalized difference vegetation index of June	CNRD	Full, uncorrelated
ndvi07	Normalized difference vegetation index of July	CNRD	Full, pruned
ndvi08	Normalized difference vegetation index of August	CNRD	Full, pruned
ndvi09	Normalized difference vegetation index of September	CNRD	Full
ndvi10	Normalized difference vegetation index of October	CNRD	Full, uncorrelated
ndvi11	Normalized difference vegetation index of November	CNRD	Full
ndvi12	Normalized difference vegetation index of December	CNRD	Full, uncorrelated
landcov	Land-cover	GLC 2003	Full, uncorrelated, pruned
GDP	Gross domestic product for 2000	CNRD	Full
HII	Human influence index	LWP-2	Full, uncorrelated, pruned
aspect	Aspect	USGS 2004	Full, uncorrelated
elevation	elevation (m a.s.l.)	USGS 2004	Full, uncorrelated, pruned
slope	Slope	USGS 2004	Full
CTI	Compound Topographic index	USGS 2004	Full

CNRD, Chinese Natural Resources Database; LWP-2, Last of the Wild Data Version 2.

Table 2 The number of training/testing data and AUC cut-off value (i.e. threshold) used for transforming the probability data to presence/absence data at each scale

	Scale					
	1 × 1 km	2 × 2 km	4 × 4 km	8 × 8 km	16 × 16 km	32 × 32 km
Training data	95	57	32	22	15	11
Testing data	22	14	7	5	3	2
AUC cut-off value	0.571	0.255	0.309	0.275	0.657	0.326

The area under the receiver operating characteristic curve (AUC) cut-off value indicating maximum training sensitivity and specificity is used.

different scales using ArcGIS 9.2 (ESRI, Redland, WA, USA), with one record per cell for each scale. Record number and threshold are given in Table 2.

We used the ROC analyses as reliability measurements to evaluate the predictive performance of the model. AUC is a threshold-independent measure of model accuracy and

ranges from 0 to 1. In general: 0.5–0.6, insufficient; 0.6–0.7, poor; 0.7–0.8, average; 0.8–0.9, good; 0.9–1, excellent (Araújo & Guisan, 2006). We evaluated model accuracy with the five-fold cross-validation AUC statistics. We assessed spatial congruence (agreement on predicted ranges) between scales based on Seo *et al.* (2009). With the baseline 1 × 1 km

records, the AUC value that compared the probability map was computed at each scale. For instance, we overlaid a species' 1×1 km presence data with its 2×2 km probability surface and computed an AUC value. The difference between these AUC values and those from 1×1 km SDM outputs represented the spatial bias probably introduced by scaled-up records and predictors.

To examine the effect of scale on the normalized area predicted, with the threshold indicating maximum training sensitivity plus specificity, we calculated and compared the area ratio (ratios of area predicted as a species' range) across scales using the extent of 1×1 km as the denominator (Seo *et al.*, 2009).

Results

Explanatory predictors and threshold-determining approaches

Jackknife analyses revealed that elevation, bio5 (maximum temperature of the warmest month), bio8 (mean temperature of the wettest quarter), bio10 (mean temperature of the warmest quarter) and bio3 (isothermality) were the five most effective predictors when used in isolation (Fig. 1); CTI, slope, aspect, GDP, NDVI07 (normalized difference vegetation index of July) made only small contributions towards model development. The predictors that decreased the training gain the most when omitted were bio1 (annual mean temperature), HII, land-cover, NDVI07 and bio02 (mean diurnal range). Omitting some predictors such as NDVI01 (normalized difference vegetation index of January) increased the gain slightly (Fig. 1).

The 11 approaches provided different thresholds. The AUC cut-off ranged from 0.004 to 0.941 and the percentage of area selected as range by the corresponding threshold revealed an apparent divergence (Fig. 2).

Predicted geographical distribution

The ROC analyses revealed that the full, uncorrelated and pruned models all performed well. Although the full model was the most accurate on the training data (AUC = 0.9999), the pruned model was the most accurate on the testing data (AUC = 0.9997). The uncorrelated model was outperformed by the other two models, although it performed better (AUC = 0.9986 and 0.9948 for the training and testing data respectively) than random prediction (AUC = 0.5).

The three model outputs showed similar spatial patterns and clearly identified regions in the eastern part of the Qinghai–Tibetan Plateau as the most suitable habitat for Przewalski's gazelle (Fig. 3a, c, e). Boolean maps, as expected, provided more conservative predictions. They identified the region around Qinghai Lake, some north-eastern and southern regions adjacent to Qinghai Lake and other scattered locations on the Loess Plateau and mid to high plain of the Hetao Ordos (Fig. 3b, d, f). Compared with the full model, binary maps of the uncorrelated and pruned

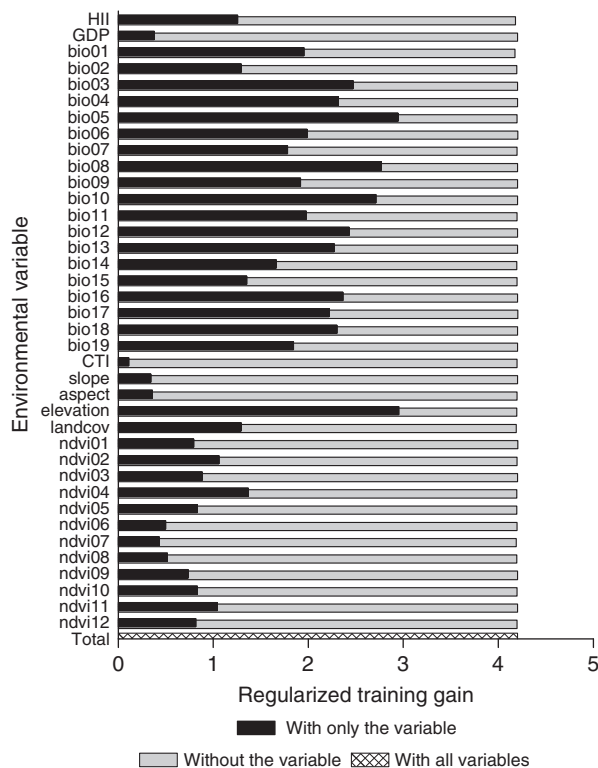


Figure 1 Jackknife analyses of individual predictor importance in the development of the full model in relation to the overall model quality or the 'total gain' (grid bar) at 1×1 km. Black bars indicate the gain achieved when including that predictor only and excluding the remaining predictors; grey bars show how much the total gain is diminished without the given predictor. HII, human influence index; GDP, gross domestic product; bio01, annual mean temperature; bio02, mean diurnal range; bio03, isothermality; bio04, temperature seasonality; bio05/06, max/min temperature of the warmest/coldest month; bio07, temperature annual range (P5–P6); bio08/09/10/11, mean temperature of the wettest/driest/warmest/coldest quarter; bio12, annual precipitation; bio13/14, precipitation of the wettest/driest month; bio15, precipitation seasonality; bio16/17/18/19, precipitation of the wettest/driest/warmest/coldest quarter; CTI, compound topographic index; landcov, landcover; ndvi01–12, normalized difference vegetation index (NDVI) of each month.

models were spatially less restrictive and the uncorrelated model was smoother.

Spatially explicit comparisons revealed few divergences among the three models (Fig. 4). $DIVERG_{min}$ did not highlight any areas. $DIVERG_{max}$ highlighted two areas (north-eastern and southern areas adjacent to Qinghai Lake, and in Shandan, Minle, Sunan, Xinghai and Tongde Counties) where the divergence was mainly due to the difference between the pruned model and the other two models.

A close-up of the predicted range of the full model is shown in Fig. 5. Besides the current ranges in Gangcha, Haiyan, Gonghe and Tianjun Counties, some parts of Qilian, Sunan, Minle, Shandan, Yongchan, Menyuan, Subei, Wulan, Xinghai, Guinan, Guide, Huangyuan,

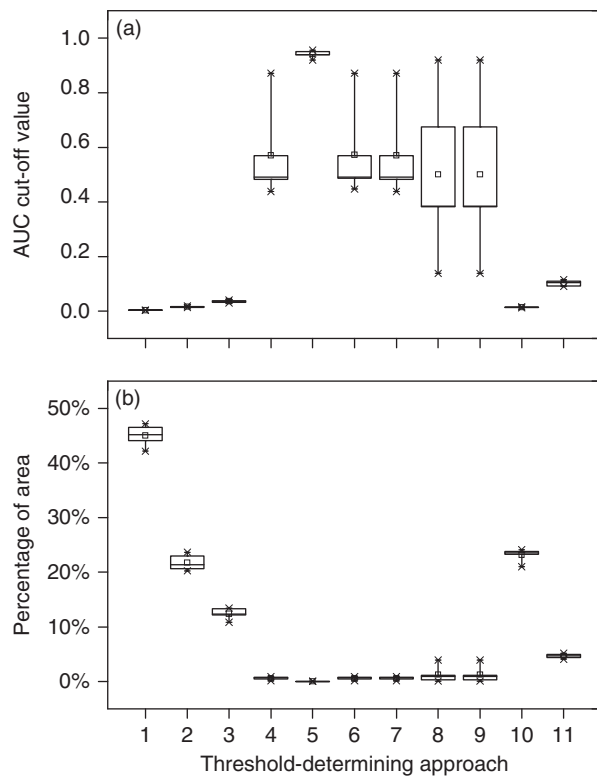


Figure 2 The area under the receiver operating characteristic curve (AUC) cut-off value (a) and percentage of area predicted as range using the corresponding cut-off value (b) determined by the 11 threshold-determining approaches of the full model at 1×1 km. Solid line, median; square, mean; edges of box, quartiles; whiskers, 5th and 95th percentiles. Approach codes: 1/2/3, fixed cumulative value 1/5/10; 4, minimum training presence; 5, 10 percentile training presence; 6/7/8/9, equal training/maximum training/equal test/maximum test sensitivity and specificity; 10, balance training omission, predicted area and threshold value; 11, equate entropy of thresholded and original distributions.

Huangzhong and Datong Counties, and small areas in Baiyin, Yinchuan and Baotou Cities were identified as suitable habitat for Przewalski's gazelle. All current and most historical presences were within the predicted ranges, except for the historical record of southern Ordos.

Model evaluation and validation across scales

The mean AUC across scales ranged from 0.9758 and 0.9017 to 0.9999 and 0.9994 for the training and testing data respectively. AUC decreased slightly as the scale increased (Fig. 6). Although the AUC values for finer scales were higher than those for coarser scales, the decreases between 1×1 and 32×32 km were only 0.0241 and 0.0977 for the training and the testing data, respectively.

As the scale increased, spatial congruence AUC fluctuated within a small range (Fig. 6b). The maximal difference was only 0.0079 and occurred between models of the 1×1 and 8×8 km probability surfaces.

The area ratio increased as the grids became coarser (Fig. 6b). Model agreements on the predicted range were relatively good below 16×16 km, the area ratio being within the range 1.00–3.58; divergence increased at greater scales, with the ratio being 8.67 times at 16×16 km and 15.56 times at 32×32 km.

Discussion

Our results indicated regions of suitable habitat for Przewalski's gazelle. In the models, scale increased from an initial resolution of 1×1 to 32×32 km, and predicted habitat deviated dramatically from current and historical distribution ranges for the species.

Sample size and model accuracy

When dealing with rare species, only a small number of occurrence records are available (Gibson, Barrett & Burbidge, 2007) and this can affect model accuracy (Pearce & Ferrier, 2000; Stockwell & Peterson 2002). Therefore, reducing the minimum number of occurrences required would considerably increase the proportion of species to which SDMs can be applied (Pearson *et al.*, 2007). In this respect, Maxent outperforms some other methods, being accurate and stable across all sample-size categories tested (Elith *et al.*, 2006; Hernandez *et al.*, 2006). This was supported by our results, which are highly accurate above 8×8 km despite small sample sizes. High cross-validation AUC and spatial congruence AUC also confirmed that generating the ROC plots using presence and randomly selected background samples, rather than pseudo-absences, provides a solution to both omission and commission errors (Phillips *et al.*, 2006; Gibson *et al.*, 2007).

Model comparison

Parolo *et al.* (2008) showed that comparisons among multiple models from various ecological hypotheses may provide a better insight into species–environment relationships and lead to a more stringent assessment of potential distribution. It is impossible to cover all likely useful predictors in SDMs and a set of predictors providing improved predictive accuracies may be adequate (Parolo *et al.*, 2008). The high accuracy of the full model supported our initial choice of predictors. As the uncorrelated and pruned models also performed well, the full model might be overly large. However, the accuracy of the full model on the testing data indicated its predictive ability outside the training data, and regularization in Maxent appears to prevent overfitting better than variable-selection methods in regression-based models (Phillips & Dudik, 2008).

The uncorrelated model was of importance as predictors are always correlated to each other (Austin, 2002). Use of non-correlated predictors in SDMs reduces the need for predictors and prevents overfitting. Although Maxent is able to build a model even with predictors of high collinearity, how stable and interpretable the model is remains to be

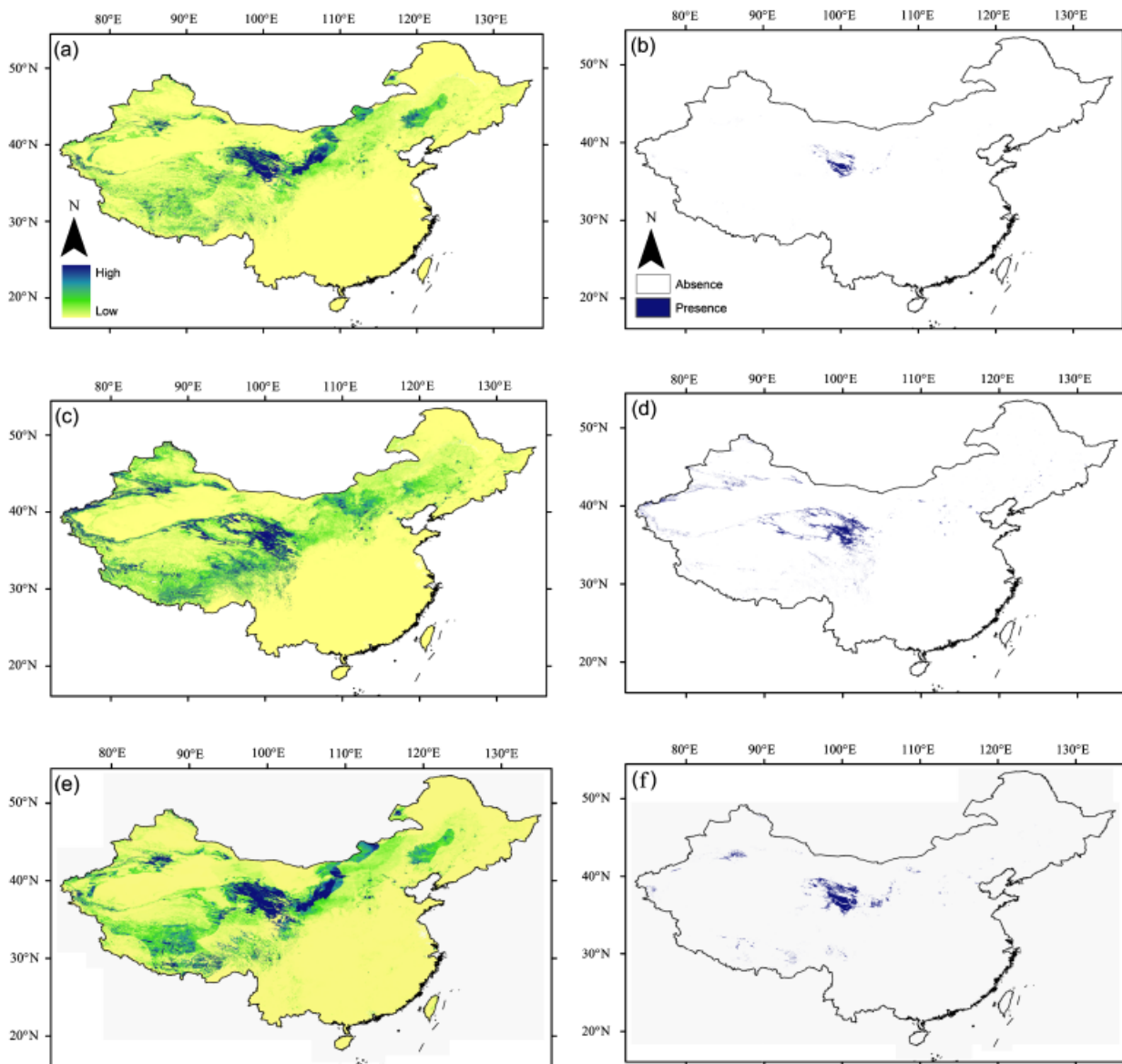


Figure 3 Predicted probability distribution and range selected using the area under the receiver operating characteristic curve (AUC) cut-off value for Przewalski's gazelle *Procapra przewalskii* based on, respectively, (a, b) the full model, (c, d) the uncorrelated model and (e, f) the pruned model at 1×1 km. The AUC cut-off value of each model indicating maximum training sensitivity and specificity is used.

determined (Maxent Google Group, 2009). The above also explains why the uncorrelated model was outperformed by the other two models; some useful predictors may have been omitted incorrectly. Concurrently, due to regularization to prevent overfitting in Maxent, it might not need to eliminate predictors with (high levels of) collinearity.

The pruned model was the most effective while addressing the need for a size-limited, non-overfitting and non-redundant model, based exclusively on significant predictors (Parolo *et al.*, 2008). It provided the highest AUC on the testing data and met the need for parsimony (accuracies being approximately equal, the simplest model is the best). Compared with larger models, parsimonious models are

also more transferable from a predicted to external areas nearby (Araújo & Guisan, 2006).

Those areas where high $DIVERG_{min}$ values represented high levels of disagreement among the models; those areas with low $DIVERG_{max}$ values represented good model fitting and are of particular interest (Parolo *et al.*, 2008). This is a step forward regarding the quantification of uncertainty in predictions based on predicted maps (Barry & Elith, 2006).

Scale effects on model outputs

Studies of scale effects on SDMs have focused mainly on identifying what model produced the highest accuracy (Elith

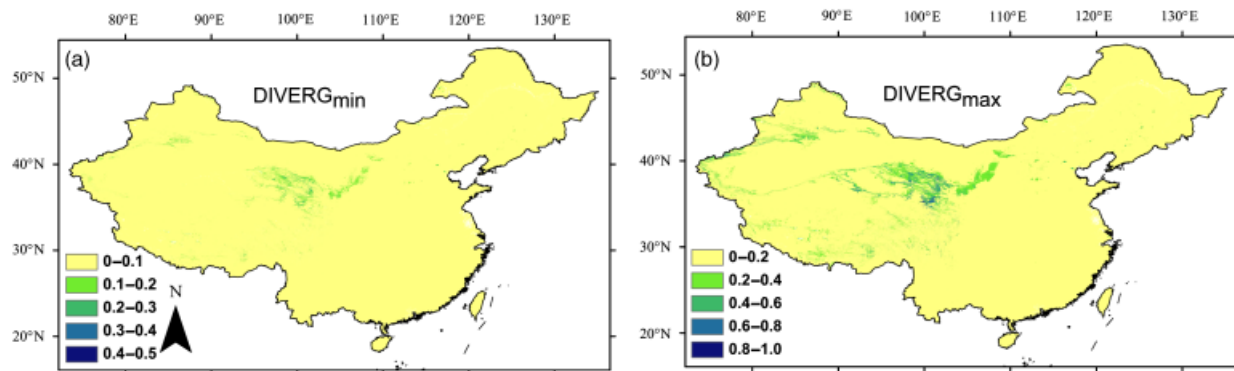


Figure 4 Disagreement among the three competing models (the full, uncorrelated and pruned models) estimated through (a) minimal ($DIVERG_{min}$) and (b) maximal ($DIVERG_{max}$) divergences at 1×1 km.

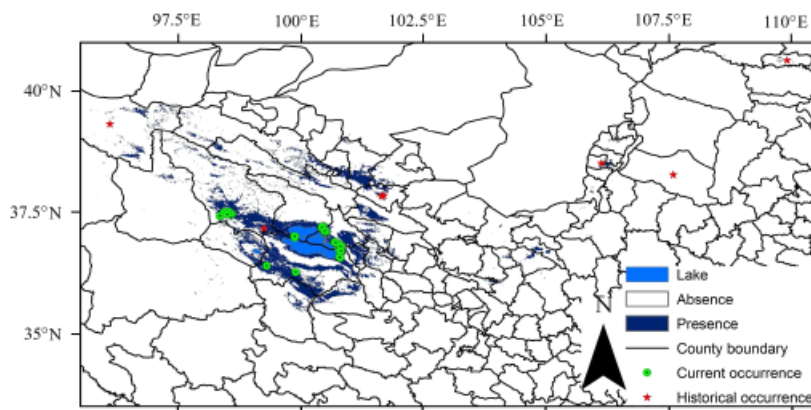


Figure 5 Close-up of the predicted range using the area under the receiver operating characteristic curve cut-off value indicating the maximum training sensitivity and specificity of the full model at 1×1 km. Historical occurrence records from the literature indicate no current Przewalski's gazelle *Procapra przewalskii* record (Jiang 2004); current records are from gazelle censuses conducted in western China during 2002–2008.

et al., 2006; Lawler *et al.*, 2006), whereas few studies have tested spatial outputs. Guisan *et al.* (2007) suggest that a 10-fold scale change will not considerably impact SDMs while Seo *et al.* (2009) indicate that model accuracy and spatial output agreement decrease when the scale increases 64-fold. Our results support the hypothesis that a species' range will be portrayed differently across scales (Seo *et al.*, 2009) but the details here are more complex.

Seo *et al.* (2009) suggest that the decline in model accuracy generally accelerates between eight- and 16-fold at a 1×1 km scale when evaluating the performance of SDMs. With the scale increased 32-fold here, cross-validation AUC decreased slightly and spatial congruence AUC fluctuated slightly; the area ratio increased sharply with an increase in scale to 16×16 km. The area ratio of 15.56-fold at 32×32 km here was greater than that of Seo *et al.* (2009), who reported a ratio of only 2.50–3.00-fold at 64×64 km for a species with a narrow range. Therefore, we should limit scale to below 16×16 km to obtain an ideal representation of the predicted range of Przewalski's gazelle.

Threshold selection

It is crucial to select an optimal threshold for transforming probability data to presence/absence data, as the latter

provide more practical information (Liu *et al.*, 2005). Although there are many approaches to determine thresholds, no general-purpose rule has been developed to determine the optimal threshold (Suarez-Seoane *et al.*, 2008), and this remains to be explored in Maxent (Phillips *et al.*, 2006). For the 11 approaches used here, some, including fixed cumulative value 1/5/10, balance training omission, predicted area and threshold value, and equate entropy of thresholded and original distributions, provided thresholds that were too low. The approach of 10 percentile training presence was not recommended as is provided too high a threshold. Based on the trade-off between investigation cost and conservation effort, the remaining approaches were recommended because of their appropriate thresholds.

Conservation implications

When species are threatened, standard methods such as simple or stratified random sampling combined with main environmental gradients may be highly inefficient (Rushton, Ormerod & Kerby, 2004). However, SDMs could be a promising tool to identify areas where species might be found (Pyrton, Burbrink & Guiher, 2008) and to help find new populations (Bourg, McShea & Gill, 2005). It is expected that the larger the predicted probability/suitability

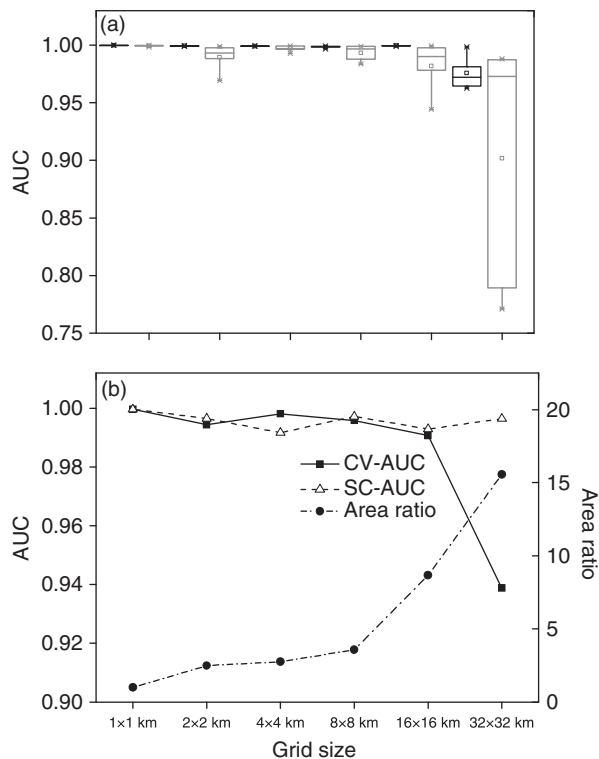


Figure 6 Model performance versus scale: (a) the five-fold cross-validation training area under the receiver operating characteristic curve (AUC) (black) and testing AUC (grey) and (b) total cross-validation AUC (CV-AUC), spatial congruence AUC (SC-AUC) and area ratio (ratios of area predicted as range between the 1 × 1-km grid size model and every other grid size). Solid line, median; square, mean; edges of box, quartiles; whiskers, 5th and 95th percentiles.

of presence at a site, the more suitable the site is to the species survival. For Przewalski's gazelle, despite there remaining only several hundred individuals after 20 years of protection, the populations are growing and its distribution ranges are expanding (Jiang, 2004; Ye *et al.*, 2006). To avoid potential conflict between gazelles and local people (Hu *et al.*, 2009), we should adopt a less restrictive strategy and purposely include some less suitable habitat in protection measures as the predicted range extends outside the current species range. There may be undiscovered or newly established populations of Przewalski's gazelle (Jiang, 2004). If aiming to discover new populations/records, the highly suitable areas predicted here would be good starting points. Moreover, priority should be given to those predicted suitable areas that are consistent with the historical distribution (no current presence; Jiang *et al.*, 1995) when identifying areas for reintroductions within the former range.

The model-based sampling of rare species, involving reiterative alternation of modelling and field sampling phases, holds great promise for strengthening and complementing conservation practice and reducing the sampling costs (Guisan *et al.*, 2006). Several investigations conducted

within historical ranges in Inner Mongolia, Gansu, Xinjiang and Qinghai Provinces of China found Przewalski's gazelles only around Qinghai Lake (Schaller, 1998; Jiang *et al.*, 2003). However, populations have recently been found around Qinghai Lake (Jiang, 2004). The highly suitable areas identified here should be surveyed to search for appropriate environmental conditions. These data can then used to update the training dataset and fit improved models to direct further sampling, and this iterative process could be repeated over several field seasons (Guisan *et al.*, 2006). Additionally, attention should be paid to areas occupied not by Przewalski's gazelle but by related species (see Phillips, 2008), such as Tibetan gazelle *Procapra picticaudata* (Zhang & Jiang, 2006).

Acknowledgements

We thank Steven Phillips for adapting Maxent, and to all our colleagues, especially Xiaoge Ping, Philippe Chouteau, Lin Zhang and Peng Luo, for their comments on earlier versions of the paper. Thanks are also due to the Editor and two anonymous reviewers. This study was funded by the Science and Technology Supporting Project of MOST (2008BAC39B04), Whitley Fund for Nature, Sir Peter Scott Fund of SSC/IUCN and the National Natural Science Foundation (30670267, 30430120).

References

- Anderson, R.P. & Martínez-Meyer, E. (2004). Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. *Biol. Conserv.* **116**, 167–179.
- Araújo, M.B. & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *J. Biogeogr.* **33**, 1677–1688.
- Austin, M.P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* **157**, 101–118.
- Barry, S. & Elith, J. (2006). Error and uncertainty in habitat models. *J. Appl. Ecol.* **43**, 413–423.
- Bourg, N.A., McShea, W.J. & Gill, D.E. (2005). Putting a cart before the search: successful habitat prediction for a rare forest herb. *Ecology* **86**, 2793–2804.
- Carnaval, A.C. & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *J. Biogeogr.* **35**, 1187–1201.
- Elith, J. & Burgman, M. (2002). Predictions and their validation: rare plants in the central highlands, Victoria, Australia. In *Predicting species occurrences: issues of accuracy and scale*: 303–313. Scott, J.M., Heglund, P.J., Hauffer, J.B., Morrison, M., Raphael, M.G., Wall, W.B. & Samson, F. (Eds). Washington: Island Press.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A.,

- Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151.
- Engler, R., Guisan, A. & Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *J. Appl. Ecol.* **41**, 263–274.
- Gibson, L., Barrett, B. & Burbidge, A. (2007). Dealing with uncertain absences in habitat modelling: a case study of a rare ground-dwelling parrot. *Divers. Distrib.* **13**, 704–713.
- GLC (2003) Global Land Cover 2000 database. European Commission, Joint Research Centre. Available at <http://gem.jrc.ec.europa.eu/products/glc2000/glc2000.php> (accessed 10 October 2009).
- Godown, M.E. & Peterson, A.T. (2000). Preliminary distributional analysis of US endangered bird species. *Biodivers. Conserv.* **9**, 1313–1322.
- Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A. & Zimmermann, N.E. (2006). Using niche-based models to improve the sampling of rare species. *Conserv. Biol.* **20**, 501–511.
- Guisan, A., Graham, C.H., Elith, J. & Huettmann, F. (2007). Sensitivity of predictive species distribution models to change in grain size. *Divers. Distrib.* **13**, 332–340.
- Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* **8**, 993–1009.
- Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**, 773–785.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978.
- Hu, J.-H., Ping, X.-G., Cai, J., Li, Z.-Q., Li, C.W. & Jiang, Z.-G. (2009). Do local communities support the conservation of endangered Przewalski's gazelle? *Eur. J. Wildl. Res.* (Online DOI: 10.1007/s10344-009-0346-4).
- IUCN SSC Antelope Specialist Group. (2008). *Procapra przewalskii*. In *IUCN 2009. IUCN Red List of Threatened Species. Version 2009.1*. IUCN. Available at <http://www.iucnredlist.org/apps/redlist/details/18230/0> (accessed 12 September 2009).
- Jiang, Z.-G. (2004). *Przewalski's gazelle*. Beijing: China Forestry Publishing House.
- Jiang, Z.-G., Feng, Z.-J. & Wang, Z.-W. (1996). Przewalski's gazelle in China. *Conserv. Biol.* **10**, 324–325.
- Jiang, Z.-G., Feng, Z.-J., Wang, Z.-W., Chen, L.-W., Cai, P. & Li, Y.-B. (1995). Historical and current distributions of Przewalski's gazelles. *Acta Theriol. Sin.* **15**, 241–245.
- Jiang, Z.-G., Lei, R.-H., Liu, B.-W. & Li, C.-W. (2003). A review on the researches of Przewalski's gazelle. *Chin. J. Zool.* **38**, 129–132.
- Jiang, Z.-G., Li, D.-Q. & Wang, Z.-W. (2000). Population declines of Przewalski's gazelle around Qinghai lake, China. *Oryx* **34**, 129–135.
- Jiang, Z.-G. & Wang, S. (2001). China. In *Antelopes. Part 4: North America, the Middle East and Asia. Global Survey and Regional Action Plans*: 168–177. Mallon, D.P. & Kingwood, S.C. (Eds). Gland/Cambridge: SSC Antelope Specialist Group/IUCN.
- Last of the Wild Data Version 2. (2005) Global Human Influence Index (HII). Wildlife Conservation (WCS) and Center for International Earth Science Information Network (CIESIN). Available at <http://sedac.ciesin.columbia.edu/wildareas/> (accessed 10 September 2009)
- Lawler, J.J., White, D., Neilson, R.P. & Blaustein, A.R. (2006). Predicting climate-induced range shifts: model differences and model reliability. *Global Change Biol.* **12**, 1568–1584.
- Lawton, J. & May, R. (1995). *Extinction rates*. Oxford: Oxford University Press.
- Li, C.-W., Jiang, Z.-G., Feng, Z.-J., Yang, X.-B., Yang, J. & Chen, L.-W. (2009). Effects of highway traffic on diurnal activity of the critically endangered Przewalski's gazelle. *Wildl. Res.* **36**, 379–385.
- Li, Z.-Q., Jiang, Z.-G. & Beauchamp, G. (2009). Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *J. Zool. (Lond.)* **277**, 302–308.
- Li, Z.-Q., Jiang, Z.-G. & Li, C.-W. (2008). Dietary overlap of Przewalski's gazelle, Tibetan gazelle, and Tibetan sheep on the Qinghai-Tibet Plateau. *J. Wildl. Mgmt.* **72**, 944–948.
- Liu, C.R., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**, 385–393.
- Maxent Google Group. (2009) A discussion group for users of the Maxent software for modelling species distributions. Available at <http://groups.google.com/group/maxent> (accessed 2 November 2009).
- Meyer, C.B. & Thuiller, W. (2006). Accuracy of resource selection functions across spatial scales. *Divers. Distrib.* **12**, 288–297.
- Papeş, M. & Gaubert, P. (2007). Modelling ecological niches from low numbers of occurrences: assessment of the conservation status of poorly known viverrids (Mammalia, Carnivora) across two continents. *Divers. Distrib.* **13**, 890–902.
- Parolo, G., Rossi, G. & Ferrarini, A. (2008). Toward improved species niche modelling: *Arnica montana* in the Alps as a case study. *J. Appl. Ecol.* **45**, 1410–1418.
- Pearce, J. & Ferrier, S. (2000). An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecol. Model.* **128**, 127–147.
- Pearce, J.L. & Boyce, M.S. (2006). Modelling distribution and abundance with presence-only data. *J. Appl. Ecol.* **43**, 405–412.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* **34**, 102–117.

- Phillips, S.J. (2008). Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). *Ecography* **31**, 272–278.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231–259.
- Phillips, S.J. & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31**, 161–175.
- Pimm, S.L. & Raven, P. (2000). Biodiversity: extinction by numbers. *Nature* **403**, 843–845.
- Primack, R. (2008). *A primer of conservation biology*. 4th edn. Sunderland: Sinauer Associates.
- Pyron, R., Burbrink, F. & Guiher, T. (2008). Claims of potential expansion throughout the US by invasive Python species are contradicted by ecological niche models. *PLoS One* **3**, e2931.
- Rushton, S.P., Ormerod, S.J. & Kerby, G. (2004). New paradigms for modelling species distributions? *J. Appl. Ecol.* **41**, 193–200.
- Schaller, G. (1998). *Wildlife of the Tibetan steppe*. Chicago: University of Chicago Press.
- Seo, C., Thorne, J.H., Hannah, L. & Thuiller, W. (2009). Scale effects in species distribution models: implications for conservation planning under climate change. *Biol. Lett.* **5**, 39–43.
- Stockwell, D.R.B. & Peterson, A.T. (2002). Effects of sample size on accuracy of species distribution models. *Ecol. Model.* **148**, 1–13.
- Suarez-Seoane, S., de la Morena, E.L.G., Prieto, M.B.M., Osborne, P.E. & de Juana, E. (2008). Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution. *Ecol. Model.* **219**, 17–29.
- Thorn, J.S., Nijman, V., Smith, D. & Nekaris, K.A.I. (2009). Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). *Divers. Distrib.* **15**, 289–298.
- Ye, R.-R., Cai, P., Peng, M., Lu, X.-F. & Ma, S.-Z. (2006). The investigation about distribution and population size of Przewalski's gazelle (*Procapra przewalskii*) in Qinghai Province, China. *Acta Theriol. Sin.* **26**, 373–379.
- Zhang, F.-F. & Jiang, Z.-G. (2006). Mitochondrial phylogeography and genetic diversity of Tibetan gazelle (*Procapra picticaudata*): implications for conservation. *Mol. Phylogenet. Evol.* **41**, 313–321.