Using habitat models to evaluate protected area designing for giant pandas

Authors: Qi, Dunwu, Xu, Chi, Hou, Rong, Chen, Peng, Owens, Jacob R., et al.

Source: Folia Zoologica, 64(1) : 56-64

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v64.i1.a7.2015

Folia Zool. – 64 (1): 56–64 (2015)

Using habitat models to evaluate protected area designing for giant pandas

Dunwu QI[1], Chi XU[2], Rong HOU[1]*, Peng CHEN[1], Jacob R. OWENS[1], Zhihe ZHANG[1], Xiaodong GU[3], Zhisong YANG[1] and Limin CHEN[4]

[1] *The Key Laboratory for Conservation Biology of Endangered Wildlife, Sichuan Province, Chengdu Research Base of Giant Panda Breeding, Chengdu, Sichuan 610081, China; e-mail: qidunwu@163.com*
[2] *Xuebaoding National Nature Reserve, Mianyang 622550, China*
[3] *Sichuan Forestry Department, Wildlife Conservation Division, Chengdu, Sichuan 610081, China*
[4] *Tangjianghe National Nature Reserve, Qingchuan 628109, China*

Received 18 December 2014; Accepted 22 March 2015

Abstract. Giant pandas (*Ailuropoda melanoleuca*) are now confined to fragmented habitats in western China, with more than 60 % of individuals inhabiting 63 protected areas. Knowledge of the environmental features required by giant pandas is critically important for protected area spatial arrangement and subsequent assessments. Here we developed a distribution model for giant pandas in the Tangjiahe Nature Reserve using Ecological Niche Factor Analysis (ENFA) model. We found that less than 40 % of this key reserve is of high suitability for giant pandas, highly suitable habitat being primarily characterized as coniferous forests away from roads within the reserve. Although there was a clear core zone occupied by giant pandas, which included the vast majority of known giant panda locations, only about 45 % of this zone was classified as highly suitable habitat (suitable and optimal). Therefore, the spatial arrangement within the reserve may need to be modified to effectively manage the remaining population of giant pandas. Of particular concern are several tourism proposals being considered by local government, which, if implemented, will increase the isolation of the local population from those in the surrounding area. Our analysis identifies Caijiaba and Baixiongping as areas that should become conservation priorities. Our approach provides valuable data to advise conservation policy and could be easily replicated across other protected areas.

Key words: ecological requirement, Ecological Niche Factor Analysis (ENFA), habitat suitability, protected area management

Introduction

The development of protected areas is a fundamental strategy for the conservation of biodiversity (Gaston et al. 2006, Pressey et al. 2007) and should provide a buffer from processes that threaten its persistence (Margules & Pressey 2000, Greve et al. 2011). To achieve these functions, protected areas often require a description of a species' geographical distribution or use of habitats (Araújo & Williams 2000). Based on the target species' requirements, the spatial arrangement of these protected areas should be optimized/managed, especially given that a large number of these areas have been established over time, often without setting their appropriate management or goals (Beresford et al. 2011). However, issues surrounding the mismanagement of these areas and conservation politics can impede conservation outcomes (Kolahi et al. 2013) due to a lack of a generalized or systematic effort across a large sample of protected areas (Terborgh & van Schaik 2002, Lester et al. 2013). Fortunately, Geographic Information Systems (GIS) and predictive habitat models based on species requirements over large areas are possible and have become invaluable to the science of conservation and wildlife management (Akcakaya & Atwood 1997, Dettmers & Bart 1999, Mateo et al. 2013) and can be broadly applied throughout a focal species' range (Brooker 2002).

For the giant panda (*Ailuropoda melanoleuca*), commercial logging, agriculture developments, infrastructure and hydropower constructions across their distribution have resulted in gradual fragmentation and degradation of their habitat (Zhu et al. 2011, 2013). As a result of China´s National Conservation Plan, the number of protected areas for pandas has increased from 4 to 63, protecting approximately 3.2 million hectares of panda habitat (Hu et al. 2011). These protected areas are critically important for the long-term survival of the giant panda (Xu et al. 2006, Shen et al. 2008, Wei et al. 2012). However, it

* *Corresponding Author*

appears that the majority of protected areas have been designed and allocated by governments, and seldom considered two fundamental questions: what are the requirements of giant pandas, and, based on this information, what design should the reserves follow (Hu 2001). Furthermore, these design deficiencies are particularly significant in China, which over the past three decades has had the world's fastest growing economy, as well as an explosive growth in the number of nature reserves (Liu & Raven 2010).

The increasing prevalence of multiple-use protected areas across the globe has prompted managers to initiate careful design strategies founded upon zoning schemes (Geneletti & van Duren 2008). The zoning areas represent a gradient, from completely off-limits to fully-available for multiple human activities (Hull et al. 2011). The Tangjiahe Nature Reserve was established in Sichuan, China in 1978 and is unique in being the only giant panda reserve completely free from human inhabitants (Wan et al. 2005). Furthermore, adjacent areas previously affected by logging and clearing have been restored for the seasonal altitudinal migration of giant pandas (Hu 2001). Currently, the reserve is classified by managers into the following three zones, based on elevation: transition zone (below 1500 m), buffer zone (1500-1900 m), and core zone (above 1900 m). Two tourist roads and 14 tourism sites were developed within the transition zone, and, as a result, concerns about how to manage these areas effectively have existed since ecotourism was initiated.

Currently, ecotourism is a rapidly expanding portion of the world's travel market (Newsome et al. 2002), and helps to protect animal habitat, but may also have negative impacts on wildlife (Müllner et al. 2004, Ménard et al. 2014). To maximize the potential of the protected areas, managers and policymakers need information on the threats and stressors that wildlife faces (Sutherland et al. 2004). This type of management only makes sense if there is a reasonable chance that these areas can continue to provide ecosystem services in the future (Cooke & O'Connor 2010). Given the current design of the reserve, and the tourism developments underway, it is important to understand the precise ecological requirements of giant pandas in this area and how these requirements are affecting their distribution. We explore these issues using the Ecological Niche Factor Analysis (ENFA) with one specific goal in mind: to identify environmental features of importance to the giant panda so that appropriate conservation practices can be implemented.

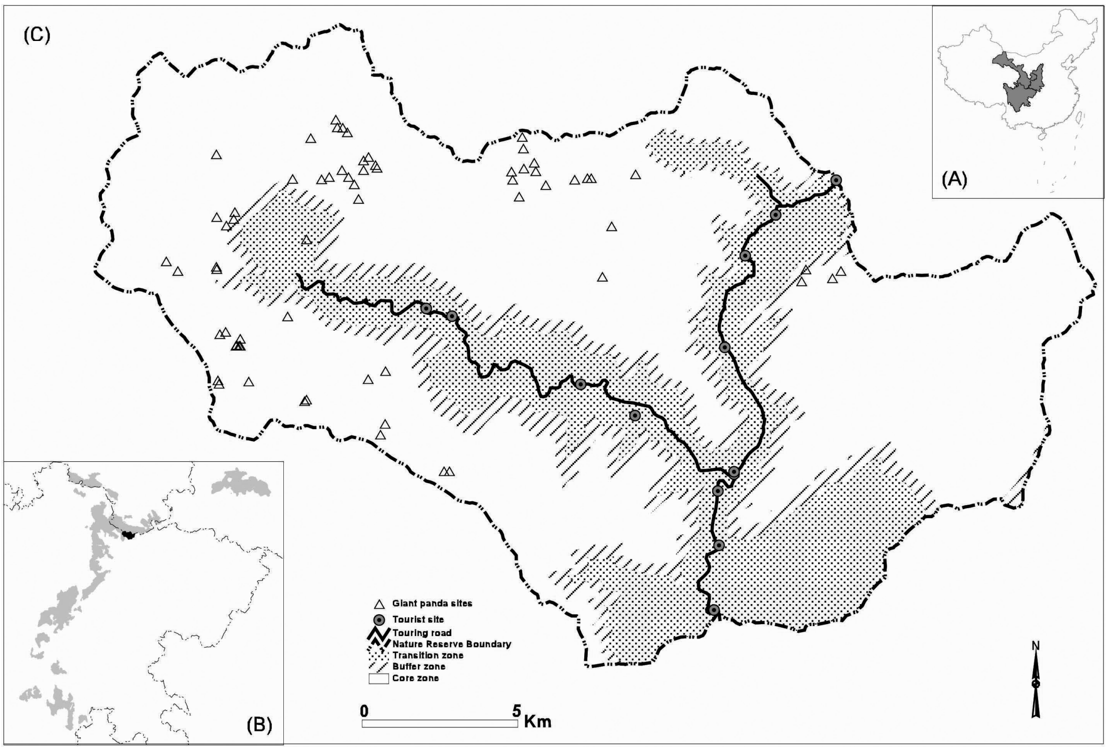

Fig. 1. Giant panda distribution within three provinces (Sichuan, Shaanxi and Gansu) where giant pandas are found currently in China (A), distribution (grey areas) of the 64 giant panda protected areas, with Tajiahe Nature Reserve highlighted in black (B), study area showing zoning (transition, buffer and core zone), the distribution of all touring site records, and tourist route design (C).

Material and Methods

Study area

The Tangjiahe Nature Reserve (E 104°36′-104°53′, N 32°32′-32°41′) encompasses approximately 374 km^2 and is located in the Qingchuan County, Sichuan, China on the north-western edge of the Sichuan Basin, on the southern slope of Motian Ridge and northwest of Longmen Mountain (Ge et al. 2001). This dynamic terrain inclines from northwest to southeast. The Motian Ridge in the north is 3000 m above sea level, while elevation the Dacaoping ridge in the northwest is 3837 m, whereas the intermediate valleys are below 1200 m. Two tourist roads are located in the study area (Fig. 1).

Table 1. Ecogeographical variables in the study.

Variable	Description
Aspect (8 classes)	Northness (0°-22.5°; 337.5°-360°), Northeastness (22.5°-67.5°), Eastness (67.5°-112.5°), Southeastness (112.5°-157.5°), Southness (157.5°-202.5°), Southwestness (202.5°-247.5°), Westness (247.5°-292.5°), and Northwestness (292.5°-337.5°); [1]Distance variables were calculated by "CircAn" of Version 1.2.0.19, and [2]Frequency variables were calculated "DistAn" of Version 1.3.1.19 in the BIOMAPPER
Elevation	Unit: m
Tourist roads	2 routes recorded; distance variables were calculated by "CircAn" of Version 1.2.0.19 in the BIOMAPPER
Slope	From 0° to 90°, seven categories: ≥ 0-≤ 10°, > 10-≤ 20°, > 20-≤ 30°, > 30-≤ 40°, > 40-≤ 50°, > 50-≤ 60°, and > 60-≤ 90°; distance variables were calculated by "CircAn" of Version 1.2.0.19, and frequency variables were calculated "DistAn" of Version 1.3.1.19 in the BIOMAPPER
Touring site	14 sites record, distance variables were calculated by "CircAn" of Version 1.2.0.19 in the BIOMAPPER
Vegetation (5 classes)	Conifer forest, mixture forest, deciduous forest, shrub, and bare land; distance variables were calculated by "CircAn" of Version 1.2.0.19, and frequency variables were calculated "DistAn" of Version 1.3.1.19 in the BIOMAPPER

[1] Distance variables (unit: km) are a measure of the distance between the same location and the closest cell containing a given feature.
[2] Frequency variables describe the proportion of cells containing a given feature within a 1200 m radius of a location where evidence of giant panda habitat use was found.

Species map and environmental variables

For the wild giant panda, presence points (including faeces, hair, tracks, scats and den sites) were obtained from a field survey using transect-line sample methods. A total of 190 transects were surveyed within the study area. Stratified random transect lines, based on the terrain, vegetation, and bamboo status, were adopted to ensure that representative habitat types were surveyed. The transects were > 1500 m in length, and lay throughout the entire range of the nature reserve. To minimize potential bias due to differences existing in giant panda detectability in dense bamboo forests, the transect lines included a two 2 m band on either side of the transect (Qi et al. 2009). Giant panda sightings were recorded systematically in the study area and all surveys were conducted on foot by experienced observers of the Fourth General Survey Project on giant panda in Sichuan. Field surveys were carried out from 19 to 27 March 2013. A GPS point was recorded at the start and end point of each transect, at vegetation transformations, and at points every 1000 m. The transect lines were tracked by GPS and the transect length was computed using Arcview GIS 3.3 (ESRI, California, USA). A total of 125 presence samples were recorded from the transects, and while most of them were located in the different transects, some transects included several presence points. Presence samples were recorded around three areas: Baixiongping, Caijiaba, and Motianling (Figs. 1, 2). All presence points were plotted in the UTM 48N reference system using WGS 1984 datum and used in the analysis.

Habitat variables related to terrain, land cover, and human disturbance (Table 1) were chosen based on known species-habitat associations of the giant panda (Hu 2001). The topographic variables were derived from a Digital Elevation Model (DEM) provided by the Computer Network Information Center, Chinese Academy of Sciences (http://datamirror.csdb.cn). Two types of human disturbances were included: tourism sites and tourist roads. To map vegetation, we used a Landsat 5 scene acquired in May 2009. This dataset was obtained from the Global Land Cover Facility (University of Maryland, College Park, USA). A supervised classification was carried out using a maximum likelihood classification algorithm, five classes were created: conifer forest, mixed forest, deciduous forest, shrub, and bare land/other (Table 1). The accuracy of the land-cover classification was 74 %. Elevation, slope, and aspect were derived from digital elevation models (DEM) with a resolution of 30 m. All analyses were performed in ERDAS IMAGINE 8.7 software (Leica Geosystems GIS and Mapping 2003) and Arc View GIS 3.3 (ESRI, Redlands, USA).

Ecological niche factor analysis

To compute ENFA, two types of qualitative data measures, frequency and distance, were prepared (Hirzel et al. 2002). Distance variables expressed the distance between a cell containing evidence of giant panda habitat use (the focal cell) and the cell containing a given feature. The module "DistAn" in version 1.3.1.19 of BIOMAPPER was used to calculate distances from focal cells to cells that contained the given variable (Hirzel et al. 2007). Under ENFA, high and negative marginality values for distance variable coefficients indicate species preference for those variables (Sattler et al. 2007). Frequency variables describe the proportion of cells containing a given feature within a 1200 m radius of the focal cell. A 1200 m radius equates to an area of 4.65 km^2, which represents the average home range of a giant panda (Schaller et al. 1985). The module CircAn in version 1.2.0.19 of BIOMAPPER was used to calculate the frequency of each variable. Under ENFA, high and positive marginality values for frequency variable coefficients indicate species preference for the variable (Sattler et al. 2007). For the ENFA analyses, 43 landscape variables of suspected importance to giant pandas were first prepared (Table 1). When two or more variables had a correlation coefficient greater than 0.5, only the most proximal was retained (Engler et al. 2004). To check for correlations amongst our data set of 43 variables, a correlation tree in BIOMAPPER was produced, and the one variable from each correlated pair was removed and launched in the ENFA again (Hirzel et al. 2007). These steps were repeated until all the eigenvalues were less than 0.5; 18 variables were retained in the final model (Table 2).

ENFA transforms the original ecogeographical variables into new uncorrelated axes (Hirzel et al. 2006). The first axis (marginality factor) is chosen to describe the marginality of the niche with respect to regional environmental conditions and maximizes the difference between the environmental mean value for where the species is found and the global mean environmental value of the region (Hirzel et al. 2002). The following axes (specialization factors) are sorted according to decreasing levels of explained variance, and are used to represent the degree of specialization compared to (orthogonal) environmental gradients across the study area (Hirzel et al. 2002). Global marginality and specialization coefficients integrate these descriptor-specific scores

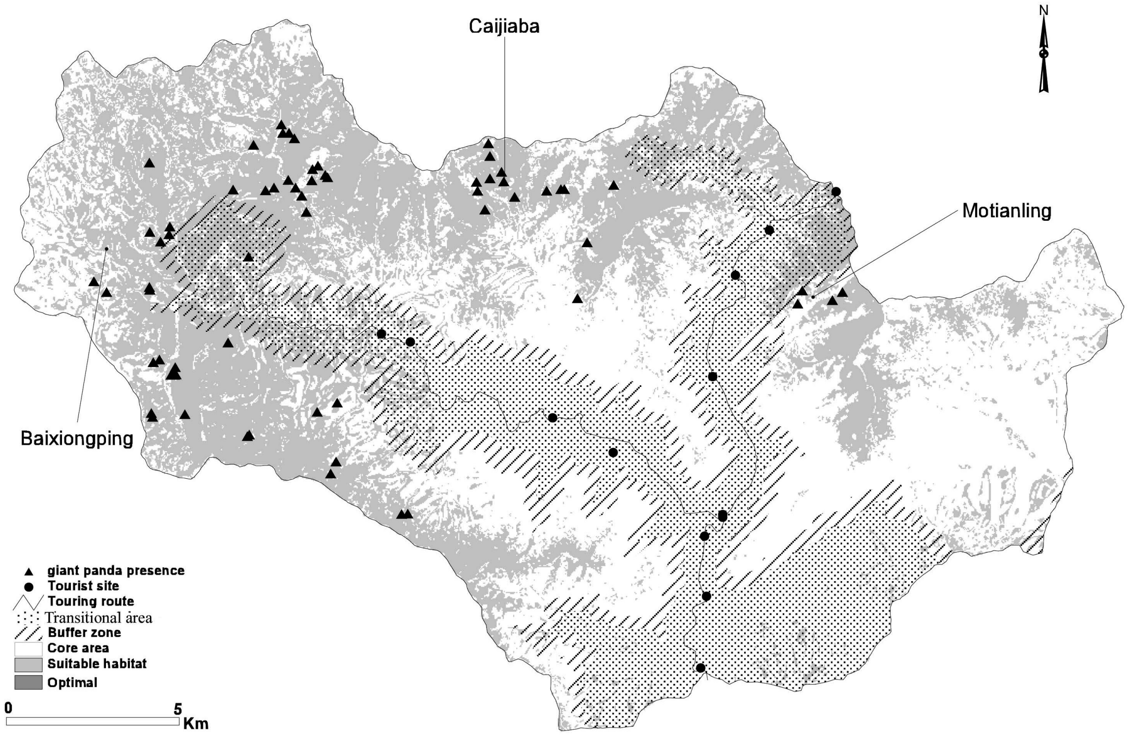

Fig. 2. Habitat suitability distribution and zoning of the Tangjiahe Nature Reserve.

and provide information about a species' niche. Global marginality generally ranges from 0 to 1 and indicates how far the species optimum is from the average condition in the study area, this can also described as its specialization (Engler et al. 2004). A global marginality value ≥ 1 indicates that the species is specialized to a particular habitat relative to the total distribution of habitats available in the reference set. The global tolerance coefficient, defined as the inverse of the specialization, is usually preferred as it ranges from 0 to 1, and indicates niche breadth (Hirzel et al. 2006).

Following Hirzel & Arlettaz (2003), the distance geometric mean algorithm in ENFA was used to predict habitat suitability across the study area. Based on predicted-to-expected frequencies (P/E curve), habitat suitability maps were then divided into four categories: optimal, suitable, marginal, and unsuitable (Hirzel et al. 2006, Sattler et al. 2007). Suitable and optimal habitat shared habitat suitability values for which presence was more frequent than expected by chance (P/E > 1), the boundary being placed so as to maximize the P/E difference between them (Hirzel et al. 2006); habitat suitability values for which presences are less frequent than expected (0 < P/E < 1) were defined as marginal habitat; habitat suitability values with no presence points (PE = 0) were defined as unsuitable habitat (Sattler et al. 2007). To evaluate model accuracy we used the Boyce index (Boyce et al. 2002, Hirzel et al. 2006). The Boyce index provides a continuous assessment of the model's predictive power (Hirzel et al. 2006), varying from –1 to 1 (Boyce et al. 2002). An index value greater than 0.5 indicates a good model, whereas 0 indicates a random model (Hirzel et al. 2006). All ENFA analyses were performed using BIOMAPPER software v4.0 (Hirzel et al. 2007).

Evaluation of nature reserve

To evaluate reserve design and identify potential sites for future monitoring of giant pandas, we overlaid the ENFA distribution model with the existing reserve zoning and the tourist areas proposed by the Tangjiahe Nature Reserve administration.

Results

Giant panda habitat selection characteristics

ENFA computed a global marginality factor of 0.75 and indicated a difference between the ecological requirements of giant pandas and mean environmental

Table 2. Correlations between ENFA factors and ecogeographic variables.

Variables	Factor 1[1] (52 %)	Factor 2[2] (32 %)
Distance to conifer forest	--------	***
Distance to eastness	+	0
Distance to northeastness	--	0
Distance to northness	+	*
Distance to tourist road	+++++	*
Distance to shrub	+++	*
Distance to slope (≥ 0-≤ 10°)	0	******
Distance to slope (> 10-≤ 20°)	-	*
Distance to slope (> 20-≤ 30°)	--	****
Distance to slope (> 30-≤ 40°)	+++	**
Distance to slope (> 40-≤ 50°)	0	***
Distance to southeastness (112.5°-157.5°)	-	**
Distance to southness (157.5°-202.5°)	+++	*
Distance to southwestness	+	*
Frequency of eastness	0	**
Frequency of northwestness	0	**
Frequency of slope (≥ 0-≤ 10°)	0	*
Frequency of slope (> 50-≤ 60°)	--	*

[1] Marginality factor: the symbol + means that the species was found in locations with higher values than average. The symbol - means the reverse. The greater the number of symbols, the higher the correlation; 0 indicates a very weak correlation.

[2] Specialization factor: the symbol * means the species was found occupying a narrower range of values than available. The greater the number of asterisks, the narrower the range; 0 indicates a very low specialization.

Table 3. Nature reserve zoning and proportion of habitat.

Function area	Optimal Suitable		Suitable		Marginal Suitable		Unsuitable	
	Area (km^2)	Ratio to study area (%)	Area (km^2)	Ratio to study area (%)	Area (km^2)	Ratio to study area (%)	Area (km^2)	Ratio to study area (%)
Core zone	13.94	5.68	97.68	39.81	60.97	24.85	72.78	29.66
Buffer zone	0.78	2.02	7.28	18.84	9.45	24.46	21.13	54.68
Transition zone	1.09	1.22	14.36	16.02	22.67	25.30	51.49	57.46
Total	15.81	4.23	119.32	31.94	93.09	24.92	145.4	38.92

conditions. The global tolerance (calculated as 1/ global specialization) was 0.12, indicating a high specialization for giant pandas inhabiting Tangjiahe Nature Reserve. The model performed well as indicated by a high and continuous Boyce index (mean = 0.71, SD ±0.42), but the large variance is a symptom of low robustness.

Distance to conifer forests and distance to 20-30° slopes were the variables with lowest negative marginality coefficients, indicating that giant pandas prefer areas closer to conifer forests and 20-30° gentle slopes (Table 2). The distance to tourist roads, southern slopes, 30-40° slopes, and shrubs were the variables with highest positive marginality coefficients, and indicated that giant pandas avoid areas rich in shrubs, medium slopes, and tourist roads (Table 2). East-facing slopes, the distance to 0-10°, 20-30°, 30-40°, and 40-50° slopes, conifer forest, and shrub have the higher coefficients for the specialization factors, indicating that the distribution of the giant panda is specifically restricted by these variables (Table 2). However, we also found that giant pandas were neutral regarding occurrence of 0-10° degree slope, eastness and northwestness slope aspect across our reserve, and indicated the species exhibited a wide niche with regard to these predictors (Table 2).

Habitat suitability distribution

About 31.94 % was classified as suitable and 4.23 % as optimal habitat: these areas are found across the reserve but are more concentrated in the northwestern region (Fig. 2). However, over 60 % of the Tangjiahe Nature Reserve was classified either as unsuitable (38.92 %) or marginal habitat (24.92 %, Table 3).

The three areas within the reserve where giant pandas are currently found, Motianling, Caijiaba and Baixiongping, are surrounded by large patches of contiguous suitable and optimal habitat (Fig. 2); however Motianling in the east and Caijiaba in the centre-north are almost completely isolated from Baixiongping in the west. Motianling is far from Caijiaba and Baixiongping and is surrounded by large sections of unsuitable landscape containing a tourist road.

Management status

The transition zone was found to cover 24 % of the Tangjiahe Nature Reserve and encompass only one location where giant pandas were found to occur (Fig. 1, Table 3). More than 83 % of the transition zone was classified as unsuitable or marginal habitat (58 % and 25 % respectively); the remaining 17 % was classified as suitable (16 %) or optimal (1 %). The buffer zone covered 10 % of the Tangjiahe Nature Reserve and 46 % of its surface was classified as marginal (25 %), suitable (19 %) or optimal (2 %). No known giant panda locations were found in the buffer zone. The core zone included the vast majority of known giant panda locations and 45 % of this zone was classified as high suitable habitat (suitable and optimal, Table 3).

Discussion

Habitat suitability models are typically produced using species presence or habitat selection data (Falcucci et al. 2009). Different factors may be considered when planning reserve design, and include information about habitat quality, species distributions, and threats (Moilanen 2005). Our results indicate that giant pandas appear to select areas with coniferous forests and those that are far from tourist roads. Giant pandas' dependence on old growth forests has been previously discussed in larger-scale studies and is likely related to giant panda requirements for cover for sheltering and food availability (Wei et al. 2000, Zhang et al. 2011). Areas containing tourist roads, which have very high marginality scores, appear not to be suitable for the species. The continued development of these roads will cause a progressive decline in giant panda habitat availability; the strong negative relationship between habitat suitability for the giant pandas and human disturbance has been previously documented (Xu et al. 2006). While some of these tourism sites are located in the transition zone, they may directly impact giant pandas by disturbing the movement of animals between core areas.

The increased ecotourism leads to increased noise, light, and other disturbances by human visitors (Farrell & Marion 2001). Since the establishment of the Tangjiahe Nature Reserve, all farmers migrated out of the reserve and farming, including the collection of bamboo shoots, has been banned (Wan et al. 2005). These steps help protect the reserve from human disturbances. However, tourism has increased in recent years; there were more than 45000 visitors to the Tangjiahe Nature Reserve in 2013. Unfortunately, the current analyses do not allow us to isolate the effects of the number of visitors on the giant panda movements. It is possible that these factors could have a stronger effect than those measured by our model index, however, as it stands, the effects of the volume or frequency of visitation on giant panda dispersion remaining untested. In addition, since tourist roads and tourist sites had a correlation coefficient greater than 0.5 ($r = 0.86$), only the tourist roads were retained for the ENFA, however, we can conclude that tourist sites may have a similar affect on giant pandas. The two touring routes and 14 tourist sites were found to be located in the transition and buffer zones and none overlapped with known giant panda locations. These tourism sites were found to contain habitat of low suitability, except for a few in the northwest, but they still may inhibit giant panda movement between Motianling and Caijiaba (Fig. 2).

Two of the most important questions to be addressed during the process of wildlife conservation planning are: 1) where does a species currently occur, and 2) where could it potentially occur (Peterson & Dunham 2003). As a result, estimating and mapping high suitability habitat plays a critical role in conservation planning and policy, but if assumptions about habitat suitability are wrong, conservation action will be misguided (Hobbs 2003). In recent years, several new nature reserves have been suggested and established in the known giant panda range (Wei et al. 2012). Unfortunately, the design of these new nature reserves has often overlooked the availability of high suitability habitat on giant panda population exchange (Wang et al. 2010). Based on the results of the ENFA reported here, all areas where giant pandas are concentrated in the highly suitable habitat category encompass less than 36 % of the total area, meaning that 64 % of the reserve is habitat of low suitability for giant pandas. The distribution pattern caused by the resulting patches of suitable and unsuitable habitat may reduce the area's ability to support the survival of a population of giant pandas.

Due in part to computational limitations, most current reserve-design efforts have previously focused on landscape patterns and overlooked ecological processes, such as demographics and genetic connectivity (Carroll et al. 2012). Maintaining this genetic exchange is essential, as molecular evidence has shown that the individuals in the Tangjiahe reserve have formed three distinct clusters with a high level of genetic distance (Wan et al. 2005). The probability of successful dispersal decreases with linkage length, but strategically located high suitability habitat used as stepping-stones can provide temporary refuge and increase dispersal success (Wikramanayake et al. 2004). High suitability habitat around one of these clusters, Motianling, has been almost completely separated by the tourist road and two tourist sites, which may explain this genetic clustering. Caijiaba and Baixiongping have an abundance of high suitability habitat and no barriers to genetic flow. Given that the results of both the molecular work of Wan et al. (2005) and the ENFA presented here indicate that this population may be highly susceptible to inbreeding, we argue that changes to the existing and planned ecotourism construction must be addressed to increase the dispersal potential between the three remaining groups.

In managed landscapes, habitat manipulation for species conservation has to also consider human needs and efficiency (Polasky et al. 2008). Our model revealed three areas of high sensitivity that should become a priority for conservation action. First, an area between Motianling and Caijiaba (see Fig. 2) is experiencing increased tourism; if this trend continues it will completely divide these two areas. Second, the area of Caijiaba where giant pandas are present, although surrounded by high suitability habitat connected with Motianling, should be prioritized for protection because of the genetic clustering already present between these two sites. Third, an area that connects highly suitable habitat in central Baixiongping, with the northern and southern habitats located west of the transition zone, has experienced the most rapid tourism development and is in need of protection. The chief concern is that this area is the main entry point for the over 45000 tourists who visit and spend an average of two days exploring the park annually, so the rate of development is likely to increase.

In summary, our findings should improve the design of this reserve and others where inter-connectivity is urgently needed. We believe that to improve the conservation status and facilitate movement of giant pandas between habitats, Tangjiahe Nature Reserve managers should make explicit the need for the divisional population management of this species. We also urge decision makers throughout the giant panda's range to incorporate the analysis used here into their conservation management planning process to increase the efficacy of their actions, specifically as they relate to reserve design and tourism.

Acknowledgements

This research is supported by the National Natural Science Foundation of China (31101649, 31372223, 31300306), Sichuan Youth Science and Technology Foundation (2012JQ0028), Sichuan Science and Technology Department Program (2012SZ0094), Chengdu Giant Panda Breeding Research Foundation (CPF Research 2012-7, 2013-17, CPF 2014-11), National Basic Research Program of China (2012CB722207), and the fourth survey on giant panda in Sichuan Province, China. Importantly, this work was made possible by the many anonymous people who participated in the fieldwork. We thank the anonymous reviewers for their comments on this manuscript.

Literature

Akcakaya H.R. & Atwood J.L. 1997: A habitat-based metapopulation model of the California gnatcatcher. *Conserv. Biol. 11: 422– 434.*

Araújo M.B. & Williams P.H. 2000: Selecting areas for species persistence using occurrence data. *Biol. Conserv. 96: 331–345.*

Beresford A.E., Buchanan G.M., Donald P.F., Butchart S.H.M., Fishpool L.D.C. & Rondinini C. 2011: Minding the protection gap: estimates of species' range sizes and holes in the protected area network. *Anim. Conserv. 14: 114–116.*

Boyce M.S., Vernier P.R., Nielsen S.E. & Schmiegelow F.K.A. 2002: Evaluating resource selection functions. *Ecol. Model. 157: 281–300.*

Brooker L. 2002: The application of focal species knowledge to landscape design in agricultural lands using the ecological neighbourhood as a template. *Landscape Urban. Plann. 60: 185–210.*

Carroll C., McRae B.H. & Brookes A. 2012: Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. *Conserv. Biol. 26: 78–87.*

Cooke S.J. & O'Connor C.M. 2010: Making conservation physiology relevant to policy makers and conservation practitioners. *Conserv. Lett. 3: 159–166.*

Dettmers R. & Bart J. 1999: A GIS modeling method applied to predicting forest songbird habitat. *Ecol. Appl. 9: 152–163.*

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. App. Ecol. 41: 263–274.*

Falcucci A., Ciucci P., Maiorano L., Gentile L. & Boitani L. 2009: Assessing habitat quality for conservation using an integrated occurrence-mortality model. *J. Appl. Ecol. 46: 600–609.*

Farrell T.A. & Marion J.L. 2001: Identifying and assessing ecotourism visitor impacts at eight protected areas in Costa Rica and Belize. *Environ. Conserv. 28: 215–225.*

Gaston K.L., Charman K., Lackson S.E., Armsworth P.R., Bonn A., Briers R.A., Callaghan C.S.Q., Catchpole R., Hopkins J., Kunin W.E., Latham J., Opdam P., Stoneman R., Stroud D.A. & Tratt R. 2006: The ecological effectiveness of protected areas: the United Kingdom. *Biol. Conserv. 132: 76–87.*

Ge B., Guan T., Powell D., McShea W.J. & Song Y. 2011: Effects of an earthquake on wildlife behavior: a case study of takin (*Budorcas taxicolor*) in Tangjiahe National Nature Reserve, China. *Ecol. Res. 26: 217–223.*

Geneletti D. & van Duren I. 2008: Protected area zoning for conservation and use: a combination of spatial multicriteria and multiobjective evaluation. *Landscape Urban. Plan. 85: 97–110.*

Greve M., Chown S.L., van Rensburg B.J., Dallimer M. & Gaston K.J. 2011: The ecological effectiveness of protected areas: a case study for South African birds. *Anim. Conserv. 14: 295–305.*

Hirzel A.H. & Arlettaz R. 2003: Modelling habitat suitability for complex species distributions by the environmental-distance geometric mean. *Environ. Manage. 32: 614–623.*

Hirzel A.H., Hausser J., Chessel D. & Perrin N. 2002: Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology 83: 2027–2036.*

Hirzel A.H., Hausser J. & Perrin N. 2007: Biomapper 4.0 laboratory of conservation biology. *Department of Ecology and Evolution, University of Lausanne, Lausanne. www.unil.ch/biomapper*

Hirzel A.H., Le Lay G., Helfer V., Randin C. & Guisan A. 2006: Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model. 199: 142–152.*

Hobbs N.T. 2003: Challenges and opportunities in integrating ecological knowledge across scales. *Forest. Ecol. Manage. 181: 223–238.*

Hu J.C. 2001: Research on the giant panda. *Shanghai Science and Technology Education Press, Shanghai. (in Chinese)*

Hu J.C., Zhang Z.J. & Wei F.W. 2011: History, current situation and prospects on nature reserves for giant pandas (*Ailuropoda melanoleuca*) in China. *Acta Theriol. Sin. 31: 10–14.*

Hull V., Xu W., Liu W., Zhou S., Vina A., Zhang J., Tuanmu M., Huang J., Linderman M., Chen X., Huang Y., Ouyang Z., Zhang H. & Liu J. 2011: Evaluating the efficacy of zoning designations for protected area management. *Biol. Conserv. 144: 3028–3037.*

Kolahi M., Sakai T., Moriya K., Makhdoum M.F. & Koyama L. 2013: Assessment of the effectiveness of protected areas management in iran: case study in Khojir national park. *Environ. Manage. 52: 514–530.*

Leica Geosystems GIS and Mapping 2003: ERDAS IMAGINE 8.7. *Atlanta Georgia, U.S.A.*

Lester S.E., Costello C., Rassweiler A., Gaines S.D. & Deacon R. 2013: Encourage sustainability by giving credit for marine protected areas in seafood certification. *PLoS Biol. 11: e1001730.*

Liu J. & Raven P. 2010: China's environmental challenges and implications for the world. *Crit. Rev. Environ. Sci. Technol. 40: 823–851.*
Margules C.R. & Pressey R.L. 2000: Systematic conservation planning. *Nature 405: 243–253.*
Mateo R.G., de la Estrella M., Felicísimo Á.M., Muñoz J. & Guisan A. 2013: A new spin on a compositionalist predictive modelling framework for conservation planning: a tropical case study in Ecuador. *Biol. Conserv. 160: 150–161.*
Ménard N., Foulquier A., Vallet D., Qarro M., Le Gouar P. & Pierre J.-S. 2014: How tourism and pastoralism influence population demographic changes in a threatened large mammal species. *Anim. Conserv. 17: 115–124.*
Moilanen A. 2005: Reserve selection using nonlinear species distribution models. *Am. Nat. 165: 695–706.*
Müllner A., Linsenmair K.E. & Wikelski M. 2004: Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biol. Conserv. 118: 549–558.*
Newsome D., Moore S.A. & Dowling R.K. 2002: Natural area tourism: ecology, impacts, and management. *Channel View Publications, New York.*
Peterson J.T. & Dunham J. 2003: Combining inferences from models of capture efficiency, detectability, and suitable habitat to classify landscapes for conservation of threatened bull trout. *Conserv. Biol. 17: 1070–1077.*
Pressey R.L., Cabeza M., Watts M.E., Cowling R.M. & Wilson K.A. 2007: Conservation planning in a changing world. *Trends Ecol. Evol. 22: 583–592.*
Polasky S., Nelson E., Camm J., Csuti B., Fackler P., Lonsdorf E., Montgomery C., White D., Arthur J., Garber-Yonts B., Haight R., Kagan J., Starfield A. & Tobalske C. 2008: Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biol. Conserv. 141: 1505–1524.*
Qi D., Hu Y., Gu X., Li M. & Wei F. 2009: Ecological niche modeling of the sympatric giant and red pandas on a mountain-range scale. *Biodiv. Conserv. 18: 2127–2172.*
Sattler T., Bontadina F., Hirzel A.H. & Arlettaz R. 2007: Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. *J. Appl. Ecol. 44: 1188–1199.*
Schaller G.B., Hu J.C., Pan W.S. & Zhu J. 1985. The giant pandas of Wolong. *The University of Chicago Press, Chicago.*
Shen G., Feng C., Xie Z., Ouyang Z., Li J. & Pascal M. 2008. Proposed conservation landscape for giant pandas in the Minshan Mountains China. *Conserv. Biol. 22: 1144–1153.*
Sutherland W.J., Pullin A.S., Dolman P.M. & Knight T.M. 2004: The need for evidence-based conservation. *Trends Ecol. Evol. 19: 305–308.*
Terborgh J. & van Schaik C. 2002: Why the world needs parks. In: Terborgh J., van Shaik C., Davenport L. & Rao M. (eds.), Making parks work: strategies for preserving tropical nature. *Island Press, Washington D.C.: 3–14.*
Wan Q.H., Fang S.G., Li J.G., Zhang L.M., Ou W.F., Xian F.H. & Chen W.L. 2005: A family net of giant pandas in the Tangjiahe Natural Reserve: assessment of current individual migration. *Chin. Sci. Bull. 50: 1879–1886.*
Wang T.J., Ye X.P., Skidmore A.K. & Toxopeus A.G. 2010: Characterizing the spatial distribution of giant pandas (*Ailuropoda melanoleuca*) in fragmented forest landscapes. *J. Biogeogr. 37: 865–878.*
Wei F.W., Feng Z.J., Wang Z.W. & Hu J.C. 2000: Habitat use and separation between the giant panda and the red panda. *J. Mammal. 80: 448–455.*
Wei F.W., Hu Y.B., Zhu L.F., Bruford M.W., Zhan X.J. & Zhang L. 2012: Black and white and read all over: the past, present and future of giant panda genetics. *Mol. Ecol. 21: 5660–5674.*
Wikramanayake E., McKnight M., Dinerstein E., Joshi A., Gurung B. & Smith D. 2004: Designing a conservation landscape for tigers in human-dominated environments. *Conserv. Biol. 18: 839–844.*
Xu W.H., Ouyang Z.Y., Viňa A., Zheng H., Liu J.G. & Xiao Y. 2006: Designing a conservation plan for protecting the habitat for giant pandas in the Qionglai mountain range, China. *Divers. Distrib. 12: 610–619.*
Zhang Z.J., Swaisgood R.R., Zhang S.N., Nordstrom L.A., Wang H.J., Gu X.D., Hu J.C. & Wei F.W. 2011: Old-growth forest is what giant pandas really need. *Biol. Lett. 7: 403–406.*
Zhu L.F., Hu Y.B., Qi D.W., Wu H., Zhan X.J., Zhang Z.J., Bruford M.W., Wang J.L., Yang X.Y., Gu X.D., Zhang L., Zhang B.W., Zhang S.N. & Wei F.W. 2013: Genetic consequences of historical anthropogenic and ecological events on giant pandas. *Ecology 94: 2346–2357.*
Zhu L.F., Zhang S.N., Gu X.D. & Wei F.W. 2011: Significant genetic boundaries and spatial dynamics of giant pandas occupying fragmented habitat across southwest China. *Mol. Ecol. 20: 1122–1132.*