

# Different habitat preferences of male and female giant pandas

Dunwu Qi<sup>1,2</sup>, Shanning Zhang<sup>3</sup>, Zejun Zhang<sup>1,4</sup>, Yibo Hu<sup>1</sup>, Xuyu Yang<sup>5</sup>, Hongjia Wang<sup>5</sup> & Fuwen Wei<sup>1</sup>

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

2 Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing, Jiangsu, China

3 China Wildlife Conservation Association, Beijing, China

4 Institute of Rare Animals and Plants, China West Normal University, Nanchong, Sichuan, China

5 Sichuan Forestry Department, Wildlife Conservation Division, Chengdu, Sichuan, China

## Keywords

habitat selection; landscape structure; sexual segregation; species distribution model.

## Correspondence

Fuwen Wei, Key Laboratory for Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 1-5 Beichenxi Road, Beijing 100101, China.  
Tel: +86 10 64807152; Fax: +86 10 64807152

Email: weifw@ioz.ac.cn

Editor: Nigel Bennett

Received 28 December 2010; revised 12 May 2011; accepted 13 May 2011

doi:10.1111/j.1469-7998.2011.00831.x

## Abstract

A feature of many endangered species management plans, is the provision or protection of habitat. However, defining exactly what constitutes habitat can be difficult. This is made more complicated when habitat preferences differ within a species such as between males and females. Using a combination of field surveys and sex identification through fecal DNA, we investigated gender differences in habitat use in wild giant pandas through ecological niche factor analysis modelling. Our results indicated that both males and females tended to prefer areas at high altitudes and with high forest cover. However, significant sexual differences in habitat selection were also observed. Furthermore, habitat preferences of females are more restrictive than those of males, and females have a stronger association with high altitude conifer forest, mixed forest, historically clear-felled forest and  $>10$  to  $\leq 20^\circ$  slopes. The more restricted habitat preferences of females could be explained by their need for dens for birthing and dense bamboo cover for concealing the young. Therefore, effective conservation and management strategies should consider these differences in habitat selection of females and males.

## Introduction

Sex-specific differences in habitat occur in many species, and can have fundamental implications on their conservation (Rubin & Bleich, 2005). Differences in habitat can affect the persistence of populations, especially if habitat features favored by one sex are disproportionately affected by spatial patterns (Safi, König & Kerth, 2007). Despite the time and effort devoted to understanding sexual segregation in animals (Bonenfant *et al.*, 2002; Loe *et al.*, 2006), little is known about gender-based patterns of habitat selection for many endangered species inhabiting complex landscapes.

Sexual segregation is traditionally defined as the differential use of space, habitat and forage by sexes outside the mating season (Bowyer, 2004). Such differences may cause males and females to use different strategies when acquiring and defending resources (Clutton-Brock, Iason & Guinness, 1987; du Toit, 2005). However, most of this work has been carried out on sexually dimorphic ungulates, in which differences in size are central to the mechanisms behind segregation (Senior, Butlin & Altringham, 2005). Sexual segregation is rarely studied in other animal groups (Ben-David, Titus & Beier, 2004) and its implications are often

overlooked when managing wild populations (Gordon, Hester & Festa-Bianchet, 2004).

Giant pandas *Ailuropoda melanoleuca* are confined to highly fragmented montane forests in remote China (Hu, 2001). Basic giant pandas habitat requirements are understood, but potential differences in female and male habitat selection have been largely ignored. This is predominantly because giant pandas are solitary, direct observation is difficult and close contact is required to accurately distinguish the sexes (Reid & Hu, 1991; Wei *et al.*, 2000). From radio-tracking studies in Wolong Nature Reserve, females spend most of their time within a discrete core area of their home range and males occupy overlapping ranges with a poorly-defined core area (Schaller *et al.*, 1985). Thus, it appears that males and females use the landscape differently, but a more thorough analysis is required if we are to guide current management protocols. Using a combination of field surveys and sex identification through fecal DNA analysis, this study aimed to resolve differences in habitat selection between male and female giant pandas. Specifically, we asked which factors explain differences in habitat use, and if different, what does this mean for the distribution

of preferred habitat for wild giant pandas inhabiting the Liangshan Mountains?

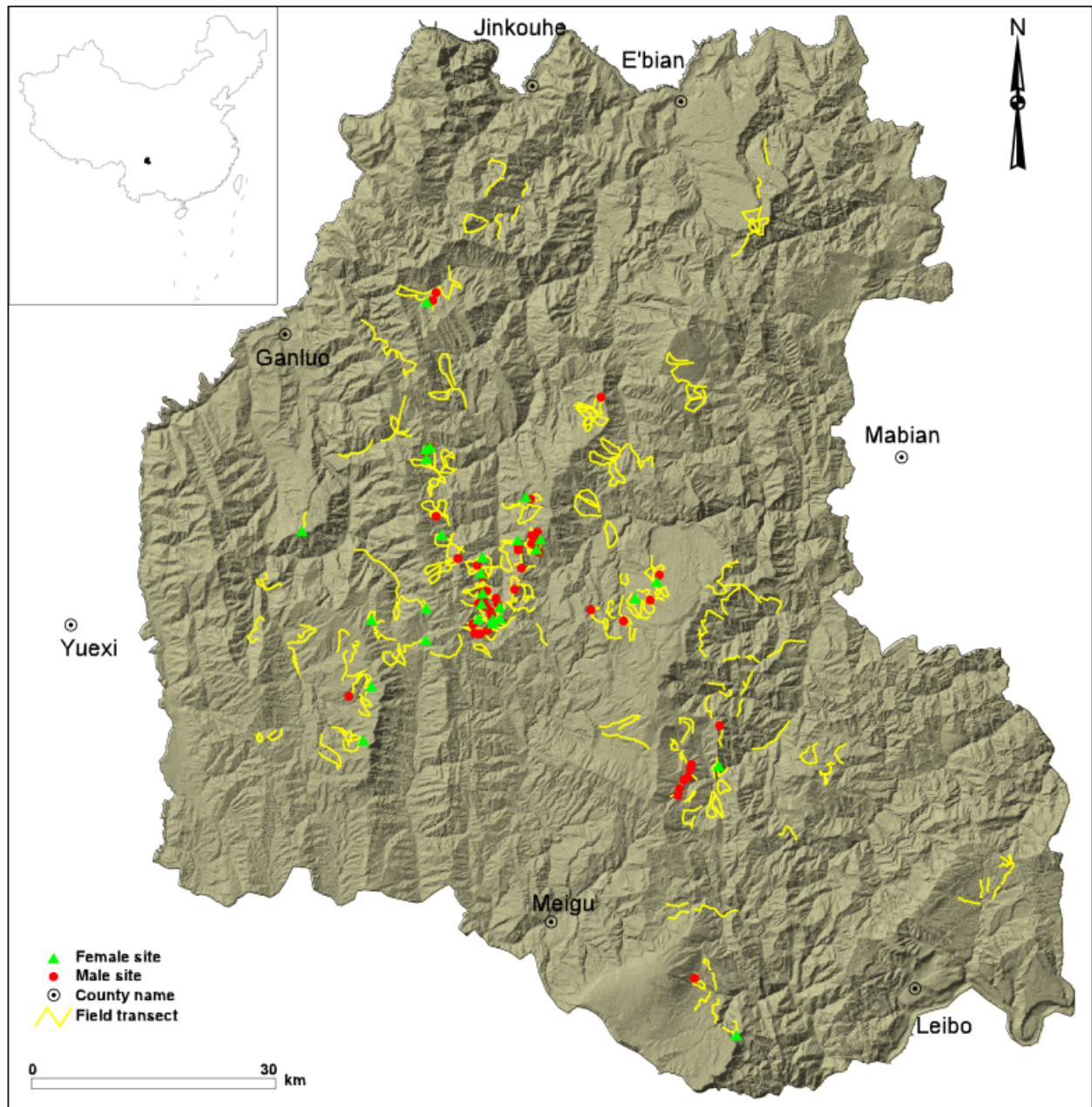
## Material and methods

### Study area and transect surveys for giant pandas

The focus of our research was a 10 067 km<sup>2</sup> area of the Liangshan Mountains located in a transition zone between the Tibetan Plateau and Sichuan Basin (102°35'–103°46'E,

28°14'–29°33'N). Elevation varies from 325 to 4287 m above sea level (Fig. 1). Feces and hair are commonly used as indirect measures of giant pandas habitat use (Wei *et al.*, 2000). We used random sampling combined with randomized line intersect sampling to survey giant pandas feces and hair (Hu *et al.*, 2010) throughout the study area.

Previous research has revealed that giant pandas select high-elevation forests at least 1500 m above sea level (Hu, 2001), and are not distributed evenly [State Forestry Administration (SFA), 2006]. Therefore, we created two strata based upon differences in population density and applied



**Figure 1** Study area in the Liangshan Mountains, Sichuan, China and distribution of sampling plots.

these across the study area. Stratum 1 (S1) represented areas of higher population density ( $>0.1$  individual  $\text{km}^{-2}$ ) and stratum 2 (S2) represented areas of lower population density ( $<0.1$  individual  $\text{km}^{-2}$ ). To improve the likelihood of sampling at least one giant panda home range S1 cells were  $5 \text{ km}^2$  and S2 cells were  $15 \text{ km}^2$  (i.e.  $3 \times 5 \text{ km}$ , where  $3 \text{ km}$  is around the average diameter of a home range and  $5 \text{ km}$  is around the average length of our transects). We used ArcGIS 9.0 to create these strata.

We surveyed 204 transect lines and a total length of  $950 \text{ km}$ . The average ( $\pm \text{SD}$ ) length of transects was  $4.64 \text{ km}$  ( $\pm 2.24$ ); 107 transects were measured within S1 (average density of  $0.2$  transects  $\text{km}^{-2}$  or 1 transect  $5 \text{ km}^{-2}$ ), and 97 within S2 (average density of  $0.07$  transects  $\text{km}^{-2}$  or 1 transect/ $15 \text{ km}^2$ ). A stratified random transect line based on terrain (valley, mid-slope and ridge) was adopted in field surveys to ensure that representative habitat types were surveyed. The transects laid across all these terrain types, and began  $1500 \text{ m}$  above sea level and near a valley or abandoned logging roads (Qi *et al.*, 2009). To minimize bias due to difference in giant pandas detectability in dense bamboo forests the transect line included  $2 \text{ m}$  either side. Giant panda sightings were recorded systematically in the same stratum and all surveys were implemented on foot by experienced observers. We carried out field surveys in September 2005, March–September 2006 and April 2007, which covered  $90.5\%$  of giant pandas habitat across the study area. We recorded a GPS point at the start and end point of each transect and points every  $300 \text{ m}$  along the transect. The transect lines were tracked by GPS and the transect length was computed using Arcview GIS 3.3 (ESRI, Redlands, CA, USA).

### Determining the gender of samples

Molecular sexing was performed using fecal samples. Total DNA was extracted from feces following Zhang *et al.* (2006). Blank controls were performed in both extractions and downstream amplifications. We screened each sample using giant pandas specific mitochondrial DNA primers (Zhang *et al.*, 2002) to ensure extracts were from our target species. A Y-linked sexing marker (ZX1,  $210 \text{ bp}$ ) in combination with an X/Y-linked amplification control (ZFX/ZFY,  $130 \text{ bp}$ ) was used to determine the sex of each sample (Zhan *et al.*, 2006). Sex identification was conducted three times for each DNA extraction. A sample was identified as male if at least two PCRs showed the positive SRY band and female if no bands were produced. Positive and negative controls were simultaneously conducted to ensure non-contamination.

### Mapping survey data

We defined a cell ( $30 \times 30 \text{ m}$ ; WGS84 UTM) as being used by a giant panda if indirect evidence (feces and hair) was found within it. Not all cells were used in the analysis as their clumped distribution would have led to problems of autocorrelation. The minimum distance between two

sampling sites was defined before sampling, according to an exploratory spatial autocorrelation study (Guisan & Zimmermann, 2000). We visually inspected each cell containing sampling point of giant pandas and then randomly chose one from each cluster using the Random Point Generator v.1.3 in ArcView GIS 3.3 (ESRI). This randomly selected point then served as the center of a circle with a radius of  $1200 \text{ m}$ , which corresponds to the radius of the average size of a giant panda's home range (Schaller *et al.*, 1985). To avoid recording the same individual more than once, we ignored point within this radius.

### Mapping habitat variables

We chose habitat variables related to terrain, land cover and human disturbance (Table 1) based on known species–habitat associations (Hu, 2001). A total of 18 topographic variables were derived from a digital elevation model provided by the Computer Network Information Centre, Chinese Academy of Sciences (<http://datamirror.csdb.cn>). To map vegetation, we used Landsat 5 scenes acquired in April 2002 and May 2006 by the Global Land Cover Facility (University of Maryland, College Park, MD, USA). Using the maximum likelihood classification algorithm in supervised classification, seven classes of vegetation cover and two classes of non-vegetation cover were created by ERDAS 8.7 (Leica Geosystems GIS and Mapping, 2003, LLC, Atlanta, GA, USA). Because logging and land clearing were once widely practiced in the region, areas affected by these historical practices were classified as either clear-cut sparse forest (SF), or fragmented forest (FF) if still intact after selective logging. Overall,  $63.0\%$  of the study area was covered by woodland ( $8.8\%$  conifer forest,  $25.4\%$  mixed coniferous and deciduous broadleaf forest,  $12.4\%$  fragmented forest and  $16.4\%$  sparse forest),  $16.7\%$  by shrubs,  $11.2\%$  by meadows,  $8.7\%$  by agricultural land,  $0.4\%$  by open areas and rocky outcrops and  $0.009\%$  by rivers. The accuracy of the land-cover classification was  $>75\%$ . All variables were converted to raster maps in ArcGIS with a  $30 \text{ m}$  pixel resolution.

Conifer forests (CF) were dominated by four conifer species: *Abies georgei*, *Abies forrestii*, *Abies fabri* and *Picea likingensis*. Mixed coniferous with deciduous broadleaf forests (MF) comprised by *Tsuga dumosa*, *Tsuga chinensis*, *Picea bruchytyla*, *Castanopsis delavayi*, *Cyclobalanopsis glaucooides*, *Lithocarpus variolosus* and *Lithocarpus cleistocarpus*. Shrub lands (SL) were dominated by *Rhododendron kuanii*, *Corylus yunnanensis*, *Rubus ichangensis* and *Lindera limprichtii*. Meadows (ME) were characterized by *Clinelymus nutans*, *Roegneria nutans* and *Festuca ovina*.

### Ecological niche factor analysis (ENFA)

ENFA calculates niche marginality and specialization using presence-only data to account for differences in ecological importance between variables (Hirzel *et al.*, 2002). Marginality refers to the degree to which the species mean differs from the global mean across the study area. Specialization measures niche narrowness relative to global variance

**Table 1** Ecogeographical variables (EGV) included in our ecological niche factor analysis (ENFA)

EGV name	Description	Discard criteria and action taken
AL-fq	Frequency of arable land (AL) within a 1200 m radius of focal cell	Correlated with distance to shrub lands ( $r=0.522$ ), discarded
Altitude	Average height in meters above sea level of focal cell	Used in analysis
CF-fq	Frequency of conifer forest (CF) within a 1200 m radius of focal cell	Used in analysis
Dis-1st road (km)	Average distance from focal cell to roads connecting counties (1st class roads), which roads had been blacktopped and more vehicles than 2nd and 3rd class roads	Used in analysis
Dis-2nd road (km)	Average distance from focal cell to roads connecting towns and villages (2nd class roads), which roads were unpaved, and fewer vehicles than 1st roads	Used in analysis
Dis-3rd road (km)	Average distance from focal cell to unpaved or abandoned logging roads (3rd class roads), which roads were unpaved, have not been used by vehicles and few human used it by foot.	Used in analysis
Dis-AL (km)	Average distance from focal cell to arable lands	Correlated with frequency of conifer forest ( $r=0.529$ ), discarded
Dis-CF (km)	Average distance from focal cell to conifer forests	Correlated with distance to fragmented forests ( $r=0.505$ ), discarded
Dis-east (km)	Average distance from focal cell to east-facing slopes ( $45\text{--}135^\circ$ )	Correlated with frequency of south-facing slopes ( $135\text{--}225^\circ$ ) ( $r=0.721$ ), discarded
Dis-FF (km)	Average distance from focal cell to patches of fragmented forest affected by historical selective-logging (FF)	Used in analysis
Dis-ME (km)	Average distance from focal cell to meadows (ME)	Correlated with distance to conifer forests ( $r=0.589$ ), discarded
Dis-MF (km)	Average distance from focal cell to mixed coniferous and deciduous broadleaf forests (MF)	Used in analysis
Dis-north (km)	Average distance from focal cell to north-facing slopes ( $315\text{--}45^\circ$ )	Correlated with distance to south-facing slopes ( $135\text{--}225^\circ$ ) ( $r=-0.512$ ), discarded
Dis-SF (km)	Average distance from focal cell to historically clear-felled sparse forests (SF)	Used in analysis
Dis-SL (km)	Average distance from focal cell to shrub lands (SL)	Correlated with distance to towns ( $r=0.575$ ), discarded
Dis-slope10 (km)	Average distance from focal cell to $\geq 0$ to $\leq 10^\circ$ slope	Used in analysis
Dis-slope20 (km)	Average distance from focal cell to $> 10$ to $\leq 20^\circ$ slope	Correlated with distance to $\geq 0$ to $\leq 10^\circ$ slope ( $r=0.637$ ), discarded
Dis-slope30 (km)	Average distance from focal cell to $> 20$ to $\leq 30^\circ$ slope	Used in analysis
Dis-slope40 (km)	Average distance from focal cell to $> 30$ to $\leq 40^\circ$ slope	Correlated with distance to $> 30$ to $\leq 40^\circ$ slope ( $r=0.637$ ), discarded
Dis-slope50 (km)	Average distance from focal cell to $> 40$ to $\leq 50^\circ$ slope	Correlated with distance to $> 10$ to $\leq 20^\circ$ slope ( $r=0.586$ ), discarded
Dis-slope60 (km)	Average distance from focal cell to $> 50$ to $\leq 60^\circ$ slope	Correlated with distance to $> 10$ to $\leq 20^\circ$ slope ( $r=0.656$ ), discarded
Dis-slope61-90 (km)	Average distance from focal cell to $> 60$ to $\leq 90^\circ$ slope	Correlated with frequency of $> 20$ to $\leq 30^\circ$ slope ( $r=0.534$ ), discarded
Dis-south (km)	Average distance from focal cell to south-facing slopes ( $135\text{--}225^\circ$ )	Used in analysis
Dis-town (km)	Average distance from focal cell to towns. A town is larger and has more facilities than a village, often including 3–10 villages. Towns are defined administratively by the local authorities.	Correlated with distance to shrub lands ( $r=0.575$ ), discarded
Dis-village (km)	Average distance from focal cell to villages. A village is the fundamental organizational unit for China's rural population and comprises <500 people.	Used in analysis
Dis-west (km)	Average distance from focal cell to west-facing slopes ( $225\text{--}315^\circ$ )	Correlated with frequency of east-facing slopes ( $45\text{--}135^\circ$ ) ( $r=0.506$ ), discarded
East-fq	Frequency of east-facing slopes ( $45\text{--}135^\circ$ ) within a 1200m radius of focal cell	Used in analysis
Easting	Sine of slope, average easting within a 1200 m radius of focal cell	Used in analysis
FF-fq	Frequency of fragmentary forest within a 1200 m radius of focal cell	Used in analysis
ME-fq	Frequency of meadow within a 1200 m radius of focal cell	Correlated with altitude ( $r=0.608$ ), discarded

**Table 1** Continued.

EGV name	Description	Discard criteria and action taken
MF-fq	Frequency of mixed coniferous and deciduous broadleaf forest in a 1200 m radius of focal cell	Used in analysis
North-fq	Frequency of north-facing slopes (315–45°) within a 1200 m radius of focal cell	Correlated with frequency of south-facing slopes (135–225°) ( $r = -0.642$ ), discarded
Northing	Cosine of slope, average northing within a 1200 m radius of focal cell	Used in analysis
SF-fq	Frequency of sparse forest within a 1200 m radius of focal cell	Used in analysis
SL-fq	Frequency of shrub land within a 1200 m radius of focal cell	Correlated with distance to conifer forests ( $r = 0.668$ ), discarded
Slope10-fq	Frequency of $\geq 0$ to $\leq 10^\circ$ slope within a 1200 m radius of focal cell	Correlated with frequency of $> 10$ to $\leq 20^\circ$ slope ( $r = 0.568$ ), discarded
Slope20-fq	Frequency of $> 10$ to $\leq 20^\circ$ slope within a 1200 m radius of focal cell	Used in analysis
Slope30-fq	Frequency of $> 20$ to $\leq 30^\circ$ slope within a 1200 m radius of focal cell	Used in analysis
Slope40-fq	Frequency of $> 30$ to $\leq 40^\circ$ slope within a 1200 m radius of focal cell	Correlated with frequency of $> 10$ to $\leq 20^\circ$ slope ( $r = -0.854$ ), discarded
Slope50-fq	Frequency of $> 40$ to $\leq 50^\circ$ slope within a 1200 m radius of focal cell	Correlated with frequency of $\geq 0$ to $\leq 10^\circ$ slope ( $r = -0.564$ ), discarded
Slope60-fq	Frequency of $> 50$ to $\leq 60^\circ$ slope within a 1200 m radius of focal cell	Correlated with frequency of $> 20$ to $\leq 30^\circ$ slope ( $r = -0.636$ ), discarded
Slope61-90-fq	Frequency of $> 60$ to $\leq 90^\circ$ slope within a 1200 m radius of focal cell	Correlated with frequency of $> 20$ to $\leq 30^\circ$ slope ( $r = -0.556$ ), discarded
Slope-mean	Mean angle of slopes within a 1200 m radius of focal cell	Correlated with frequency of $\geq 0$ to $\leq 10^\circ$ slope ( $r = -0.788$ ), discarded
South-fq	Frequency of south-facing slopes (135–225°) within a 1200 m radius of focal cell	Correlated with frequency of north-facing slopes (315–45°) ( $r = -0.642$ ), discarded
West-fq	Frequency of west-facing slopes (225–315°) within a 1200 m radius of focal cell	Correlated with frequency of east-facing slopes (45–135°) ( $r = -0.750$ ), discarded

Frequency variables describe the proportion of cells containing a given feature within a 1200 m radius of a location where evidence of giant pandas habitat use was found; distance variables are a measure of the distance between the same location and the closest cell containing a given feature.

(Hirzel *et al.*, 2002) and high absolute values of specialization indicate a more restricted range for the species and a given variable (Engler, Guisan & Rechsteiner, 2004). Global marginality and specialization coefficients integrate these descriptor-specific scores and provide overall information about a species' niche. Global marginality is a measure of how much the average environmental conditions selected by the species are different from the average environmental conditions inside the study area (the higher the marginality, the more extreme the conditions with regard to the area studied). Theoretically, the global marginality ranges from 0 to 1. However, Hirzel, Hauser & Perrin (2007) suggested the main biasing effect is the study area. One species can have a high marginality, if the study area has a large extent, but will show almost no marginality if the study area fit closely to its spatial distribution. The global marginality value of  $\geq 1$  means that the species occupies a particular habitat relative to the distribution of all habitats across the area studied (e.g. Hirzel *et al.*, 2002; Costantini *et al.*, 2009). The global tolerance coefficient defined as the inverse of the specialization, ranges from 0 to 1, and indicates niche breadth of species, with low values indicating a specialist species and high values indicating a tolerant species (Hirzel *et al.*, 2004).

ENFA in BIOMAPPER v4.0 (Hirzel *et al.*, 2007) were used for giant pandas habitat suitability modelling. We prepared all habitat variables maps for ENFA using a Box-Cox transformation to normalize the distribution of values in each map (Sokal & Rohlf, 1994) and then developed a series of quantitative raster maps describing habitat variables. For qualitative data, we transformed two types of measures: frequency and distance. Distance variables expressed the distance between a cell containing evidence of giant pandas habitat use (the focal cell) and the nearest cell containing a given feature and were calculated using DistAn v1.3.1.19 in BIOMAPPER. Under ENFA, high and negative marginality values for distance variable coefficients indicate species preference for those variables. Frequency variables describe the proportion of cells containing a given feature within a 1200 m radius of the focal cell. CircAn v1.2.0.19 in BIOMAPPER was used to calculate these frequency variables. Under ENFA, high and positive marginality values for frequency variable coefficients indicate species preference for the variable. Within our estimates of giant pandas home ranges, 46 landscape variables of suspected importance to giant pandas were first prepared (Table 1). According to Engler *et al.* (2004), when two or more variables have a correlation coefficient  $> 0.5$  only the most proximal should

be retained. To check for correlations among our dataset of 46 variables, we produced a correlation tree in BIOMAPPER and removed one variable from each correlated pair and launched ENFA again. We repeated this step until all the eigenvalues were  $<0.5$ ; 21 variables were retained in the final model (Table 2).

### Comparing the habitat preferences of males and females

Discriminant analysis was used to compare the habitat preferences of males and females. This model is a standard factor analysis and computes the factor that maximizes the inter-specific variance between distributions while minimizing the intra-specific variance (Hirzel *et al.*, 2007). Using the spatial distributions simultaneously, the discriminant factor is the direction along which the two species differ the most, that is, it is correlated with the variables on which they are distributed most differently (Sattler *et al.*, 2007). The value of the coefficient of the discriminant factor indicates a difference in habitat selection across ecogeographic vari-

ables (Sattler *et al.*, 2007). These discriminant analysis computations are integrated in BIOMAPPER (Hirzel *et al.*, 2007). In addition, as we cannot confirm that every variable in our research was normally distributed, both one-way ANOVA and the Mann–Whitney *U*-test were used to compare the means for each variable between the sexes. ANOVA could be applied under the condition that the distribution of the corresponding variable is normal; the Mann–Whitney *U*-test is nonparametric and applies for variables of non-normal or ambiguous distribution (Lu, 2002). In all statistical tests, significance was set at  $P < 0.05$ .

### Mapping suitable habitat for males and females

Habitat suitability maps are calculated by the median algorithm based on several factors obtained by the ENFA (Hirzel *et al.*, 2002). These factors were results from a comparison of variables' eigenvalues based on a MacArthur's broken-stick distribution, and the eigenvalues is a count of all cells from the species distribution that lay at

**Table 2** Coefficients of each ecogeographical variable (EGV) in the final ecological niche factor analysis (ENFA) model, and the discriminant coefficient for habitat characteristics of females and males

EGV	Female		Male		Mean of females (se)	Mean of males (se)	Coefficient value <sup>d</sup>	P <sup>e</sup>
	Marginality factor <sup>a</sup> (50%) <sup>b</sup>	Specialization factor <sup>c</sup> (24%) <sup>b</sup>	Marginality factor <sup>a</sup> (28%) <sup>b</sup>	Specialization factor <sup>c</sup> (26%) <sup>b</sup>				
Altitude	0.48	-0.35	0.41	-0.08	2.963(0.057)	2.862(0.031)	-0.157	0.02*
CF-fq	0.51	-0.24	0.56	0.02	0.26 (0.05)	0.27(0.03)	-0.487	NS
Dis-1st road	-0.07	-0.01	-0.19	-0.04	8.221(1.151)	6.494(0.735)	-0.332	0.023**
Dis-2nd road	0.01	0.39	-0.03	-0.39	8.902(0.528)	8.249(0.736)	0.156	NS
Dis-3rd road	-0.32	-0.08	-0.22	-0.31	3.694(0.530)	5.023(0.727)	0.282	0.018**
Dis-FF	-0.08	-0.2	-0.09	-0.01	0.479(0.088)	0.448(0.081)	-0.257	<0.000**
Dis-ME	-0.12	0.3	-0.11	0.42	1.099(0.213)	1.116(0.103)	-0.032	NS
Dis-north	-0.08	0.04	-0.01	-0.05	0.090(0.017)	0.108(0.021)	-0.123	NS
Dis-slope10	-0.19	-0.16	-0.18	-0.03	0.076(0.014)	0.074(0.011)	0.091	NS
Dis-slope30	-0.11	-0.4	-0.12	0.12	0.036(0.009)	0.031(0.004)	0.100	NS
Dis-slope61-90	0.22	0.05	0.12	-0.01	2.854(0.281)	2.789(0.195)	-0.049	NS
Dis-south	-0.07	-0.03	-0.16	-0.13	0.098(0.018)	0.070(0.011)	0.034	0.010*
Dis-village	0.2	-0.01	0.22	0.18	4.847(0.360)	4.981(0.255)	-0.012	NS
East-fq	0.08	0.16	0.18	-0.12	0.29 (0.03)	0.32(0.03)	0.223	NS
Easting	-0.07	-0.01	-0.01	-0.06	-0.03(0.01)	0.02(0.01)	0.008	NS
FF-fq	-0.14	-0.39	-0.12	0.67	0.07 (0.02)	0.08(0.01)	-0.119	NS
MF-fq	0.18	0	0.18	-0.02	0.35 (0.04)	0.35(0.02)	-0.382	NS
Northing	-0.04	0.14	0	-0.02	-0.04(0.01)	0.05(0.01)	-0.019	NS
SF-fq	0.26	0.01	0.25	0.06	0.24 (0.03)	0.24(0.02)	-0.293	NS
Slope20-fq	0.09	0.44	-0.05	0.13	0.24 (0.03)	0.19(0.02)	-0.352	0.009**
Slope30-fq	0.31	0.05	0.37	0.06	0.34 (0.02)	0.36(0.01)	-0.007	NS

<sup>a</sup>Positive values of marginality mean that giant pandas prefer locations with higher values of the corresponding variable than the mean location in Liangshan Mountains, whereas a negative value indicates that giant pandas prefer areas with lower values of the variable than generally found in the study area;

<sup>b</sup>The amount of marginality or specialization accounted by each factor for is given in parentheses;

<sup>c</sup>Signs of coefficient have no meaning on the specialization factor;

<sup>d</sup>The positive values indicate variables that the female favours, whereas the negative values indicate that the male has a closer association. The higher the absolute value of a coefficient, the better its corresponding EGV separates the gender niche;

<sup>e</sup>P, one way ANOVA (\*) and Mann–Whitney *U*-test (\*\*), and NS, not significant.

least as far apart from the median as the focal cell (Sattler *et al.*, 2007). The number of factors to keep was defined by the broken-stick method (Jackson, 1993). Overall habitat suitability for each cell is calculated by combining the score of each factor (Hirzel & Arlettaz, 2003). Habitat suitability varies from 0 to 100 and indicates how the environmental combination of a single cell suits the requirements of the focal species (Hirzel *et al.*, 2002).

Using the means of 10-fold cross-validation, we tested the accuracy of our habitat suitability model (Fielding & Bell, 1997). The quality of the habitat suitability was modeled by The Boyce index (*B*; Boyce *et al.*, 2002) whose value > 0.5 indicated good models (Hirzel *et al.*, 2006).

## Results

Our transect design meant that we surveyed 90.5% of giant pandas habitat across the Liangshan Mountains. We are confident that we have sampled the majority of giant pandas living in this area (Fig. 1). We located 401 fecal and 30 hair samples but could not identify the sex of all samples due to low quantities and/or quality of DNA. Molecular sexing revealed that 36 samples from 34 transects were male and 80 samples from 26 transects were female.

The ENFA habitat model for females was built using a three-factor map explaining 100% of the marginality and 86% of the specialization. ENFA computed a global marginality coefficient of 1.164 and global tolerance of 0.169 for females, showing that females habitat differed drastically from the mean condition in the Liangshan Mountains and that they are quite restrictive in the range of conditions they tolerate. The scores for our ecogeographical variables (EGV) (Table 2) indicate a strong preference for high-altitude forest. The frequency of slopes > 10 to  $\leq 20^\circ$  was found to influence niche specialization the most. The model performed well as indicated by a high and continuous Boyce index ( $0.66 \pm 0.423$ , mean  $\pm$  SD), but the large variance is a symptom of low robustness.

The ENFA model for males was built with a four-factor map explaining 100% of the marginality and 80% of the specialization. The global marginality coefficient remained almost identical (1.195 vs. 1.164), indicating that male

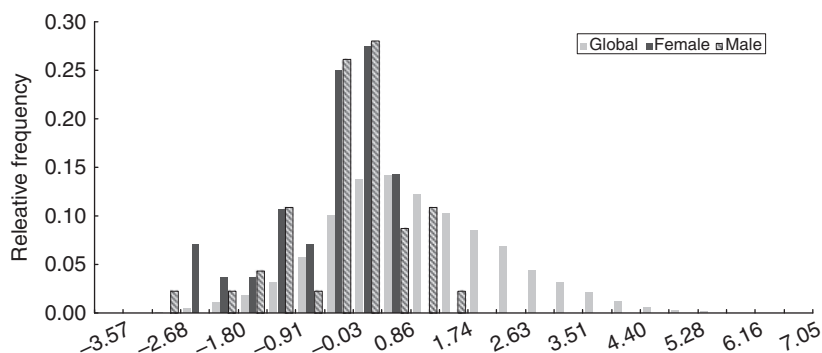
habitat follows a similar pattern of females that differed from average environmental conditions inside the study area. However, the global tolerance coefficient was larger (0.246 vs. 0.169), indicating that niche breadth was wider for males. The overall fit of the model was good as indicated by a continuous Boyce index of  $0.75 \pm 0.37$  (mean  $\pm$  SD).

The discriminant analysis across all EGV revealed sex-based differentiation (Table 2). Females were found to have a stronger association with habitat containing conifer forest, mixed forest, sparse forest, slopes > 10 to  $\leq 20^\circ$ , first class roads and fragmented forest. Males had a closer association with habitat containing east-facing slopes and of a given distance from village roads, slopes  $\geq 0$  to  $\leq 10^\circ$ , > 20 to  $\leq 30^\circ$  and south-facing slopes. The distribution range of species observations along the discriminant axis indicated that the habitat preferences of females are narrower than those of males (Fig. 2). We found that males and females are associated with habitat of different altitude, containing a different proportion of historically clear-cut forest and of different proximity to slopes with a southern aspect, fragmented forest patches, first and third class roads ( $P < 0.05$ , Table 2).

Although habitat selection analysis revealed significant differences between male and female giant pandas for some variables, we found no difference in 15 of the 21 variables included in the final models. Both males and females tended to prefer areas with conifer forest. Further, both sexes were found to occur near gentle slopes  $\geq 0$  to  $\leq 10^\circ$ , and far from areas with a high frequency of > 60 to  $90^\circ$  slopes and east-facing slopes ( $45\text{--}135^\circ$ ). Last, both sexes were found to avoid areas with villages.

## Discussion

Giant pandas are solitary animals and because they feed exclusively on nutrient-poor bamboo the availability of forage impacts their activity (Schaller *et al.*, 1985). Our data show that giant pandas tended to prefer areas at high altitudes and with high forest cover. The association between giant pandas and habitat within a narrow altitudinal range is not surprising as they do not visit higher peaks lacking bamboo and avoid lower areas dominated by



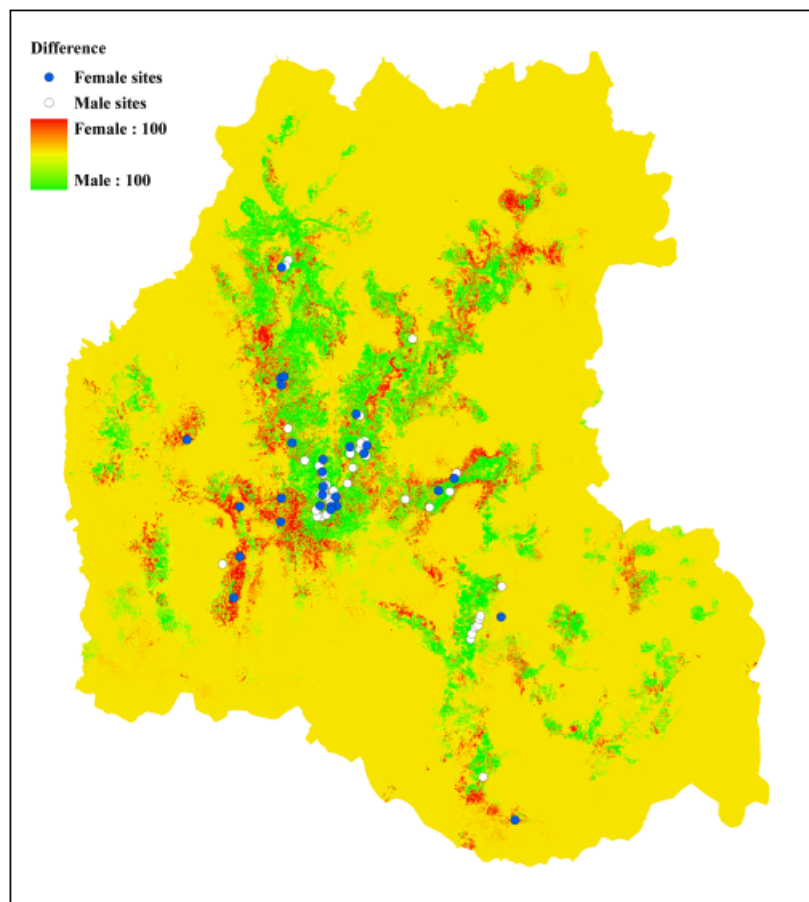
**Figure 2** Habitat characteristics for female (black) and male (diagonal) giant pandas in relation to the global distribution of all cells across the study area (gray) along the discriminant factor.

people. This preference becomes even clearer when the Liangshan distribution map of giant pandas and a geographical map are compared: giant pandas are concentrated in high altitude conifer forest and avoid valleys dominated by people. This pattern was especially strong for females (Fig. 3). Habitat type and structure affect the distribution of bamboo (Ouyang *et al.*, 2001) and we posit that basic forage requirements explain the overlap in habitat selection for both males and females but that other factors are responsible for the differences found this study.

Our models confirm sexual differences in habitat selection in giant pandas. Differences in the ecology and reproduction of males and females can cause them to use habitats differently (Thirgood, 1995). Hu *et al.* (1985) suggested that asymmetry in breeding costs between male and female giant pandas may result in different patterns of habitat use. We found that habitat favoured by females was of a narrower range than that for males and that females have a stronger association with high altitude conifer forest, mixed forest, historically clear-felled forest and  $>10$  to  $\leq 20^\circ$  slopes. This more restricted niche can be explained by the female need for den sites for birthing and dense bamboo cover to

conceal young (Zhang *et al.*, 2004). Female giant pandas are particular in selecting dens and dens are most likely found in large trees more than 200 years old among conifer forests. However, few old trees survived in the logging area and den sites may now be a limiting factor for females (Zhang *et al.*, 2007).

Roads can cause the fragmentation of habitat (Nicholson & Van Manen, 2009), whereas, the actual ecological impact of the fragmentation depends on road characteristics (Jaarsma & Willems, 2002). An interesting result from our modelling is that roads may not negatively impact giant pandas to the extent previously thought. Our results suggest that giant pandas habitat selection may be positively correlated with roads across the study area as females use habitat in close proximity to abandoned logging trails and males use habitat close to first class roads with more vehicles. The association between females and abandoned logging trails may be an artefact of the number of roads of this type that crisscross the region (Hu, 2001). Abandoned logging trails may still pose a negative effect on giant pandas even if they are used by giant pandas as a conduit across the landscape. The limited movement of females may mean they are able to



**Figure 3** Map illustrating difference of habitat suitability between females and males and presence points (blue circles: female sites, and white circles: male sites) used in the ecological niche factor analysis (ENFA). Deeper red and green represent more difference between genders, whereas yellow indicates less difference.



exist close to a road without having to interact with it. In contrast, males were found to use habitat closer to vehicles roads that, while posing a risk, reflects their wider home ranges and need to traverse the home ranges of several surrounding females. In the Qinling Mountains, Pan *et al.* (2001) found that males crossed roads within their home range when migrating to lower elevations in spring.

Assessing the predictive power of a model is of paramount importance for the practical conservation management (Hirzel *et al.*, 2006). Our use of ENFA was based on a large amount of giant pandas spatial information collected through non-invasive sampling across the Liangshan Mountains. Previous attempts to characterize giant pandas habitat selection have relied on small numbers of radio-collared animals (Hu *et al.*, 1985; Pan *et al.*, 2001), whereas we were able to utilize data from more than 50 individuals of known gender. Despite the high predictive power of our models, the conclusions we can draw are limited by two factors. First, our 'sightings' or samples comprised different sources (tracks, feeding, resting and den sites), and we treated these as equal in the model. Future analyses should partition each type of sample to provide finer scale differences in habitat use as it is known the longer giant pandas spend in an area, the more feces they deposit (Reid & Hu, 1991). Second, we did not consider seasonal differences in habitat use, a potentially important factor for this species as animals undergo an annual elevational migration.

### Conservation implications

Forest exploitation, fragmentation and degradation have caused a decline in wild giant pandas and their habitat (Hu, 2001). Our results confirm that conifer forest is an important ecological requirement for giant pandas (Zhang *et al.*, 2011). However, little research into sex-specific habitat use in giant pandas has been conducted, despite being one of the most endangered species in the world. Our results suggest that the habitat preferences of females are narrower than males and we posit that females have likely been disproportionately affected by anthropogenic habitat exploitation and habitat loss. Giant pandas are often managed under broad habitat preference criteria. However, our findings suggest that conservation and management strategies should consider the differences in habitat selection of females and males. Specially, for reintroduction plan of giant pandas, sex-specific niche requirements should be given more attention to improve panda's adaptation to novel environment and increase reintroduction success rate.

### Acknowledgments

This research was supported by the National Nature Science Foundation (30830020), Key Program of Knowledge Innovation Program of Chinese Academy of Sciences (KSCX2-EW-Z-4) and the China Postdoctoral Science Foundation (200904501111). Thanks are given to Zongming Cao, Kui Fang, Guji Yang, Tianjian Gong, Zhuo Wang, Zhihong Li,

Yongbin Liao, Weimin Yang and Bin Wang from the Sichuan Forestry Bureau and many other volunteers for assistance during this study. We would like to thank anonymous referees for constructive comments on the earlier drafts of this paper.

### References

- Ben-David, M., Titus, K. & Beier, L.R. (2004). Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* **138**, 465–474.
- Bonenfant, C., Gaillard, J.M., Klein, F. & Loison, A. (2002). Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography* **25**, 446–458.
- Bowyer, R.T. (2004). Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *J. Mammal.* **85**, 1039–1052.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002). Evaluating resource selection functions. *Ecol. Model.* **157**, 281–300.
- Clutton-Brock, T.H., Iason, G.R. & Guinness, F.E. (1987). Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). *J. Zool. (Lond.)* **211**, 275–289.
- Costantini, C., Ayala, D., Guelbeogo, W.M., Pombi, M., Some, C.Y., Bassole, I.H., Ose, K., Fotsing, J.-M., Sagnon, N., Fontenille, D., Besansky, N.J. & Simard, F. (2009). Living at the edge: biogeographic patterns of habitat segregation conform to speciation by niche expansion in *Anopheles gambiae*. *BMC Ecol.* **9**, 16.
- du Toit, J.T. (2005). Sex differences in the foraging ecology of large mammalian herbivores. In *Sexual segregation in vertebrates: ecology of the two sexes*: 35–52. Ruckstuhl, K.E. & Neuhaus, P. (Eds.) Cambridge: Cambridge University Press.
- 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.
- Fielding, A.H. & Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**, 38–49.
- Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004). The management of wild large herbivores to meet economic, conservation, and environmental objectives. *J. Appl. Ecol.* **41**, 1021–1031.
- Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–186.
- Hirzel, A., Hausser, J. & Perrin, N. (2007). *Biomapper 4.0*. Lausanne: Laboratory of Conservation Biology, Department of Ecology and Evolution, University of Lausanne. Available at <http://www.unil.ch/biomapper>.

- Hirzel, A.H. & Arlettaz, R. (2003). Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environ. Mgmt.* **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., 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.
- Hirzel, A.H., Posse, B., Oggier, P.A., Crettenand, Y., Glenz, C. & Arlettaz, R. (2004). Ecological requirements of reintroduced species and the implications for release policy: the case of bearded vulture. *J. Appl. Ecol.* **41**, 1103–1116.
- Hu, J.C. (2001). *Research on the giant panda*. Shanghai: Shanghai Science and Technology Education Press [in Chinese].
- Hu, J.C., Schaller, G.B., Pan, W.S. & Zhu, J. (1985). *The giant pandas of Wolong*. Chengdu: Sichuan Publishing House of Science and Technology Press [in Chinese].
- Hu, Y.B., Zhan, X.J., Qi, D.W. & Wei, F.W. (2010). Spatial genetic structure and dispersal of giant pandas on a mountain-range scale. *Conserv. Genet.* **11**, 2145–2155.
- Jaarsma, C.F. & Willems, G.P.A. (2002). Reducing habitat fragmentation by minor rural roads through traffic calming. *Landsc. Urban Plan.* **58**, 125–135.
- Jackson, D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* **74**, 2204–2214.
- Loe, L.E., Irvine, R.J., Bonenfant, C., Stien, A., Langvatn, R., Albon, S.D., Mysterud, A. & Stenseth, N.C. (2006). Testing five hypotheses of sexual segregation in an arctic ungulate. *J. Anim. Ecol.* **75**, 485–496.
- Lu, W.D. (2002). *SPSS for windows*. Beijing: Publishing House of Electronics Industry [in Chinese].
- Nicholson, J.M. & Van Manen, F.T. (2009). Using occupancy models to determine mammalian responses to landscape changes. *Integr. Zool.* **4**, 232–239.
- Ouyang, Z.Y., Liu, J.G., Xiao, H., Tan, Y.C. & Zhang, H.M. (2001). An assessment of giant panda habitat in Wolong Nature Reserve. *Acta Ecol. Sin.* **21**, 1869–1874. [In Chinese].
- Pan, W.S., Lü, Z., Zhu, X.J., Wang, D.J., Wang, H., Long, Y., Fu, D.L. & Zhou, X. (2001). *A chance for lasting survival*. Beijing: Peking University Press. [in Chinese].
- Qi, D.W., Hu, Y.B., Gu, X.D., Li, M. & Wei, F.W. (2009). Ecological niche modeling of the sympatric giant and red pandas on a mountain-range scale. *Biodivers. Conserv.* **18**, 2127–2141.
- Reid, D.G. & Hu, J.C. (1991). Giant panda selection between *Bashania fangiana* bamboo habitats in Wolong Reserve, Sichuan, China. *J. Appl. Ecol.* **28**, 228–243.
- Rubin, E.S. & Bleich, V.C. (2005). Sexual segregation: a necessary consideration in wildlife conservation. In *Sexual segregation in vertebrates: ecology of the two sexes*: 379–391. Ruckstuhl, K.E. & Neuhaus, P. (Eds.) Cambridge: Cambridge University Press.
- Safi, K., König, B. & Kerth, G. (2007). Sex differences in population genetics, home range size and habitat use of the parti-colored bat (*Vespertilio murinus*, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biol. Conserv.* **137**, 28–36.
- 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*. Chicago: The University of Chicago Press.
- Senior, P., Butlin, R.K. & Altringham, J.D. (2005). Sex and segregation in temperate bats. *Proc. Roy. Soc. Lond. Ser. B* **272**, 2467–2473.
- Sokal, R.R. & Rohlf, F.J. (1994). *Biometry: the principles and practice of statistics in biological research*. London: W. H. Freeman and Co.
- State Forestry Administration (SFA). (2006). *The third national survey report on giant panda in China*. Beijing: Science Press.
- Thirgood, S.J. (1995). The effects of sex, season and habitat availability on patterns of habitat use by fallow deer (*Dama dama*). *J. Zool. (Lond.)* **235**, 645–659.
- 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.
- Zhan, X.J., Li, M., Zhang, Z.J., Goossens, B., Chen, Y.P., Wang, H.J., Bruford, W.M. & Wei, F.W. (2006). Molecular censusing doubles giant panda population estimate in a key nature reserve. *Curr. Biol.* **16**, 451–452.
- Zhang, B.W., Li, M., Ma, L.C. & Wei, F.W. (2006). A widely applicable protocol for DNA isolation from fecal samples. *Biochem. Genet.* **44**, 503–512.
- Zhang, Y.P., Wang, X.X., Ryder, O.A., Li, H.P., Zhang, H.M., Yong, Y.G. & Wang, P.Y. (2002). Genetic diversity and conservation of endangered animal species. *Pure Appl. Chem.* **74**, 575–584.
- Zhang, Z.J., Swaisgood, R.R., Wu, H., Li, M., Yong, Y.G., Hu, J.C. & Wei, F.W. (2007). Factors predicting den use by maternal giant pandas. *J. Wildl. Mgmt.* **71**, 2694–2698.
- 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.
- Zhang, Z.J., Wei, F.W., Li, M., Zhang, B.W., Liu, X.H. & Hu, J.C. (2004). Microhabitat separation during winter among sympatric giant pandas, red pandas, and tufted deer: the effects of diet, body size, and energy metabolism. *Can. J. Zool.* **82**, 1451–1458.