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Habitat Relations

Measures of Giant Panda Habitat Selection Across Multiple Spatial Scales for Species Conservation

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ABSTRACT Examining ecological processes across spatial scales is crucial as animals select and use resources at different scales. We carried out field surveys in September 2005, March–September 2006, and April 2007, and used ecological niche factor analysis to determine habitat preferences for the giant panda (*Ailuropoda melanoleuca*) across 4 spatial scales: daily movement, core range, home range, and seasonal elevational migration. We found that giant pandas prefer conifer forest and mixed forest at higher than average elevation (2,157 m) of study area in the 4 scale models. However, we also observed significant scale differences in habitat selection. The strength of habitat preference increased with scale for the 2 disturbed forests (sparse forest and fragmented forest), and decreased with scale for 0–30° gentle slope and south- and north-facing aspect. Furthermore, habitat suitability patterns were scale-dependent. These findings highlight the need to determine species–environment associations across multiple scales for habitat management and species conservation. © 2012 The Wildlife Society.

KEY WORDS ecological niche factor analysis (ENFA), giant panda, habitat selection, hierarchy, scale, spatial heterogeneity.

Examining ecological processes across numerous spatial scales is widely recognized (Wiens 1989, Forman 1995, Wu and Hobbs 2002) as animals select and use resources at different scales (Kotliar and Wiens 1990, Bergin 1992, Schmidt 1993, Ward and Saltz 1994, Boyce et al. 2003). Habitat selection is now considered an inherently scale-sensitive process, and researchers realize the need to investigate multiple scales (Kie et al. 2002, Wilson et al. 2011). However, in some cases, scales employed in habitat studies were chosen arbitrarily and lacked biological relevance (Wheatley and Johnson 2009). The influence of spatial scales on the selection of habitat components is expected because limiting factors vary with scale (Mayor et al. 2009). The need for a sensible and biologically relevant spatial scale cannot be overstated (Addicott et al. 1987, Wiens 1989, Kie et al. 2002), as failing to select the correct scale in spatial analyses can lead to misinterpretations of data (Wiens 1989, Powell 1994, Bowyer et al. 1996).

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One of the cornerstones of animal conservation is to understand the relationship between animals and their habitat (Nams et al. 2006). Multi-scaled investigations of habitat use are essential because different selection processes may operate at different scales (Luck 2002, Mitchell et al. 2001). Selectivity at multiple scales has been observed in bears (Mcloughlin et al. 2002, Nielsen et al. 2004), but these studies did not explicitly test whether habitat preferences vary at different biological scales. Habitat selection is a hierarchical process that may yield various patterns depending on scales of investigation (Rettie and Messier 2000). However, generalizations about the effect that scales will have on habitat selection are few, because enormous variations in landscapes and patterns of processes influence resource selection (Boyce 2006). Landscape heterogeneity measured at large spatial scales appears to be necessary for characterizing habitat selection (Kie et al. 2002).

Wildlife absences, especially in the case of endangered and rare species, may originate from chance, sampling error, poor sampling effort, and stochastic demographic processes rather than environmental incompatibilities (Hirzel et al. 2002), and do not necessarily reflect habitat unsuitability in landscape scales (Jaquiéry et al. 2008, Nicholson and Van Manen 2009). Therefore, habitat selection analyses based on only presence data are needed to avoid problems associated with false absences (Hirzel et al. 2002). Ecological Niche Factor Analysis (ENFA) uses only species presence data and computes habitat suitability functions by comparing a species' distribution in ecogeographic space with that of entire study area (Hirzel et al. 2002). This approach is based on Hutchinson's (1957) ecological niche theory and predicts the potential distribution of a species using presence-only data and habitat suitability maps (Hirzel et al. 2002). This tool is valuable for managing animals that are rare and patchy, such as the giant panda (*Ailuropoda melanoleuca*).

The giant panda is an elusive and highly endangered animal inhabiting montane forest across southeastern China (Schaller et al. 1985). For this species, the establishment of a home range and decisions regarding movement within or beyond an established home range may be influenced by a range of environmental factors at different biological scales. The majority of research on the giant panda has not considered multiple scale effects, and has been conducted at a small spatial scale (i.e., the sampling unit <400 m^2; Wei et al. 1997, 2000; Zhang et al. 2004), or across a single nature reserve range (e.g., Ouyang et al. 2001, Liu et al. 2002, Linderman et al. 2006). Conclusions from these studies are valid only within the scale at which they were conducted as many habitat characteristics are scale dependent.

Although home range characteristics such as maximum size are informative, measures of spatial use within home ranges and across scales are more valuable for effective management (Gaillard et al. 2010). Comprehensive investigations of these relationships must incorporate environmental variables at multiple spatial scales since species' responses to the environment vary with scale (Grand and Cushman 2003). For habitat selection and use in giant pandas, we derived 4 scales of high relevance: 1) core area of home range—giant pandas frequently visit as little as 10% of their home range (Schaller et al. 1985); 2) daily movement—daily movement patterns are dependent on slope and are energetically limited because of pandas' unusual bamboo diet; 3) home range—a scale at the basis of many studies of habitat use; and 4) seasonal elevational migration—giant pandas undertake a seasonal elevational migration. Specifically, we aim to determine what factors influence habitat selection of the giant panda and at what scales giant pandas respond to environmental heterogeneity. We also assess which categories of habitat selection or scale are more relevant to giant panda management and conservation.

STUDY AREA

Our study area covered 10,067 km^2 across the Liangshan Mountains (LSM) located between the Tibetan Plateau and Sichuan Basin (102°35′–103°46′E, 28°14′–29°33′N). Altitude in the area ranged from 325 m to 4,287 m above sea level (Fig. 1). Here, giant pandas were found in seven counties, but mainly in Mabian, Meigu, and Ebian. The landscape was characterized by mountain slopes of conifer and deciduous woodland, and occasional open areas of grassland and shrubbery. Valley floors throughout the region were intensively cultivated or urbanized and human activities occurred in 113 small towns and 249 villages. A diversity of bamboos lived in the LSM. Although pandas foraged on 17 species of bamboo, they showed a preference for *Yushania brevipaniculata*, *Y. ailuropodina*, *Qiongzhuea macrophylla*, and *Y. tineloata*. Pandas mainly fed on the leaves of *Qiongzhuea* spp. during winter, whereas in spring, they foraged on both *Qiongzhuea* and *Yushania* spp. shoots. The pandas fed on the stem of these two bamboos in summer and on shoots and new leaves of *Chimonobambu*s spp. in the fall.

METHODS

Surveying Giant Pandas

The presence of giant pandas was determined by indirect evidence (including feces, hair, tracks, and den sites) along transect lines during field surveys. Giant panda feces are easily distinguished from that of other sympatric species such as the red panda (*Ailurus fulgens*). Fresh feces (<15 days) have a white mucosal outer-layer, strong bamboo odor, and are green in color. Old fecal samples are identifiable because of sun bleaching, a pale brown or black outer-layer and dry interior. During field surveys, we recorded a Global Positioning System (GPS) point if indirect evidence was found along the transect line. We did not use all presences in the analysis, as their clumped distribution would have led to problems of autocorrelation. We defined the minimum distance between 2 sampling points prior to sampling, according to an exploratory spatial autocorrelation study (Guisan and Zimmermann 2000). To avoid recording the same individual more than once, we randomly chose 1 from these sample points using the Random Point Generator v.1.3 in ArcView GIS 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA). This randomly selected point then served as the center of a circle with a radius of 300 m, which corresponded to a core area of giant panda (Schaller et al. 1985); we excluded other points within this radius from analysis. A previous study indicated that an area with a greater density of sign points is thought to be an area with higher habitat quality (Liu et al. 2005).

We surveyed 204 transect lines and 950 km, covering 90.5% of giant panda habitat across the study area. The average (±SD) length of transects was 4.64 km (±2.24). We recorded GPS coordinates at the start and end points of each transect and at points every 300 m along the transect. The transect lines were tracked by GPS as we walked along them and then we computed transect length using ArcView GIS 3.3. We surveyed transects over 3 sampling periods: 11 transects in September 2005, 167 transects in March–September 2006, and 26 transects in April 2007.

Habitat Mapping

We chose habitat variables related to terrain and land cover, and those variables that indicate habitat suitability for giant pandas (Xu et al. 2006). Furthermore, since human activities may cause habitat degradation, we also considered factors related to human activities for modeling habitat suitability (Liu et al. 1999). We derived 18 topographic variables from a

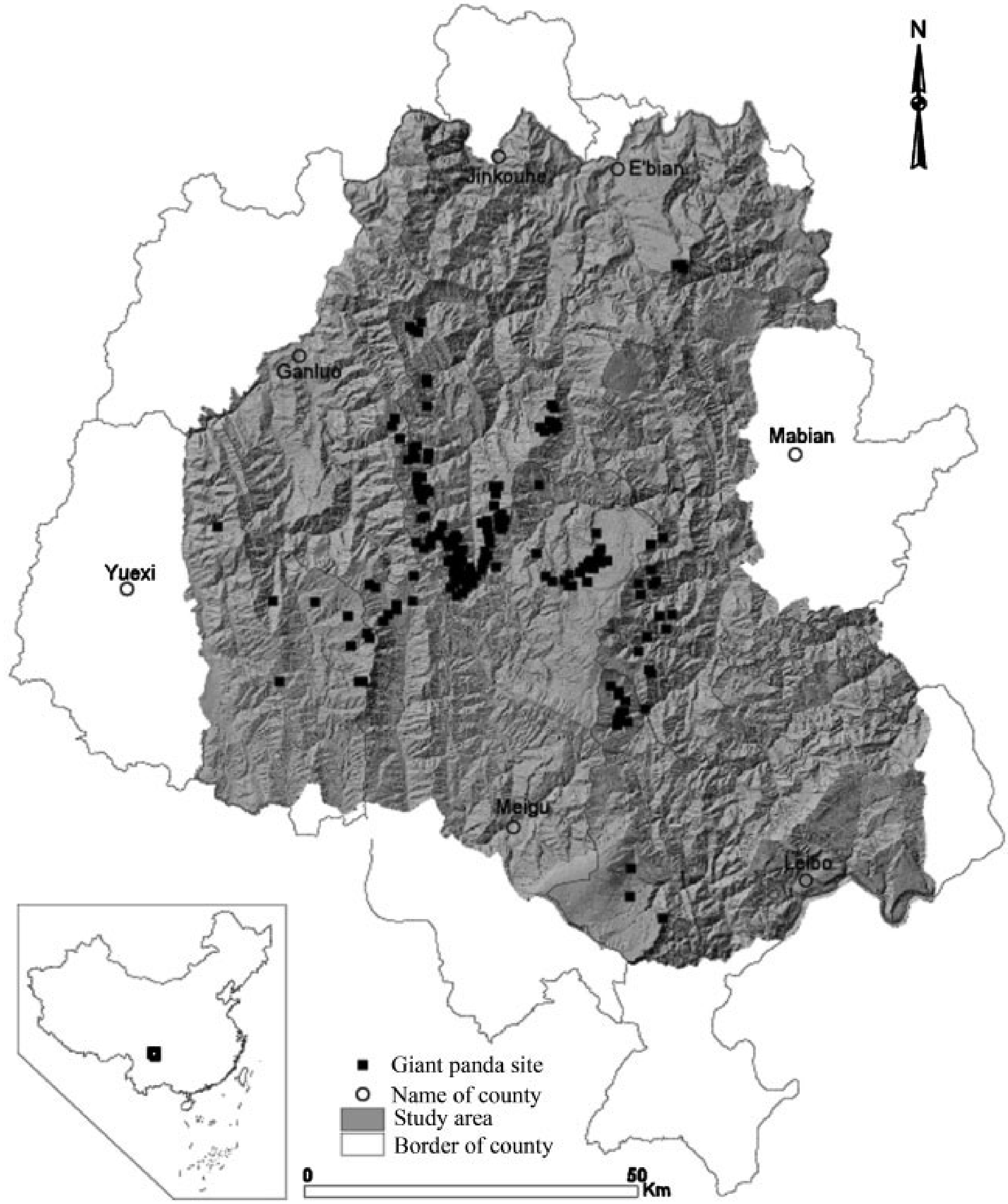

Figure 1. Giant panda study area within the Liangshan Mountains, Sichuan province, China, 2005–2007.

digital elevation model (DEM) provided by the Computer Network Information Center, Chinese Academy of Sciences (http://datamirror.csdb.cn, accessed 28 Aug 2007).

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). We divided giant panda habitat (e.g., conifer forest) into small patches because logging and land clearing were once widely practiced in the region. For example, forest cover across the LSM decreased from 11,600 km^2 in the 1950s to 2,490 km^2 in the 1980s (Hu 2001). We classified areas affected by these historical practices as either clear-cut sparse forest or fragmented forest. Clear-cut sparse forests were characterized by areas where almost all trees were logged and where small trees have been retained and bamboo forest is dense. Fragmented forests are un-logged patches next to clear-cut sparse forests.

Using the maximum likelihood classification algorithm in supervised classification, 7 vegetation classes and 2 classes of nonvegetation cover were created by ERDAS 8.7 software (Leica Geosystems Trade Co., Ltd., Beijing, China). 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% clear-cut sparse forest). In conifer forest, 4 conifer species (*Abies georgei*, *A. forrestii*, *A. fabri,* and *Picea likiangensis*) were the most common. The mixed forest was comprised of 3 main conifers (*Tsuga dumosa*, *T. chinensis*, and *P. brachytyla*) and 4 common broad-leafed trees (*Castanopsis delavayi, Cyclobalanopsis glaucoides, Lithocarpus variolosus*, and

L. cleistocarpus). Shrub lands were dominated by *Rhododendron kuanii*, *Corylus yunnanensis*, *Rubus ichangensis,* and *Lindera limprichtii*, and covered 16.7% of the total area. Meadows were characterized by cover from *Clinelymus nutans*, *Roegneria nutans,* and *Festuca ovina* and accounted for 11.2% the total area. Remaining areas were characterized as agricultural land (8.7%), open areas and rocky outcrops (0.4%), and rivers (0.009%).

Scale Hierarchy

We defined available resource units across our 4 spatial scales using the following methods. For the core area scale, we extended a 28.26-ha circular plot with a buffer radius of 300 m around each presence point, as 300 m corresponds to the radius of average core area for giant pandas (Hu et al. 1985). We calculated the daily movement scale using an 87.57-ha circular plot around each presence point corresponding to an area with a radius of 500 m (Schaller et al. 1985). For the home range scale, we computed the frequency of occurrence of the habitat characteristic within a circular area of radius 1,200 m representing the average home range of giant pandas (Schaller et al. 1985). For the seasonal elevational migration scale, we mapped the occurrence of environmental features within a 3,600-m circular area, as this distance represents the average distance between winter habitat and summer habitat (Pan et al. 2001).

Spatial Analysis

We used ENFA implemented in the ecogeographical package Biomapper 4.0 (Hirzel et al. 2002) to calculate niche marginality and specialization using presence-only data to account for differences in ecological importance between variables. Prior to running the ENFA, we normalized the ecogeographical variable maps using a Box-Cox transformation. We transformed the maps into raster layers using the Av2Idris extension in ArcView GIS 3.3. The raster maps describing habitat variables were quantitative, and 2 types were included: frequency and distance. We calculated frequency variables with the module CircAn of Biomapper (Hirzel et al. 2002) and distance variables with the module Distance of IDRISI 32 (Clark Labs, Worcester, MA). We measured frequency variables as the number of a certain ecogeographical properties (e.g., north facing slopes) within 1,200 m of the focal point. Variables with larger coefficients indicated more preference in the study area and those with coefficients of 0 (or near to 0) indicated a very weak effect of the variable. We calculated distance variables as the distance from the nearest given ecogeographic property (e.g., nearest north facing slope) to the focal point. Larger values for this variable indicated more avoidance by pandas in the study area.

We prepared 46 ecogeographical variables using the raster version of ENFA, but we did not use all of variables in the final ENFA models. When 2 variables had a correlation coefficient >0.5, we retained only the most proximal (Engler et al. 2004, Hirzel et al. 2007). To check for correlations among our data set of 46 variables, we produced a correlation tree in Biomapper, removed 1 variable from each correlated pair, and launched ENFA again. We repeated this step until all eigenvalues were <0.5. As a result, 21 variables (Table 1) remained in the final ENFA model across the core range, home range, daily movement, and seasonal elevational migration scales.

Under the ENFA, 2 key parameters: marginality and specialization are measured (Hirzel et al. 2002, Engler et al. 2004). Marginality refers to the degree to which giant panda selection (or preference) differs from the average of the variables across the LSM range. Positive values mean that we found the giant panda in locations with greater marginality values, and negative values mean the reverse. Specialization measures niche narrowness relative to global variance (Hirzel et al. 2002) and greater absolute values indicated that pandas were more restricted to a range of the given variable. The $\pm$signs are meaningless and 0 indicates a very low specialization.

To provide overall information about the giant panda's niche, 1 marginality factor and several specialization factors are integrated into global marginality and global specialization coefficients (Hirzel et al. 2004). Global marginality ranges from 0 to 1 and indicates how far giant panda selection is from average conditions across the LSM. A global marginality value of ≥ 1 means that pandas occupy a particular habitat relative to the distribution of all habitats across the study area. The global tolerance coefficient, defined as the inverse of the specialization, ranges from 0 to 1, and indicates niche breadth of giant pandas, with small values indicating a specialist species and large values indicating a tolerant species.

We calculated habitat suitability maps with the median algorithm based on several factors obtained by the ENFA (Hirzel et al. 2002). These factors resulted from a comparison of variables' eigenvalues based on a MacArthur's broken-stick distribution, and the eigenvalues were a count of all locations from the species distribution that were at least as far apart from the median of the study area (Sattler et al. 2007). We defined the number of factors to retain with the broken-stick method (Jackson 1993). Habitat suitability varies from 0 to 100 and indicates how the environmental combination of a single point 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 and Bell 1997). We computed 3 presence-only evaluation measures, that is, the Absolute Validation Index (AVI), the Contrast Validation Index (CVI; Sattler et al. 2007) and the continuous Boyce's Index (B; Hirzel et al. 2006). The AVI indicates how well the model discriminates high-suitability from low-suitability areas and ranges from 0 to 1, whereas the CVI indicates how much the AVI differs from what would have been obtained with a random model and varies from 0 to AVI. The Boyce index provides an assessment of model predictive power and varies from -1 to 1, with 0 indicating a random model (Hirzel et al. 2006). For all these measures (AVI, CVI, and B), larger mean values indicate a greater consistency with evaluation datasets, and lower standard deviations indicate more robust predictions. Using the predicted/expected (P/E) curve (Hirzel et al. 2006), we defined

Table 1. Correlation between factors of Ecological Niche Factor Analysis and ecogeographical variables across 4 models for giant pandas in the Liangshan Mountains, Sichuan province, China, 2005–2007.

	Core range		Daily movement		Home range		Elevational migration	
Ecogeographic variable	Marginality factor[a] (19%)[b]	Specialization factor[c] (20%)	Marginality factor (21%)	Specialization factor (21%)	Marginality factor (26%)	Specialization factor (23%)	Marginality factor (25%)	Specialization factor (23%)
Average height above sea level	0.51	0.13	0.50	0.13	0.45	0.20	0.43	0.01
Frequency of conifer forest	0.63	0.00	0.64	−0.02	0.68	−0.07	0.65	−0.11
Distance to first class roads (connecting counties)	−0.08	−0.17	−0.08	−0.15	−0.07	−0.15	−0.07	−0.14
Distance to second class roads (connecting counties and towns)	0.00	0.39	0.00	0.30	0.00	0.24	0.00	0.45
Distance to third class roads (connecting towns and villages, and abandoned logging roads)	−0.27	0.44	−0.26	0.41	−0.24	0.35	−0.22	0.20
Distance to fragmented forests	−0.12	0.06	−0.12	0.05	−0.11	0.01	−0.10	0.01
Distance to meadows	−0.15	−0.74	−0.14	−0.78	−0.13	−0.74	−0.12	−0.64
Distance to north-facing slope (315–45°)	−0.05	0.03	−0.05	0.03	−0.04	0.04	−0.04	0.04
Distance to slope (0–10°)	−0.18	0.02	−0.17	0.03	−0.16	0.04	−0.15	−0.04
Distance to slope (20–30°)	−0.11	0.03	−0.11	0.07	−0.10	0.10	−0.09	0.03
Distance to slope (60–90°)	0.13	−0.01	0.13	−0.01	0.12	−0.01	0.11	−0.01
Distance to south-facing slope (135–225°)	−0.07	−0.04	−0.07	−0.05	−0.06	−0.03	−0.06	−0.01
Distance to villages	0.29	−0.19	0.28	−0.19	0.26	−0.21	0.24	−0.11
Frequency of east-facing slope (45–135°)	0.11	0.03	0.14	0.07	0.13	0.13	0.25	0.11
Sine of slope	0.05	−0.05	0.05	−0.06	0.04	−0.05	0.04	−0.05
Frequency of fragmented forest	−0.03	−0.07	−0.04	−0.14	−0.08	−0.33	−0.11	−0.49
Frequency of mixed coniferous and deciduous broadleaf forest	0.16	0.06	0.18	0.04	0.18	−0.01	0.23	−0.02
Cosine of slope	−0.01	0.00	0.00	0.01	0.00	0.01	0.00	0.01
Frequency of sparse forest	0.06	−0.01	0.08	−0.05	0.13	−0.13	0.07	−0.21
Frequency of slope (10–20°)	0.03	−0.02	0.03	−0.03	0.03	−0.02	0.06	0.00
Frequency of slope (20–30°)	0.16	−0.07	0.19	−0.08	0.21	−0.10	0.27	−0.02

[a] Positive values of marginality mean that giant pandas prefer locations with greater values than the mean of the corresponding variable in Liangshan Mountains, whereas negative values indicate that giant pandas avoid areas with less values than the mean of the corresponding variable in the study area.
[b] The amount of marginality or specialization accounted by each factor is given in parentheses.
[c] Signs of coefficient have no meaning for the specialization factor.

4 classes of habitat suitability: 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 ($0 < P/E < 1$) was defined from marginal habitat; habitat suitability values with no presence points ($PE = 0$) were defined from unsuitable habitat (Sattler et al. 2007).

Concomitant to the ENFA analyses, we sampled values of each habitat variable at each giant panda location using ArcView GIS 3.3. Then, we used the K–W test to compare the means for each variable (Lu 2006) and to identify habitat selection differences across the 4 scales. For all statistical tests, significance was set at $P < 0.05$.

RESULTS

We recorded 400 signs of giant panda habitat use across the study area. These included 30 hair sites, 2 tracks, 8 den sites, and 360 fecal samples. Using the random point generator, we reduced the number of actual signs of giant panda habitat selection to 177 in the final model.

Ecological Niche Factor Analysis

The global marginality of the ENFA models was large for each of the 4 spatial scales (Table 2), indicating that giant panda habitat differs drastically from the mean conditions across the LSM. For example, global marginality was 0.952 for the core area scale, 0.985 for the daily movement scale, 1.080 for the home range scale, and 1.146 at the elevational migration scale. Although marginality increased with scale hierarchy, global tolerance decreased (Table 2). These indices suggest that giant pandas are quite restrictive in the range of conditions they tolerate, and these restrictions declined at larger scales.

Table 2. Ecological Niche Factor Analysis parameters of marginality, specialization, and tolerance for giant pandas in the Liangshan Mountains, Sichuan province, China, 2005–2007, across 4 models.

	Model scales			
Model parameters	Core range	Daily movement	Home range	Elevational migration
Marginality	0.952	0.985	1.080	1.146
Specialization	1.954	2.004	2.177	2.351
Tolerance (1/S)	0.512	0.499	0.459	0.425

A range of habitat characteristics was associated with giant panda habitat selection regardless of the measurement scale and thus we could discern little effect of the spatial hierarchy. Among a subset of the ecogeographical variables, elevation had the second largest marginality (Table 1). Giant pandas preferred habitat at higher elevations across all 4 models. However, scores for the first specialization factor indicated giant pandas are most restricted by the elevation of habitat at the home range scale and weakly at the scale of elevational migration (Table 1). Giant pandas were associated with habitat containing large amounts of conifer forest, mixed forest, and sparse forest, and few fragmented patches of forest across all spatial scales. We found giant pandas to be mixed forest specialists at all scales, but detected the strongest association in the core range model. We also found that giant pandas preferred sparse forest and avoided fragmented forest, and preferred areas containing first and third class roads far away from villages at all 4 scales (Table 1).

Using the K-W test, the frequency of fragmented forest, sparse forest, 10–20° slopes, and distance to fragmented forest, north-facing slopes, south-facing slopes, and 0–10° and 20–30° slopes differed significantly among the plot types at the 4 scales ($P < 0.05$). Giant pandas preferred habitat with a high frequency of 10–20° slopes, especially at the core range scale. Giant pandas preferred 0–10° and 20–30° slopes in all 4 models, but again, the effects were the weakest at the largest spatial scale of elevational migration (Table 1). The relationship between 2 measures of disturbed forest (frequencies of sparse forest and fragmented forest) and the distribution of giant pandas also varied across scales. However, the relative strength of marginality and specialization for the fragmented forest increased with spatial hierarchy; sparse forest use was consistent at the 3 small spatial scales and although still associated with giant pandas at the elevational migration scale, the association was weaker.

Predictive Accuracy of Multi-Scale Models

The predictive success of the ENFA model was high (Table 3). Although the overall explanatory power and model fit declined with spatial scale as indicated by a decreasing Boyce index from the core range to the elevational migration models, all values were near the theoretical maximum of 1 attesting to very good predictive power. The home range scale model also had good predictive power (0.815 ± 0.368), but the large standard deviation is a symptom of low robustness (Table 3). Although the AVI value for the elevational migration model was slightly less than those for models at the 3 small spatial scales (Table 3), all models received values approaching 0.5, indicating that the fractions of correctly classified presence points and evaluation partition were comparable. We can conclude that the 4 models show good discrimination power between high-suitability and low-suitability habitat areas in the LSM. A calculation of CVI showed that the model at the migration scale ($CVI = 0.441 \pm 0.248$) was the best model, but wide standard deviation in the migration model ($SD = 0.248$) indicated low robustness for the prediction. The standard deviation around the CVI estimate was narrow for the core range scale ($SD = 0.161$), meaning high robustness for this prediction model. Although different across the 4 scales, the CVI values indicated appropriate habitat prediction mapping, indicating that the modeling of the 21 selected variables was able to distinguish habitat preferred by giant pandas from other habitat across the LSM.

DISCUSSION

Our findings showed that the spatial scale over which habitat characteristics are measured will influence estimates of habitat selection and suitability. For species of concern such as the giant panda, these differences may have a profound impact on the type and extent of management. Using a spatial model based on a scale representing the broadest form of landscape use in this species (seasonal elevational migration), we found that giant pandas are associated with slopes of <30° and avoid fragmented forest. At the small scales of core range and daily movement, we found that the most influential ecogeographic variables are the proximity to south-facing and north-facing slopes. Habitat features selected might offer one of the clearest illustrations of scaling effects (Schaefer and Messier 1995) and should permit animals to avoid the effects of factors likely to limit individual fitness. Selection patterns should be the strongest at the largest scale of selection (Rettie and Messier 2000) whereas less influential limiting factors may influence selection patterns only at small scales (Mcloughlin et al. 2002).

Habitat selection is often viewed as a hierarchical process that implies selection or avoidance of habitat types at various

Table 3. Mean evaluation indices and standard deviations for giant panda habitat suitability models across 4 spatial scales in the Liangshan Mountains, Sichuan province, China, 2005–2007.

Spatial scale	Boyce Index[a]		Absolute Validation Index[b]		Contrast Validation Index[c]	
	Mean[d]	SD[e]	Mean	SD	Mean	SD
Core range	0.930	0.092	0.502	0.167	0.402	0.161
Daily movement	0.900	0.105	0.495	0.195	0.392	0.187
Home range	0.815	0.368	0.507	0.218	0.420	0.209
Elevational migration	0.895	0.101	0.484	0.256	0.441	0.248

[a] Boyce index (B) provides an assessment of model predictive power and ranges from −1 to 1.
[b] Absolute Validation Index (AVI) indicates how well the model discriminates between high-suitability and low-suitability habitat areas and ranges from 0 to 1.
[c] Contrast Validation Index (CVI) indicates how much the AVI differs from what would have been obtained with a random model and ranges from 0 to AVI.
[d] Larger mean values indicate a greater consistency with evaluation data sets.
[e] The smaller the SD, the more robust the prediction.

spatial scales (Dussault et al. 2005). In this study, although we found that giant pandas avoid fragmented forest, differences across the 4 scales were apparent and appeared to be driven by environmental factors directly related to movement and forage availability, especially at the elevational migration scale. Given the large body size of giant pandas, dense bamboo in the fragmented forest may inhibit movement (Wei et al. 2000). In addition, its bamboo-specialized diet and limited capacity for long-distance movement may restrict them to certain areas (Hu 2001).

The use of different spatial scales yielded different estimates of the extent to which the slope was preferred by giant pandas. Small-scale models based on core area and daily movement revealed a stronger association with habitat slope than other 2 larger scale models. Core area and daily movement scales typically contained habitats of biologically critical importance for giant pandas such as foraging areas (Hu 2001); thus, the nonrandom utilization of landscape elements at these 2 scales was due to the limited presence of those habitats containing resources used by giant pandas. The daily energy intake of giant pandas is only marginally greater than daily energy expenditure (Schaller et al. 1985, Wei et al. 1997) and a preference for gentle slopes may be a strategy to minimize energy expenditure (Hu et al. 1985, Reid and Hu 1991, Wei et al. 2000). In terms of habitat selection based on aspect, we found different effects of south-facing sunny and north-facing shaded habitat across all 4 models and little discrimination for east-facing habitat. This is in agreement with the notion that south-facing habitats that receive direct sunshine are preferred by giant pandas (Hu 2001).

To minimize anthropogenic disturbance, giant pandas usually avoid roads and prefer dense cover of coniferous vegetation (Zhang et al. 2011). Several empirical studies have concluded that giant pandas do avoid roads within nature reserves (Ouyang et al. 2001) and across entire mountain ranges (Xu et al. 2006, Wang et al. 2009). Our results found that panda's habitat selection may occur close to first and third class roads across the study area at all 4 scales, suggesting that we should comprehensively understand the

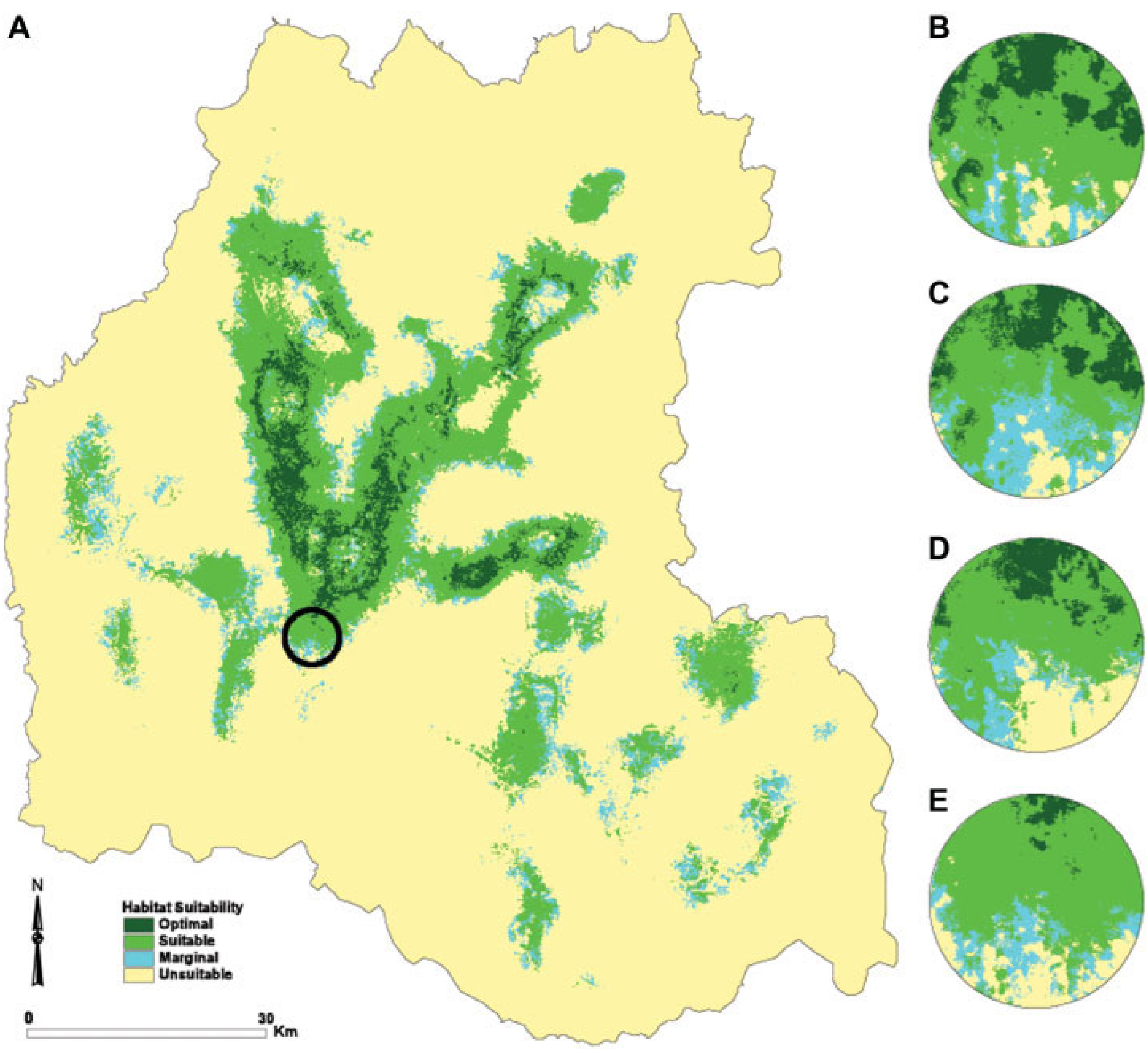

Figure 2. Habitat suitability maps for giant pandas in the Liangshan Mountains, Sichuan province, China, 2005–2007 for (A) the study area computed using ecological niche factor analysis based on a spatial scale akin to distances traveled during giant panda seasonal migration; the 3,600-m radius dark circular area shows suitability mapping in detail resulting from the (B) core range, (C) daily movement, (D) home range, and (E) migration scale models. Dark green areas denote optimal habitat, green denotes suitable habitat, blue denotes marginal habitat, and beige represents unsuitable habitat.

effect of roads on the giant panda. Based on our habitat map, a selection for such 2 types of roads may result from 2 reasons: these roads passed through giant panda habitat where they have to use them for movement or dispersal because of spatial proximity; and/or the whole or parts of these roads are away from human settlements, and these roads have no physical barriers such as fences. For example, 1 first class road connecting Ebian and Meigu counties crossed the core panda habitat, but we found that giant pandas still live on both sides of this road during our field surveys. Compared to first class roads, however, the second class roads with fewer vehicles appeared to be not used by giant pandas, most likely because this kind of road is far away from giant panda habitat. Therefore, these findings indicate that the spatial distribution of roads may be an influential factor affecting habitat use of giant pandas.

No studies have examined habitat use of giant panda using multi-scale methods across the landscape, and therefore decision makers may be making ill-informed decisions based on a single scale. For example, Wang et al. (2009) found that giant pandas prefer gentle slopes $<20^\circ$ within the scale of home range. However, our results suggest the selection of the slope varied at other scales. Our finding is the first comprehensive assessment across 4 scales with immediate conservation relevance to this endangered species.

Our results show consistencies in the influence of vegetation cover among our models, which may be explained by the role of this variable in meeting the nutritional and reproductive needs of giant pandas. For example, we found natural forests such as conifer forest and mixed forest at high elevations had a stronger association at the 4 scale models perhaps because of continuous canopy cover (Hu 2001) and presence of dens (Zhang et al. 2007), both necessary features for giant pandas, further strengthening support for the selection of old forest (Zhang et al. 2011). Generally, the giant panda is known to be extremely particular in selecting dens and dens are most likely found in large trees over 200 years old living in old-growth conifer forest. Although the number of giant pandas has reportedly increased since the population census in the 1980s, the degree of habitat fragmentation and degradation is now the critical issue for conservation managers (Yan 2005).

MANAGEMENT IMPLICATIONS

The multi-scale approach of identifying spatial habitat suitability can increase the knowledge of habitat management for a species (Piorecky and Prescott 2006). Our findings reveal the preference of giant pandas for the conifer forest at higher than average elevations at all 4 scales, and highlight scale dependence in habitat selection and habitat suitability distributions of giant pandas (Fig. 2). Thus, we recommend that management efforts for forested areas be concentrated within distribution areas of giant pandas, particularly for the conifer forests. Especially, because the giant panda is a flagship species for conservation in forest habitat, understanding multi-scale habitat use will have implications for the conservation of other forest-dwelling animals in China.

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