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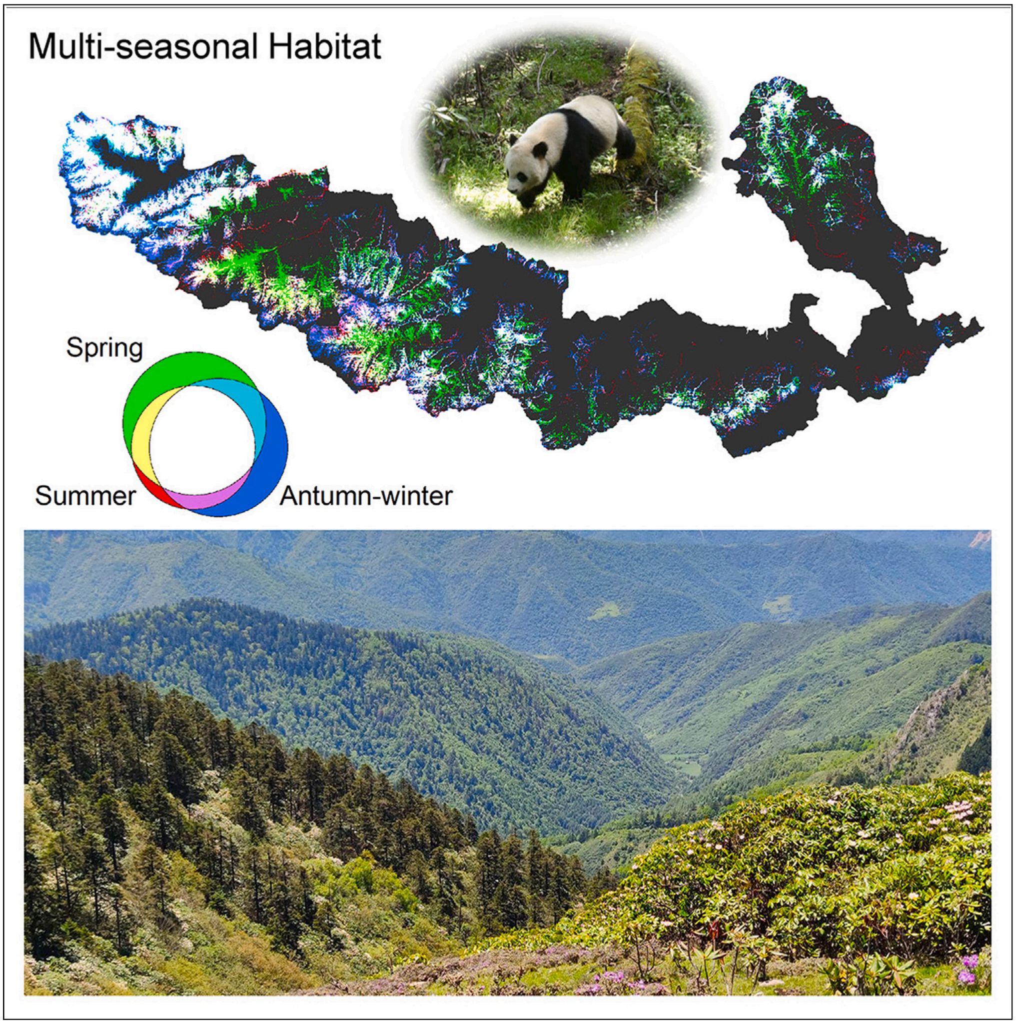

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Highlights

We mapped multi-seasonal habitat of giant pandas throughout the reserve

Giant panda habitats were mostly distributed in the west of the reserve

The existing reserve does efficiently cover the conservation needs

Developing a cohesive conservation management plan is needed

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Mapping multi-seasonal habitats of giant pandas to identify seasonal shifts

Yapeng Chang,[1] Chuanyan Zhao,[1,3,*] Xingming Liu,[2] and Liwen He[2]

SUMMARY

As a flagship species of biodiversity conservation globally, the giant panda has seasonal migration to cope with seasonal changes in available resources. Here, we have mapped the spatial distribution of multi-seasonal habitats of the giant panda across the Baishuijiang reserve in China. Results show that the spatial patterns are different in different seasons, generally, large patches are observed in the western part, while staggered clusters occur in the middle and eastern parts. That is, suitable habitats for giant pandas are mostly distributed in the west part. More than 75% of the predicted suitable habitats are within the core zone of the reserve year-round, indicating the core zone essentially meet giant panda's ecological needs, although this range could potentially be expanded. This study provides valuable insights into the spatiotemporal migration patterns of endangered species and helps to guide conservation planning.

INTRODUCTION

Biodiversity includes the totality of living organisms and the ecological complexity in which they occur and is essential to the welfare of the earth and humans.[1,2] The intensification of human activities, however, has resulted in the rapid loss of biodiversity and constitutes an international crisis.[2,3] The establishment of protected areas is a key tool for biodiversity conservation.[4,5] The survival of species depends on the integrity of the habitats to which they are adapted. Loss and fragmentation of habitats lead to species extinctions and reduced biodiversity.[6] To mitigate this global destruction, scientific assessments of the habitat need of species and predictions of the areas suitable for their survival are essential for the planning and management of protected areas.

Species distribution models (SDMs) have been developed to simulate the spatial distribution pattern of species habitats.[7] SDMs can inform studies of ecology and conservation management and can predict anthropogenic effects on the distribution patterns of species at different spatial scales.[7,8] The maximum entropy (Maxent) algorithm is the most prevalent SDM program because of its robust predictive power, high computational efficiency, and ease of use,[9–11] and has been widely used to simulate species' distributions.[12–14]

The giant panda (*Ailuropoda melanoleuca*) is an endemic and endangered species in China. It is the world's most widely recognized conservation flagship species,[15] and the symbol of the World-Wide Fund for Nature (WWF). The government of China has included the giant panda in its key biodiversity conservation program. Conservation researchers[15,16] have recommended that future emphasis should focus on improving the management of giant panda habitats, which has spurred research into the evaluation of habitat suitability. The spatial distribution of the species' preferred habitat was characterized using models constructed on climatic variables, which may have overestimated the impact of climate change.[12,17] On the other hand, models based on species present data involved either a single season (usually summer) or all seasons combined, failing to consider changes due to seasonality.[18,19] Such models possibly overestimated the long-term effectiveness of protected areas and underestimated the species' susceptibility to short-term changes in resource availability, and its plasticity in habitat selection. In a highly seasonal habitat, the species' ecological requirements are likely to show annual variations, which may result in seasonal changes in spatial distribution. Basing conservation plans on the habitats projected by correlative models may be insufficient because the seasonal fragmentation of suitable habitats can isolate populations.[20] The species' full annual range should be characterized by overlaying the distributions in different seasons to ensure its survival.[21]

Short-term changes in species' habitats are a recent focus in conservation biology. Most studies have been based on statistical information regarding species' presence and environmental characteristics, qualitatively analyzing the main characteristics of species habitat selection, and seasonal migration.[22,23] A comprehensive map of seasonal habitat changes for giant pandas across their entire range remains a gap, which limits our understanding of the seasonal migration of the species and hampers effective and holistic conservation.[24] So far, a detailed habitat analysis for different seasons is lacking, few studies have focused on the giant panda's seasonal habitat preferences or quantifying habitat shifts induced by seasonal changes. Investigating the seasonal migratory behavior of giant pandas based on their spatial movements will allow a better understanding of their habitat needs.

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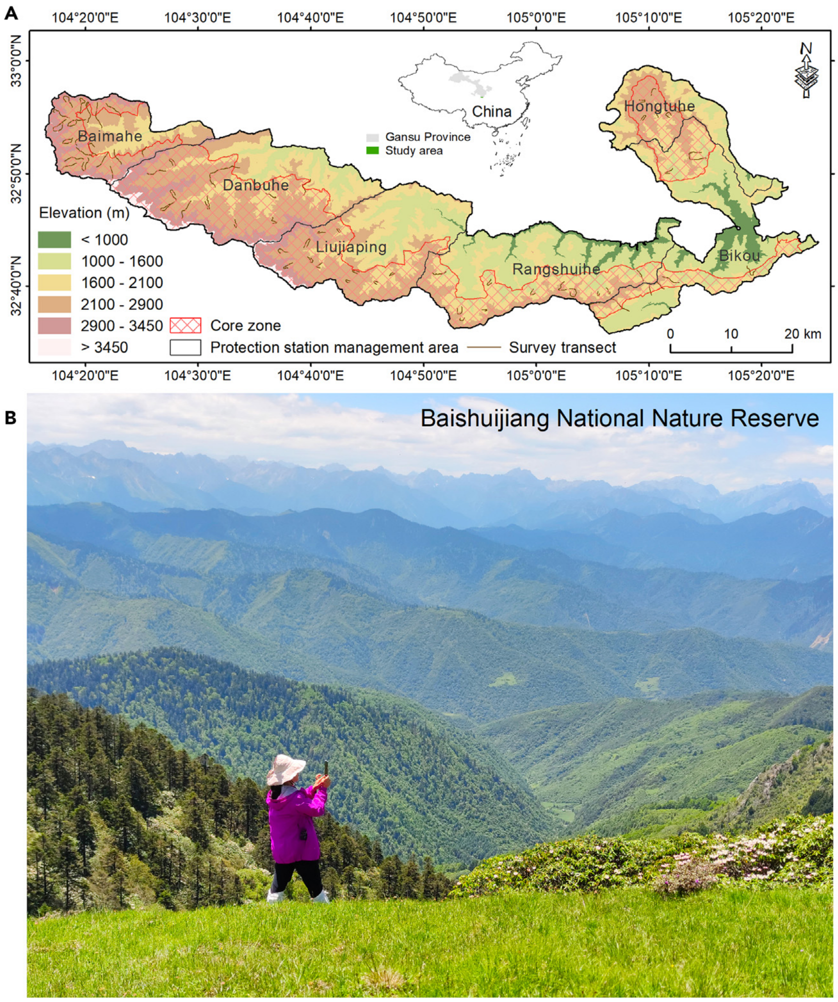

Figure 1. Location and landscape of the study area

(A) Topography and management areas, (B) The beautiful natural scenery of Baishuijiang National Nature Reserve. It is in the southern region of Gansu Province, in the Min Mountains.

Additionally, the current protected areas network is static and delineated according to conditions at a specific time, while the ecosystem and its threats are dynamic and change with the social or natural environment.[13,25] Conservation of species within static nature reserves does not effectively deal with the dynamic nature of threatened areas.[12,26] Shifting geographic ranges may influence the effectiveness of the protected area networks. The delineation of protected areas for threatened species should correspond to their suitable habitats. Hence, a detailed analysis of seasonal habitat preferences is urgently needed by policymakers to assess the conservation effectiveness of reserves, optimize the spatial distribution of existing reserves, and maintain their long-term usefulness.

Here, we present a case study of giant pandas in Baishuijiang National Natural Reserve, one of three key nature reserves for giant pandas in China. It includes the most pristine panda habitat and is a priority area for biodiversity conservation. We combine environmental information with a dataset of giant panda trace points in different seasons to identify possible seasonal shifts. Our aims were to: (1) identify the main environmental variables influencing the ranges of giant panda presence; (2) build a seasonal model of habitat suitability and map potential multi-seasonal giant panda habitat for the reserve; (3) evaluate changes in the distribution and extent of giant panda habitat under different seasons. We further defined conservation gaps in existing key areas to enhance conservation efforts. We hope that our results will improve habitat management in space and time throughout the range of giant pandas, and provide useful data for establishing a Giant Panda National Park in the Minshan Mountains of China.

Study area

Baishuijiang National Nature Reserve is located in the Minshan Mountains (104°16′ to 105°25′ E and 32°36′ to 33°00′ N), in the southern part of Gansu Province, northwest China (Figure 1). The reserve is one of three key reserves in China for the protection of giant pandas, covering an area

Table 1. Analysis of contribution and permutation importance of environmental variables

Environmental variable	Spring		Summer		Autumn- Winter	
	Contribution (%)	Permutation importance	Contribution (%)	Permutation importance	Contribution (%)	Permutation importance
Elevation	40.7	41.4	34.1	42.4	47.2	48.2
Distance to road	21.1	25.3	23.5	17.6	19.1	14.9
Distance to river	15.6	21.5	14	21.9	11.6	20.1
Land-cover type	6.3	3.3	16.6	8.5	10.2	4.2
Slope	8.1	3.8	4.9	5.2	7.3	7.7
Topographic position index	4.8	3	4.9	1.9	3.6	3.3
Aspect	3.4	1.7	2	2.5	0.9	1.6

of more than 1800 km^2. It has the only natural landscape and supports a rich biodiversity for the northern subtropics in Gansu Province. The reserve is divided into a core zone of 901.58 km^2, a buffer zone of 261.32 km^2, and an experimental zone of 675.09 km^2. Forest coverage is 87.3%. The reserve lies on the northern slope of Motianling. Its elevation ranges from 595 to 4072 m above sea level and has a northern subtropical mountain climate. The mean annual precipitation is 800 mm, with most of the rain falling between July and September. The mean temperature is 14.8°C, with means of 3.7°C in January and 24.6°C in July. The frost-free period ranges from 140 to 338 days per year. Vegetation types vary with increases in elevation, following the sequence: evergreen broad-leaved forest, evergreen deciduous broad-leaved mixed forest, deciduous broad-leaved forest, coniferous and broad-leaved mixed forest, subalpine coniferous forest, and alpine shrub meadow.[27]

RESULTS

Model evaluation and contribution of the variables

The average area under curve (AUC) values were above 0.8 for all models of the three periods: 0.85, 0.87, and 0.82, respectively, in the spring, summer, and autumn-winter habitats, which indicated good performance. The Jackknife test results indicated the relative contribution of

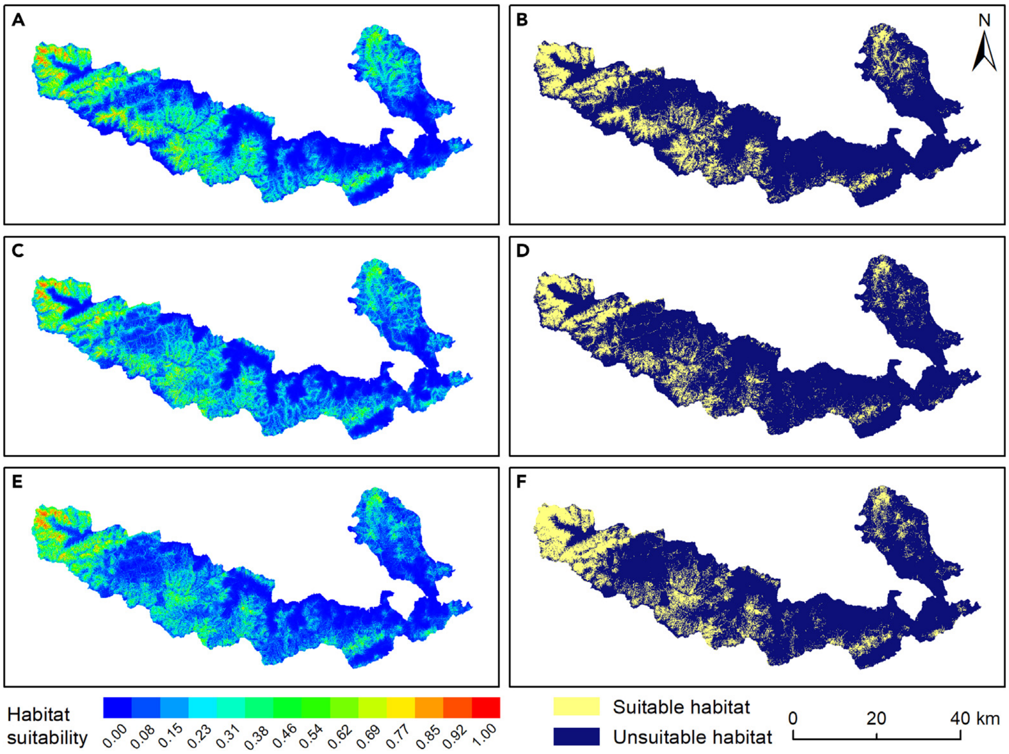

Figure 2. Habitat suitability maps of the giant panda in different seasons

The left (A, C, and E) and right (B, D, and F) columns of the figure represent habitat probability maps and binary distribution, respectively. Warmer colors show areas with better-predicted conditions. (A and B) Spring; (C and D) Summer; (E and F) Autumn-winter.

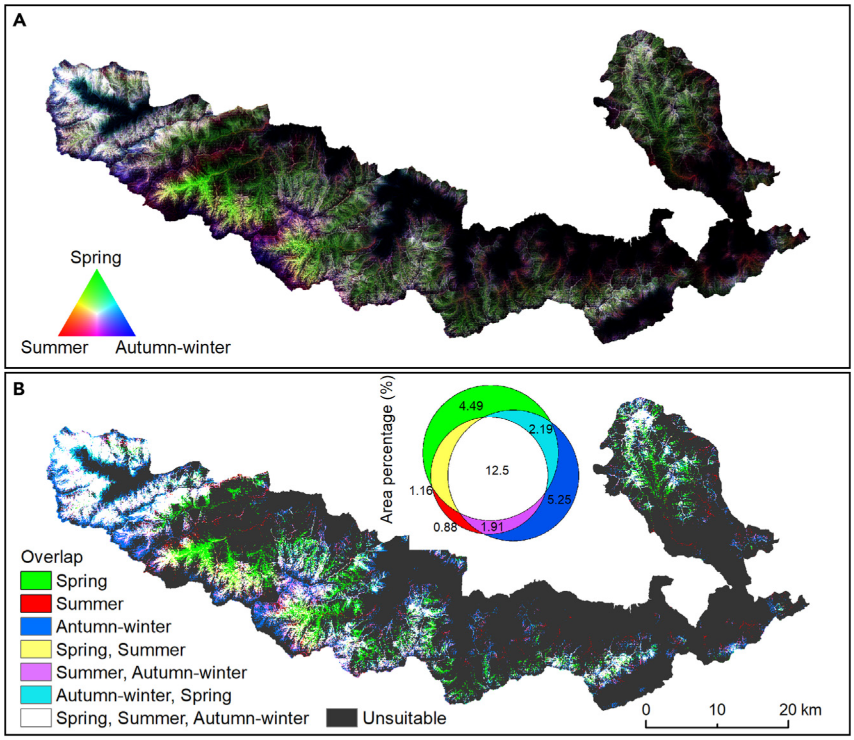

Figure 3. Multi-seasonal habitat map

(A) Habitat probability map, green, red, and blue colors indicate the suitable habitat in spring, summer, and autumn-winter, respectively. The mixtures of the three colors indicate overlaps of suitable habitats in different seasons.

(B) Distribution of giant panda habitat over the annual cycle. Venn diagram shows the overlap of seasonal habitats (numbers in the circles refer to the proportion of seasonal habitat area within the reserve area).

selected variables for predicting giant panda distribution. As shown in Table 1, the variable that contributed most to the area prediction during the three periods was elevation; its contributions were 40.7%, 34.1%, and 47.2% in spring, summer, and autumn-winter, respectively. Distance to roads and rivers, and land-cover type were also major contributors to panda distribution. The cumulative contribution of these four important variables was higher than 80%. The remaining variables appeared to have no significant effect (cumulative contributions <10%) in determining panda distribution.

Seasonal habitat suitability distribution

The habitat suitability distribution map for giant pandas is shown in Figure 2. The predicted seasonally suitable habitat effectively captured the observed giant panda traces-presence locations according to model-accuracy evaluations. Particularly the western part of the reserve contained large areas of suitable habitat in our predictions, and the area had higher suitability. In total, potential habitat in spring accounted for 20.34% of the reserve; in summer, for 16.45% of the reserve; and in autumn-winter, for 21.85%. These percentages comprise 378.01 km^2, 305.90 km^2, and 406.26 km^2, respectively. Summer and autumn-winter habitat occurred in similar areas, but potential summer habitat was more restricted (Figure 2). In general, suitable habitat was mainly found in Baimahe, Danbuhe, and Liujiaping and was scarce in Rangshuihe, Bikou, and Hongtuhe.

We combined the habitat models for spring, summer, and autumn-winter to develop an annual habitat model. Figure 3 showed that the western part of the reserve comprised large areas of multi-seasonal suitable habitat. Annually, 28.38% of the reserve provided potential giant panda habitat according to our predictions (Figure 3). Suitable habitats in different seasons overlapped considerably (Figure 4). The overlapping area of spring and summer habitats accounts for 67.16% of spring habitats and 83.04% of summer habitats, while the summer and autumn-winter habitat overlap accounts for 87.60% of summer habitats and 65.95% of autumn-winter habitats. The spring and autumn-winter habitat overlap accounts for 67.23% of spring habitats and 72.22% of autumn-winter habitats. The ratio of the area of overlap in the three periods to the total potential habitat was 62.58%.

Seasonal shift of habitat

The projected habitat in one season was overlaid on that of the following season to identify areas that would be lost or gained, or remained. The results showed that the range of suitable habitats changed in different seasons, and most changes happened in the central parts of the

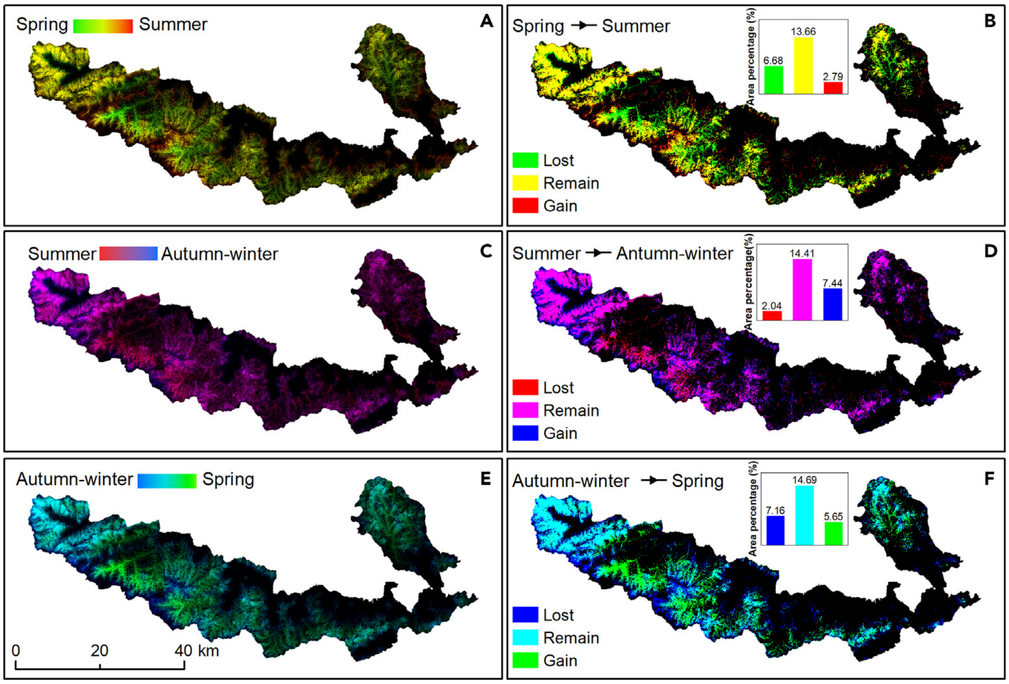

Figure 4. Projected shifts of giant panda habitats in different seasons

The left column (A, C, and E) shows a suitable habitat probability map in two seasons. Green, red, and blue colors indicate suitable habitats in spring, summer, and autumn-winter, respectively. The mixtures of the two colors indicate overlaps of suitable habitat for the two seasons. The right column (B, D, and F) expresses the seasonal shift of suitable habitats.

reserves (Figure 4). From spring to summer, the suitable area gained 51.87 km^2, while 253.96 km^2 remained, and 124.19 km^2 was lost. From summer to autumn-winter, 138.32 km^2 of suitable habitat was gained, 267.90 km^2 remained, and 37.93 km^2 was lost. From autumn-winter to spring, the suitable area gained 105.04 km^2, 273.11 km^2 remained, and 133.11 km^2 was lost.

Conservation gaps

Overlaying suitable habitats in different seasons with the core zone of the Baishuijiang reserve, we found that the core zone had high coverage of suitable habitats over all seasons (Figure 5B). For Individual periods, the core zone of the reserve encompassed 79.57% of spring habitat, 79.40% of summer habitat, 75.46% of autumn-winter habitat, and 76.60% of annual habitat (Figure 5B). The ratio of suitable habitat in the core zone to the core zone area was several times the ratio of suitable habitat outside the core zone to the area outside the core zone (Figure 5A), reflecting that the core area delineated in Baishuijiang National Nature Reserve was highly representative of suitable habitat for giant pandas. This means that the existing core zone in the reserve is adequate, but some suitable habitats exist outside the core zone. The conservation gaps were mainly located in Baimahe, Liujiaping, and Hongtuhe (see blue circles in Figure 5C). Among management areas, the Baimahe had more suitable habitat, but the gap area was also larger (Figure 5C).

DISCUSSION

Distribution and shifts of seasonal habitat

Multi-seasonal habitat modeling allowed us to estimate the entire annual survival range of giant pandas in Baishuijiang National Nature Reserve. The spatial patterns of seasonal habitats were different, and the seasonal distributions of habitats were staggered in the central part of the reserve. These findings were not unanticipated. We could be attributing the seasonal habitat changes to the limitation of giant panda activity for acclimation. Giant pandas are behaviorally buffered against seasonal changes due to their capacity for selective use of resources.[20] Seasonal shifts reflect inter-habitat differences in resource availability, which influence the presence or absence of species at both temporal and spatial scales.

Large areas of seasonally suitable habitats were predicted to occur mainly in the western part of the reserve. Since giant pandas have a specialized trophic relationship with bamboo, the spatial match of trophic interaction between giant pandas and bamboo has ensured their survival.[20] *Fargesia denudate* is one of the main edible bamboo species for giant pandas, and the most widely distributed species in the Baishuijiang reserve,[28] and is concentrated in the western part.[29] The distribution of giant panda habitats in our study is similar to *Fargesia denudate* distribution as reported by Hu and He.[29]

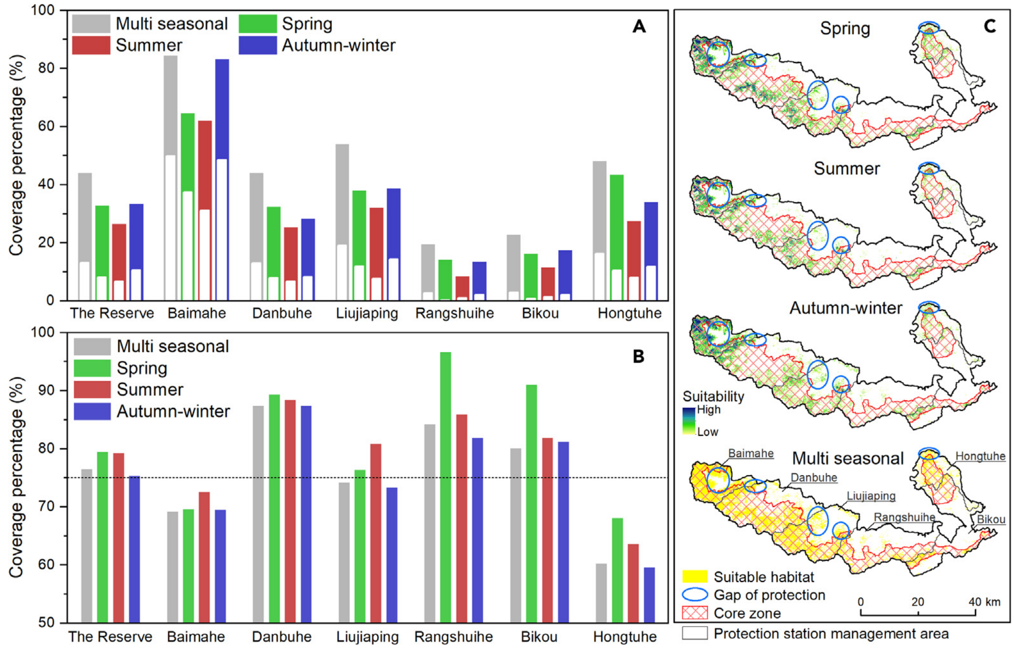

Figure 5. Comparison of habitat coverage for the giant panda across seasons

(A) The ratio of suitable habitat inside or outside the core zone to the whole distribution area inside or outside the core zone in the reserve. Colorless and colored bars represent statistics outside and inside the core zone, respectively.

(B) The ratio of the suitable habitat inside the core zone to the suitable habitat area in the reserve. The dotted line represents a ratio of 75%.

(C) The current core zone of the reserve and the distribution of suitable habitats (the blue circle indicates areas of suitable habitat outside the core zone).

The main variable influencing seasonal shifts in distribution was found to be elevation, which is consistent with other studies.[30] Elevation controls resource availability and habitat suitability in different seasons, leading to the seasonal vertical migration of giant pandas (Figure 6). Annually, the suitable habitat remaining across seasons was between 1500 m and 3500 m, with the highest relative frequency at 2500 m. From spring to summer, the suitable habitat gained occurred mostly in high-elevation and low-elevation areas, while the suitable habitat lost was concentrated in low-elevation areas. From summer to autumn-winter, gains in suitable habitat involved two elevations (i.e., about 2100 m and 3200 m), and habitats lost were at the middle elevation. From autumn-winter to spring, the suitable habitat gains affected mainly low-elevation areas, and habitats were lost across the entire distribution. The giant panda can occupy a larger area at lower elevations in the cool season, but they may be forced to abandon low-elevation habitats because of heat stress in the warm season, even if bamboo is abundant. Fundamentally, heat stress should only drive pandas upwards, while food resource can drive pandas upward or downward. This finding is in accordance with reports that giant pandas are sensitive to high temperatures, and control their ranging appropriately.[22,31]

Migration enables animals to maintain the environmental and nutritional conditions needed to ensure the survival of individual animals and enable reproduction.[32] The giant panda is no exception. To adapt to seasonal changes, giant pandas migrate seasonally to obtain the sufficient resource and to cope with extreme environmental conditions.[20,33,34] Despite this migration, the spatial overlap of seasonal habitat ranges remained stable and occupied a large proportion of all potential habitats. The pandas did not need to travel long distances for some special purpose (e.g., mating, foraging), thereby reducing energy expenditure and potential risks.

Most studies of the seasonal vertical migration of giant pandas have used indirect methods such as infrared camera monitoring and global positioning system (GPS) collar tracking.[22,34,35] These technologies can capture the giant panda image, including the site data, the time of discovery and other key data. But data are limited, and make it impossible to characterize the spatial pattern of giant panda's population across the entire area. However, the model makes it possible to accurately explain the spatial distribution of giant panda's population in whole area, although there may be some level of uncertainty involved.

Implications for conservation

Function zone designation is the foundation of scientific management of the reserve, and its effectiveness largely determines conservation outcomes.[36] Findings from gap analysis in key conservation areas provide valuable information to assess the appropriateness of functional zone designation, and we carried out such an analysis for a key conservation area in the Baishuijiang reserve to evaluate the conservation efficacy of the core zone.

A substantial portion (more than 75%) of all seasonally suitable habitats was located in the core zone of the reserve, indicating that the current key conservation area of the reserve offers effective conservation for giant panda activities. However, some suitable habitats were

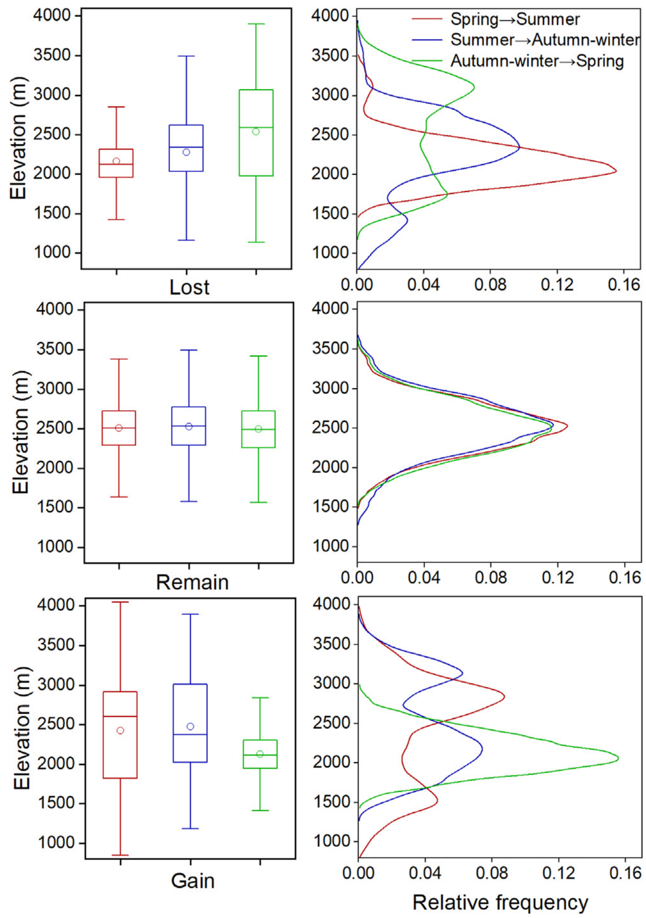

Figure 6. Elevation distribution of changes in suitable giant panda habitat

The curves represent the Kernel probability of relative frequencies of suitable habitat at certain elevations. In the boxplot, the horizontal lines represent minimum and maximum values of elevation; the middle line and circle within the boxplot show the median and mean value, respectively; the left and right edges of the boxes represent the 25th and 75th percentiles.

outside the key conservation area, especially in Baimahe. We should hence re-examine this conservation gap, and revise the reserve's management plan to include these gaps within the core zone. At the same time, we need to consider factors such as farmland, residential land, and highways in drawing up the new management plan, to balance habitat conservation with social development. We found that large areas of predicted contiguous habitat were in the west and southwest of the reserve, and their distribution extended to the reserve boundaries, indicating a need for cross-broader conservation. Fortunately, the establishment of the Giant Panda National Park will provide opportunities for cooperation with adjacent reserves.

Challenges of conservation and management

In our field survey, six types of human interference: the livestock grazing, the collection of Chinese medicinal herbs, the collection of other non-wood forest products, logging, tourism, and poaching have been recorded in different seasons, with the major interference attributable to livestock grazing and the collection of medicinal herbs. Grazing was concentrated mainly in the western part of the reserve (especially within the management area of Baimahe), while the collection of medicine herbs spans most of the reserve (Figure 7). Related studies have shown that overgrazing and the collection of medicinal herbs pose a threat to the suitability of giant panda habitat.[37,38] In our study area, we did not observe any bamboo forest degradation caused by excessive grazing and the vegetation damage resulting from medicine collection was not severe. The locations of these disturbances were not fixed permanently throughout the year, and giant pandas returned to these areas after the livestock and collectors had left. Gill et al., argued that wildlife can generally return to utilize the remaining resources after disturbances,[39] and Wei et al., found this to be the case for pandas.[40] In other words, livestock grazing or medicine collection does not pose a direct threat to the pandas' core habitat and survival in the Baishuijiang reserve at present, but may do so as they expand. Human activity is considered to be the paramount disturbance to giant panda survival.[15] Disturbance control will effectively conserve the giant panda habitats.[38,41] Hence, future conservation actions should be enforced, and illegal human activities should be strictly controlled in the reserve. Unfortunately, most human

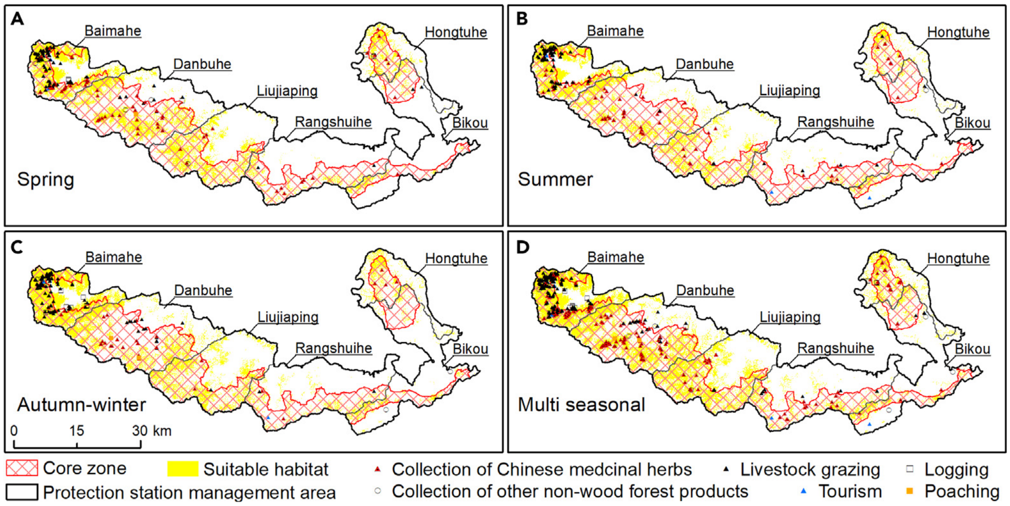

Figure 7. Distribution of human disturbance in different seasons in multi-years

(A) Spring, (B) Summer, (C) Autumn and winter, (D) Multi seasonal (annual).

disturbances are closely related to the livelihoods of residents, which may require more management efforts to reduce the dependence of local residents on natural resources, to resolve conflicts between human development and giant panda conservation.

Limitations of the study

Although our models performed very well, we recognize that there are inherent uncertainties in our predictions. Furthermore, we did not consider other biotic and abiotic factors (i.e., food resources, interspecific relationships, and climate factors) that could affect the distribution range of the studied species, which may limit the comprehensiveness of our predictions regarding the impact of seasonal changes.

Conclusions

To the best of our knowledge, this is the first study modeling of the seasonal habitat shifts by giant pandas in reserve. A data-driven Maxent model allowed us to map potential seasonal habitats for giant pandas in reserve. We identified the range of seasonal habitat distribution for giant pandas and understood the seasonal dynamics of suitable habitat, predicting the lost, remaining, and gained a range of the habitat. We have considered that the current reserve has efficiently protected the suitable panda habitat. Furthermore, our study highlights the need to monitor and assess seasonal habitat suitability for giant pandas.

To conclude, we believe that the study can serve as a reference for the habitat management of other endangered species. We propose that seasonal changes in habitats caused by the seasonal migration behavior of endangered animals, and the response to seasonal changes in the environment should be considered in the current conservation actions. Reserve managers and policymakers should adjust the conservation management plan promptly to form a cohesive one. This will enhance the conservation effectiveness of endangered animals.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- METHOD DETAILS
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AUTHOR CONTRIBUTIONS

C.Z. and Y.C. designed the research. Y.C and. L.H. did the fieldwork and data curation. X.L. and L.H. contributed to data. Y.C. analysis and prepared the initial draft. C.Z. reviewed and edited the final draft.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Digital Elevation Model	ASTER Global Digital Elevation model	https://earthdata.nasa.gov/
Land cover data (Sentinel-2)	United States Geological Survey	http://earthexplorer.usgs.gov/
Software and algorithms		
ArcGIS (Version 10.2)	ESRI	https://www.esri.com/enus/arcgis/products
Maxent (Version 3.4.4)	Maxent software for modeling species niches and distributions	http://biodiversityinformatics.amnh.org/open_source/maxent/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and data should be directed to and will be fulfilled by the lead contact: Chuanyan Zhao (zhaochy@lzu.edu.cn).

Materials availability

This study did not generate new unique reagents or materials.

Data and code availability

- The giant panda location data from the reserve is protected and cannot be shared in an online repository. Please contact the Administration of Baishuijiang National Nature Reserve for data access. No code is generated in this study.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

METHOD DETAILS

Survey data

The giant panda occurrence data used in this study were obtained from field population surveys conducted within the reserve between 2015 and 2018. A total of 66 fixed survey transects were placed in the whole giant panda distribution range. Walking along line transects, once a panda or its signs (i.e., feces, food trails, footprints, and nests) were found, its location is recorded using GPS (Global Position system). Details of the survey methods are available (http://www.baishuijiang.com.cn). In addition, infrared cameras have been placed within the reserve to capture photos of giant pandas. These photos included location and time of discovery. The length of one line-transect was controlled to be around 5 km. This survey transects were visited in March, June, September, and December per year. Due to the difficulty to visiting most places in winter, we can obtain limited data, so we divided the year into three periods: spring (March to May), summer (June to August), and autumn-winter (September to February the following year). A total of 339 trace points were collected, including 173 trace points in the spring period, 91 trace points in the summer, and 75 trace points in autumn-winter.

Additional data, including the reserve boundary layer, functional zone layer, etc., were obtained from the Baishuijiang National Nature Reserve Administration.

Environmental variables

We collected environmental data such as topography, land cover, and human activities, which affect the giant panda's habitat. The topographic variables include elevation, slope, aspect, and topographic position index, derived from a digital elevation model (DEM) with a resolution of 30 m, obtained from ASTER GDEM (https://earthdata.nasa.gov/). River data from the Baishuijiang National Nature Reserve Administration was used to extract the Euclidean distance from a surface raster to rivers by the distance analysis tool in ArcGIS 10.2.

To obtain high-resolution land-cover data in the reserve, we downloaded Sentinel-2 data with a spatial resolution of 10 m in 2018 from the United States Geological Survey (USGS) (http://earthexplorer.usgs.gov/). Data preprocesses mainly included radiometric calibration, atmospheric correction, seamless mosaic, and clipping, all of which were completed by ENVI 5.2.2 software. We then performed oriented-object classification and random forest classification on the image using eCognition software to obtain land cover classes with an overall 0.83 accuracy and 0.79 Kappa coefficient. We compiled a map with nine land cover classes (shrub forest, broad-leaved forest, coniferous forest, mixed broadleaf-conifer forest, grassland, alpine shrub land, cultivated land, built-up land, and water).

Human disturbance was measured as the Euclidean distances to roads.[42] Areas in the reserve, where the road intrudes, are disturbed by human activities.[43] Thus, roads were considered an important indicator of human activity in this study, and road data were obtained from the Baishuijiang National Nature Reserve Administration.

All environment variables were resampled to 30 m resolution and transformed in a WGS-1984-UTM-Zone-48N coordinate system. All data analyses were conducted in ArcGIS.

Mapping potential habitat

We modeled the seasonal habitat suitability of giant pandas in the reserve using the maximum entropy algorithm,[9] which predicts the potential distribution of species using species occurrence records and environmental variables based on the principle of maximum entropy.[11,44] In the present study, we randomly selected 75% of the occurrence data for model training with the remaining 25% to use for testing. A subsample procedure was performed for repeated iterations, repeatedly run ten times with the model output grid format as "logistic", and other parameters at their default value in model settings. To estimate the distribution of the species more reliably, only the average value of model outputs for each season was used for subsequent analyses. We used the jackknife test method to assess the importance of environmental variables and their contributions. We evaluated the model performance using the receiver operating characteristic (ROC) curve and the area under curve (AUC) analysis.[10,45] The larger the AUC value (ranging from 0 to 1), the higher the accuracy of the model prediction. Models with AUC >0.8 can be considered as providing good to excellent performance.[46]

The Maxent model output is the probability of species' occurrence in each cell. We selected the maximum training sensitivity plus specificity as a threshold to convert the continuous model outputs into binary values. The threshold method is a promising approach for species distribution using either presence/absence data or presence-only data when random points are used.[47,48] We then defined the cells with probability values greater than the threshold as indicating the presence of giant pandas, and vice versa, thereby obtaining presence and absence output for the giant pandas in each period. We assessed the seasonal shift of habitat based on the presence information using the ArcGIS spatial analysis tool. The seasonal habitat shift was quantified by overlapping the suitable habitat maps for two arbitrary periods. In this way, we could identify shift areas projected as being lost, remaining, or gained. Areas that remained indicated that suitable habitat was present in both seasons; gained areas indicated where suitable habitat increased from one season to another, and lost areas indicated where suitable habitat was lost from one season to another.

Gap analysis of key conservation area

The core zone is considered a key conservation area where the priority is biodiversity conservation. There is a degree of vulnerability if the giant panda population is not limited to the fully protected core zone.[36] Thus, the giant panda habitat should be covered by key conservation areas to better protect the population. We overlaid the projected suitable habitat map with the boundary of the core zone of the reserve to find gaps outside the core zone that would require protection.