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Microhabitat selection by giant pandas

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ABSTRACT

Understanding habitat selection is important for effective habitat management and recovery of species. However, many habitat selection studies are based on presence and absence data and do not differentiate the intensity of use and its association with fine-scale habitat characteristics. Such information is critical for improving our understanding of habitat suitability to inform conservation planning and practices, particularly for vulnerable species such as the giant panda (Ailuropoda melanoleuca) in China. We integrated Global Positioning Systems (GPS) tracking data of 5 giant pandas in Wolong Nature Reserve, China with detailed vegetation surveys to understand habitat selection by giant pandas. We compared microhabitat characteristics between the core and secondary home range areas of giant pandas and determined their relative importance using a resource selection function (RSF). We found that giant panda core areas had higher elevations, shorter distance to animal paths, shorter trees, and higher density of bamboo than the secondary area. Our findings shed new light on the importance of microhabitat characteristics that are generally overlooked in coarse-scale models in influencing giant panda habitat selection within the home range, such as bamboo density and accessibility to habitat that play important roles in the determination of core areas. We suggest prioritizing dense bamboo forests and areas with animal paths to improve giant pandas' habitat management, restoration, and corridor construction. The methods we used here regarding combining GPS-tracking derived intensity of use data and detailed habitat surveys could also be applied to better understand habitat selection strategies of a variety of other wildlife species.

1. Introduction

The heterogeneity of habitat influences habitat selection by animals, whereby animals select the most suitable habitat conducive to their survival and reproduction (Johnson, 1980). One important area of research involves understanding the microhabitat selection by individual animals in their home range, as reflected in different intensities of habitat utilization across available habitat in heterogeneous space. For example, approaches that link resource selection functions to individual animal utilization distributions help pinpoint factors that drive habitat selection across the entirety of an animals home range beyond a simplified "used" and "unused" (Marzluff et al., 2004; Millspaugh et al.,

2006). Such approaches often reveal that subtle features measured at the fine scale such as vegetation density, structure, and composition play more significant roles in impacting habitat selection than previously appreciated. Habitat selection is an important topic of study for conservation because habitat loss and degradation are major threats to biodiversity and can lead to species extinction (Hanski, 2011), improving habitat quality, and creating new habitat and improving habitat connectivity are effective ways to support species conservation (Hu, 2001; Yan, 2005; State Forestry Administration, 2015). Therefore, understanding species-specific habitat selection preferences is key to effective habitat management and restoration, particularly for the recovery of charismatic flagship species.

The giant panda (*Ailuropoda melanoleuca*), an icon of global wildlife conservation, is a species for which more in-depth habitat selection research is needed. The latest national giant panda survey indicates that the wild giant panda population covers a mere 25,800 km^2 area across six mountain ranges in southwestern China (State Forestry Administration, 2015). Although giant pandas have recently been downgraded to vulnerable status by the International Union for Conservation of Nature (IUCN) ("IUCN Red List of Threatened Species", n.d.), habitat conservation is still top priority for continued recovery of the wild giant panda population (State Forestry Administration, 2015; Wei et al., 2015; Qing et al., 2016; Xu et al., 2017a; Swaisgood et al., 2018). Therefore, understanding habitat selection is important for effective conservation, especially for species like giant panda that is in urgent need of habitat restoration and increased habitat connectivity (Qing et al., 2016; Xu et al., 2017a).

Previous studies have examined a variety of factors affecting giant panda habitat selection, including abiotic factors (e.g. climate, terrain, solar radiation, and water sources) (Hu and Schaller, 1985; Songer et al., 2012; Hull et al., 2014; Zang et al., 2017; Bai et al., 2018), biological factors (e.g. vegetation structure, food resources, and tree cavities) (Viña et al., 2008; Z. Zhang et al., 2011; Tuanmu et al., 2011; Hong et al., 2015, 2016; Wei et al., 2017, 2019), and nature-human impacts (e.g. protection status, earthquakes, livestock grazing, and road distribution) (Yan, 2005; Liu et al., 1999, 2001; Hull et al., 2011; J. Zhang et al., 2011; Zhang et al., 2017; Liu et al., 2016; Wei et al., 2018; Li et al., 2019; Wang et al., 2019). Overall, studies on giant panda habitat selection have revealed that giant pandas generally select forests with moderate to high bamboo densities, at mid-elevations, with gentle and moderate slopes, primary or secondary forests, and areas more distant from human activities (Hu, 2001; Yang et al., 2006; Hull et al., 2014; Wei et al., 2015; Hull et al., 2016). Presence of bamboo, forest age, as well as terrain topography, are key predictive variables dictating habitat selection at various scales (Z. Zhang et al., 2011; Ouyang et al., 2001; Liu et al., 2005). Most of these studies were done using transect or survey data by comparing environmental characteristics between areas with and without giant panda signs. However, with varying detectability and survey effort rarely accounted for, such methods can be problematic (MacKenzie et al., 2005; MacKenzie and Royle, 2005). For example, when suitable niches are not fully occupied at a site or detectability and survey effort is low, a mischaracterization and potentially an underestimation of suitable areas could occur (MacKenzie and Royle, 2005; Kéry and Schmidt, 2008). In the case of giant pandas, this could mean that habitats that are less accessible or marginal (e.g., steeper, degraded) have been undersampled, thus misrepresenting how pandas use these areas (Hull et al., 2016). To help overcome these biases, incorporation of data spanning an entire home range can bring in data points missed by other methods.

In addition, detailed vegetation surveys (e.g., on tree species, diameter at breast height (DBH), density) often contribute greatly to understanding wildlife habitat selection at the fine scale (e.g., 20 × 20 m^2 or smaller) (Z. Zhang et al., 2011; Wei et al., 2019). Generally, acquisition of detailed undergrowth vegetation data is extremely difficult without field survey. Due to logistical constraints, many studies on giant panda habitat use and selection have often been completed without fine-scale data on habitat characteristics (Xu et al., 2006; Hull et al., 2016; Xu et al., 2017b; Yang et al., 2017). These studies thus overlook key attributes of the undergrowth vegetation. The aforementioned giant panda habitat selection studies are largely based on coarse data on environmental conditions at broad geographical scales, for instance, slope and vegetation (just forest or no forest) at a coarse resolution (e.g., 250 × 250 m^2 scale) (Yang et al., 2017; Bai et al., 2018). Of the existing studies that do include fine-scale data on habitat, specifically understory vegetation condition (e.g. bamboo density, height), the studies are based on panda feces presence/non-presence data (Zhang et al., 2009) and there is no way to connect the findings to habitat use intensity of individual giant pandas. Variables such as the

structural characteristics and demographics of bamboo forest could contribute greatly to an improved understanding of habitat quality and may be important for giant panda habitat selection.

With advances in high-resolution wildlife telemetry technology, there are increasing opportunities to integrate target animal presence data with fine-scale habitat data to study wildlife-habitat relationships (Hull et al., 2016; Liu et al., 2005; Stabach et al., 2016). Such approaches go beyond comparisons of presence vs. pseudo absence of wildlife in different habitat types by allowing for comparisons across different degrees of intensity of use by the animals across their home ranges (Liu et al., 2005; Hull et al., 2016). Our study integrates GPS collar data on giant pandas with data on fine-scale habitat characteristics to examine differences in habitat selection of giant pandas in different parts of their home ranges for the first time. We used a unique field dataset to differentiate habitat selection between core and secondary home range areas of the giant panda to determine which habitat characteristics were correlated with varying intensities of use. This study provides insight for improving our understanding and approaches for studying habitat selection in giant pandas and other species. Our findings also have important implications for improving wildlife conservation and management across species.

2. Methods

2.1. Study area

The study area is located in Wolong Nature Reserve (102°52′–103°24′E, 30°45′–31°25′N), which lies in Sichuan Province, southwest China (Fig. 1). The reserve is located within the center of the Qionglai Mountain range, a high-density area for the giant panda. It is part of a global biodiversity hotspot (Myers et al., 2000; Liu et al., 2003), and is one of the largest nature reserves established for conserving giant pandas and other rare wildlife inhabiting an alpine forest ecosystem. Wolong contains ample forest stretching across mountains with steep slopes, and sufficient bamboo for giant pandas (Hu, 2001; Hu and Schaller, 1985). According to the most recent survey in 2012, the reserve is home to an estimated 104 wild giant pandas and has around 905 km^2 of potential habitat for giant pandas (Sichuan Forestry Department, 2015).

The area of interest in our study is known as Hetaoping. Roughly 40 km^2 in size and located in the northeastern portion of the reserve, the area spans an altitudinal range of 1800 to 3200 m (Hull et al., 2016). There are coniferous forests, broadleaf forests and mixed forests, while understory bamboo species include arrow bamboo (*Bashania fangiana*), umbrella bamboo (*Fargesia robusta*) and Yushan bamboo (*Yushania bravipaniculata*). Hetaoping is geographically bounded by pasture, a national highway, and a river (Hull et al., 2016). It is one of the main distribution areas of giant pandas in Wolong Nature Reserve. Camera trapping and genetic testing of DNA extracted from field-collected feces suggest that a local population of 16–25 giant pandas exists within this area (Huang et al., 2015).

2.2. Giant panda subjects

Five giant panda individuals were captured using anesthetization dart guns loaded with weight-dependent doses of ketamine in our study area (Table 1). They were fitted with GPS collars (Lotek GPS_4400 M: Lotek Engineering Inc., Newmarket, Ont., Canada) in < 30 min and released, and all GPS collars were equipped with TRD-L drop-off function. The staff and veterinarian of the China Conservation and Research Center for the Giant Panda (CCRCGP) ensured animal safety. The GPS collars recorded locations every 2 h. Duration of tracking varied across individuals from 7 months to one year between 2010 and 2012 (Table 1).
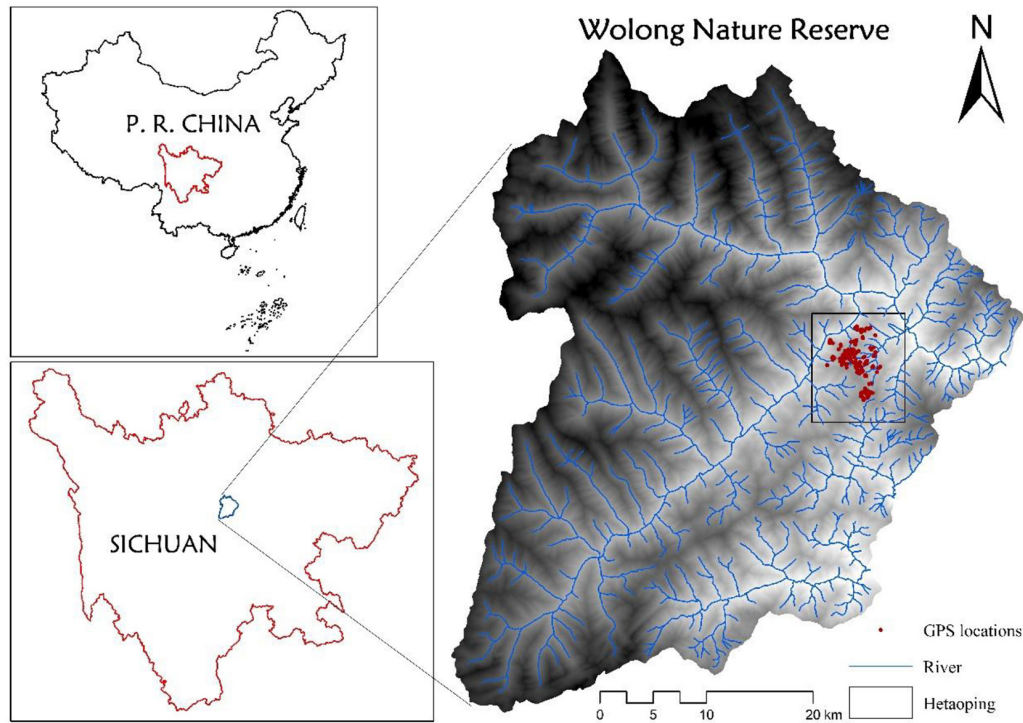
Fig. 1. Map and location of Wolong Nature Reserve, Sichuan, China, study area.

Table 1
Summary statistics of studied pandas and GPS tracking data (n = 1511). Names are appellations (in Chinese) of individual giant pandas in our study.

Name	Sex	Age	Start date	End date	Days monitored
Panpan	Female	Adult	4/16/2010	11/26/2010	226
Longlong	Female	Sub-adult	4/10/2011	10/12/2011	195
Meimei	Female	Adult	3/18/2011	3/17/2012	365
Zhongzhong	Female	Adult	4/11/2011	4/10/2012	365
Chuanchuan	Male	Adult	4/1/2011	3/25/2012	360

2.3. Home range estimation

Kernel density estimation (KDE) is a non-parametric algorithm widely used to estimate the probability density function and the associated home range based on presence data (Kernohan et al., 2001; Hemson et al., 2005). It was used in this study to estimate the giant panda home range (Zhang et al., 2015; Bai et al., 2017). The probability density function of KDE is defined as:

$$\widehat{f}_{(x)} = \frac{1}{nh^2} \sum_{i=1}^{n} K\left[\frac{x - X_i}{h}\right]$$

where $\widehat{f}_{(x)}$ is the KDE, n is the number of samples, h is the smoothing parameter, x is a given point in the home range estimated, X is a random sample of n independent points from an unknown utilization distribution, contains the horizontal and vertical coordinates of n presence location (Silverman, 1986; Worton, 1989), and $K[\ ]$ is a two-dimensional equilibrium density probability function (Worton, 1989). Likelihood Cross-Validation (CVH) was used to calculate the smoothing parameter (h) using Animal Space Use 1.3 Beta (Bai et al., 2017; Silverman, 1986; Zhang et al., 2013). We estimated the home range in ArcGIS 10.5 (ESRI, 2017).

Similar to many home range estimation methods, the KDE method assumes that each data point is independent. To address the temporal autocorrelation of the GPS fixes, we calculated KDE for each panda using only a subset of the data. For each panda-day, we selected one

record at 10:00 (UTC + 08:00), one of the most active times for giant pandas (Zhang et al., 2015). In the days when the data at 10:00 were missing, we used the closest record from that day. A total of 1511 fixes were selected and analyzed. The core area of each home range was delineated to encompass the 50% kernel density estimation area, and the secondary home range was set to include their 50–95% kernel density area (Fieberg, 2007; Bosch et al., 2010). In other words, the core areas were used most often by giant panda relative to the secondary areas of their home range. We then merged the core and secondary home range areas across the five pandas to create a single layer representing the aggregated core and secondary areas of use across Hetaoping (Fig. 2). The merged core area represented any habitat identified in the core area of one or more of the five studied pandas. The merged secondary area represented any area that was excluded from the core areas of all five individuals. Due to overlap among pandas, the area of the merged layers (core and secondary areas) was less than the sum of the areas of the five giant pandas' individual home ranges.

2.4. Habitat survey and environmental variables

We surveyed the habitat at 248 locations across the giant panda home ranges in summer 2016 (n = 134 in the aggregated core area and n = 114 in the aggregated secondary area). The locations were selected randomly from the pool of the previously referenced 1511 GPS fixes. We excluded any points that were within 50 m of each other (Fig. 2). We did not survey the vegetation at the same time as giant pandas were being monitored because pandas have small home ranges, are highly sensitive to human presence, and can detect humans by scent and sound at long distances and subsequently flee to avoid encounters. Their behavior and space use patterns would thus not be representative of natural conditions had we sampled simultaneously while tracking them. However, our knowledge of the ecology of the study area suggests that the vegetation characteristics that we measured largely did not change between the tracking and sampling periods.

At each survey location, we measured tree, shrub and bamboo characteristics. Each 20 × 20 m tree plot contained 4 shrub sub-plots
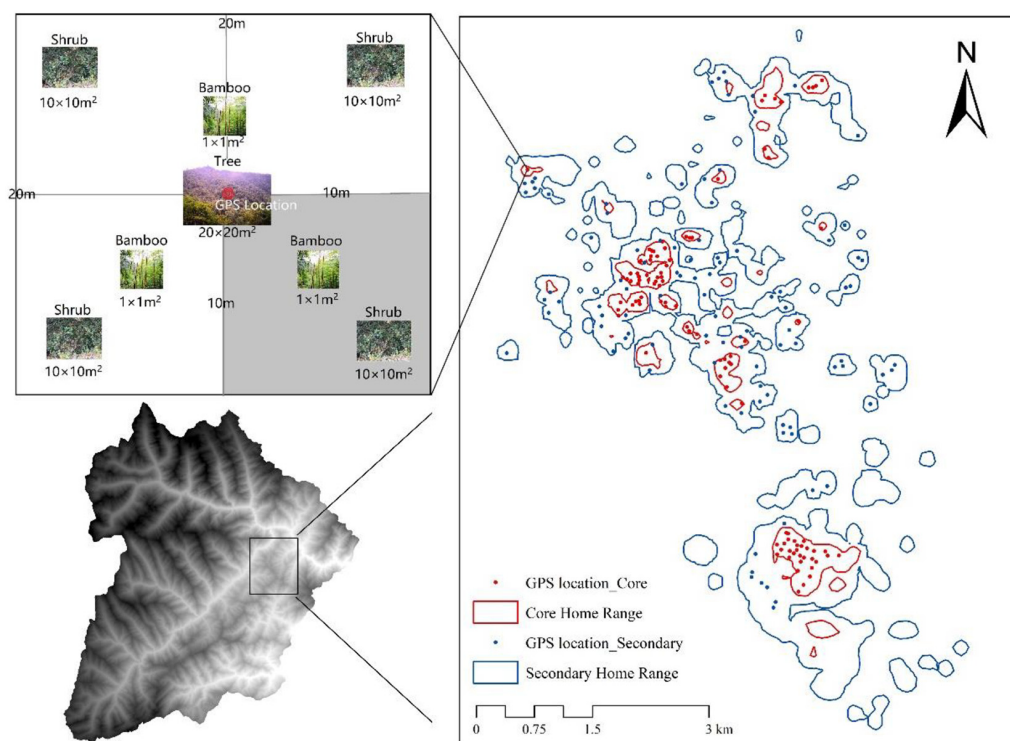
Fig. 2. Distribution of GPS locations in the study area of Wolong Nature Reserve, China, and study design for vegetation plots. Depicted are the merged core and secondary areas, which represent an aggregate across 5 studied pandas. Merged core area includes core areas of one or more of the five individuals.

Table 2
Habitat characteristics measured in the vegetation plots set up in Hetaoping, Wolong Nature Reserve, China.

Habitat characteristics	Definition (measuring method[a])
Elevation	Elevation at center of the tree plot (handheld GPS)
Slope	Slope at center of the tree plot (handheld GPS)
Distance to water (m)	Distance between center of the tree plot and a flowing stream
Distance to animal path (m)	Distance between center of the tree plot and passable path of animals (such as natural paths on ridges and paths created by all animals)
Forest age	Primary forest: forest that has not been logged, including native residual forest
	Secondary forest: forest that is naturally restored after logging
Vegetation types	Coniferous forest, Broadleaf forest, or Mixed forest
Tree crown diameter (m)	Average diameter of the canopy in the vertical direction
Number of trees	Number of trees with the height > 5 m in the tree plot
Height of trees (m)	Average height of all counted trees in the tree plot
Diameter of the tree (cm)	Average diameter at 1.5 m of all counted trees in the tree plot (breast diameter ruler)
Height under tree branches (m)	Average height of the lowest branch of all counted trees in the tree plot
Tree crown diameter (m)	Average length of canopy in horizontal and vertical directions of all counted trees in the tree plot
Shrub coverage (%)	Average estimation of the shrub coverage in the 4 shrub sub-plots
Number of shrubs	Average number of shrubs and trees < 5 m tall in the 4 shrub sub-plots
Height of shrub (m)	Average height of all counted shrubs in the 4 shrub sub-plots
Diameter of shrub (cm)	Average diameter at main stem of all counted shrubs in the 4 shrub sub-plots
Bamboo coverage (%)	Average estimation of the bamboo coverage in the 3 bamboo sub-plots
Number of bamboo shoots	Average number of bamboo shoots in the 3 bamboo sub-plots
Basal diameter of bamboo shoots (mm)	Average basal diameter of 10 bamboo shoots in 3 bamboo sub-plots; or average of all when < 10 present (Vernier caliper)
Height of bamboo shoots (cm)	Average height of all measured bamboo shoots in the 3 bamboo sub-plots (tape measure)
Number of young bamboos	Average number of young bamboos in the 3 bamboo sub-plots
Basal diameter of young bamboo (mm)	Average basal diameter of 10 young bamboos in 3 bamboo sub-plots, or average of all when < 10 present (Vernier caliper)
Height of young bamboo (cm)	Average height of all measured young bamboo in the 3 bamboo plots (tape measure)
Number of adult bamboos	Average number of adult bamboos in the 3 bamboo sub-plots
Basal diameter of adult bamboo (mm)	Average basal diameter of 10 adult bamboos in 3 bamboo sub-plots, or average of all when < 10 present (Vernier caliper)
Height of adult bamboo (cm)	Average height of all measured adult bamboos in the 3 bamboo sub-plots (tape measure)
Number of dead bamboos	Average number of dead bamboos in the 3 bamboo sub-plots, including flowering bamboo and residual eaten bamboo

[a] Measurement method was visual estimation if not otherwise stated.

(10 × 10 m) and 3 bamboo sub-plots (1 × 1 m) (Fig. 2). The tree plot was centered on the GPS location and was positioned perpendicular with the slope direction. Shrub sub-plots were positioned as four quadrants within each tree plot. Bamboo sub-plots were placed to form a triangle shape within each tree plot, so that they were at least 6 m from each other (the only bamboo species in our plots was arrow bamboo). Definitions and measurement methods of all habitat characteristics measured in the plots are shown in Table 2. To compare the

habitat characteristics between plots located in the core and secondary areas, we conducted *t*-tests. The significance level was set to 0.05 and the results are shown by mean $\pm$ SD.

2.5. Resource selection models

Resource selection functions (RSF) are commonly used to quantify species/habitat relationships and predict species occurrence on the landscape (Gillies et al., 2006; Johnson et al., 2006; Roever et al., 2012; Stabach et al., 2016). We modeled resource selection differences between the aggregated core (1) and secondary (0) areas using the generalized linear model (GLM) with the following formula:

$$g(\mu_i) = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \cdots + \beta_n x_{ni}$$

where $g(\mu_i)$ is the RSF, β_n is the coefficient for the *n*th predictive environmental variable x_n. The small sample size of subjects prevented modeling core and secondary areas of each panda individually.

Before building the model, all continuous variables were normalized. We first built a full variable generalized linear model based on logistic regression (exponential family distribution = 'binomial'), then obtained the optimal model among all possible combinations of environmental variables using the dredge function in 'MuMIn' package (Barto'n, 2019). Quadratic terms were also included in the models, and multiple interaction terms among habitat variables were also tested. We initially tested for multicollinearity among all possible variables using the variance inflation factor (VIF) using the vifstep function in 'usdm' package (Naimi, 2017) and then on the optimal model using the vif function in the 'car' package (Nilsson and Fox, 2019). VIF of all variables included in the final model were < 2 and thus below the recommended cut-off of 5 (Rogerson, 2001). We also plotted the relative probability of selection against each of predictors in the top model to show the direction of giant panda habitat preference for the microhabitat characteristics (Stabach et al., 2016). Model performance was evaluated based on Akaike Information Criteria (AIC) (Barto'n, 2019; Burnham et al., 2002). We used variable importance to evaluate the contribution of each factor to the model and the important values of variables in the model with ΔAIC < 4 were averaged (ΔAIC is the difference of AIC value from the top performing model). We set the significance level to 0.05 and all statistical analyses were conducted in R v3.4.0 (R Development Core Team 2013).

3. Results

3.1. Core and secondary home range areas

Giant panda home ranges spanned 1.28 to 4.07 km^2 for the period of study, with a total aggregated area of 10.41 km^2 (Table 3). Core areas ranged from 0.27 to 0.72 km^2 and secondary areas ranged from 1.01 to 3.35 km^2, aggregating to 2.07 km^2 and 8.34 km^2, respectively (Fig. 2, Table 3). Because giant panda home ranges overlap, the aggregates are less than the sum of individual values.

Table 3
Home range (and component core and secondary areas) among 5 giant pandas. Core area: 50% kernel density area, secondary area: 50–95% kernel density area.

Name	Area (km^2)		
	Core area	Secondary area	Home range
Panpan	0.27	1.01	1.28
Longlong	0.22	1.35	1.57
Meimei	0.48	2.04	2.52
Zhongzhong	0.51	2.47	2.98
Chuanchuan	0.72	3.35	4.07
Aggregated area	**2.07**	**8.34**	**10.41**

3.2. Microhabitat differences between the core and secondary areas

A total of 14 habitat characteristics, including 7 bamboo structure attributes were significantly different between the aggregated core and secondary areas ($P < 0.05$, Table 4). Core areas were found in higher elevations, closer to animal paths, and in areas with lower tree height, lower tree diameter at breast height, lower height under tree branches, and higher shrub coverage compared to secondary areas. Core areas also had greater numbers of bamboo shoots, young bamboo culms, adult bamboo culms, and dead bamboo culms than secondary areas. Smaller basal diameters of bamboos of all ages were also seen in the core areas compared to the secondary areas.

3.3. Habitat selection in the home range

The best model predicting differences between core areas and secondary areas included eight factors: elevation, distance to animal path, forest age, height of trees, height of bamboo shoots and numbers of young bamboo, adult bamboo, and dead bamboo. Of these variables, all but height of bamboo shoots and forest age were significant ($P < 0.05$, Table 5). Lower ranking models with ΔAIC < 1 (n = 5) are listed in Appendix 1.

The most important factors in the model were distance to path and number of adult bamboos (Importance value = 1.00), followed by height of trees (0.98), number of dead bamboos (0.97), elevation (0.86), and number of young bamboos (0.84) (Table 5). Compared with secondary areas, core areas had higher elevation, were closer to animal paths, had higher tree height, and had higher numbers of bamboo culms of all ages (Table 5, Fig. 3). In our study area, giant pandas are more willing to live in primary forests at high-altitude, choosing close to animal paths, lower trees and dense bamboo forests as their core active areas.

4. Discussion

Habitat selection is a complex process that involves numerous factors (Wei et al., 1998), and is dynamic in both spatial and temporal dimensions. The distribution of resources is heterogeneous across space and animals spend more time in a resource-rich area (Powell, 2000), which leads to differential intensity of use. Fine spatial scale analyses and detailed field investigations are the basis for research on animal microhabitat preferences. Studies on microhabitat selection within the home range are growing across species (Millspaugh et al., 2006). However, for some species, the work lags behind because it is difficult to integrate detailed undergrowth vegetation survey data with tracking data.

Many habitat selection studies on the giant panda using tracking data have focused on animal migration or space use while ignoring microhabitat characteristics (Zhang et al., 2015; Hull et al., 2016). Our study makes novel a contribution to understanding giant panda habitat selection by integrating GPS collar data with fine-scale habitat characterization for the first time. The novelty of our results for informing giant panda ecology and conservation support the value of investing in detailed microhabitat studies, an approach which can also be valuable for other species around the world whose microhabitat selection processes are understudied.

One of our findings worth noting was that slope was not a significant predictor of core versus secondary habitat use areas. Traditionally, slope is considered one of the most important habitat factors for giant pandas. It was believed that giant pandas prefer areas of lower slope to facilitate more energetically efficient travel (Hull et al., 2014; Liu et al., 1999; Yang et al., 2006; Ouyang et al., 2001). The most optimal slope range is considered to be < 15° (Liu et al., 1999; Ouyang et al., 2001), however, we found that giant pandas used habitat with steeper slopes (on average > 35°) in both their core and secondary home ranges. This could be due to the steep topography of

Table 4

Difference tests (t-tests) comparing habitat characteristics between core and secondary areas.

Habitat characteristics	Mean ± SD		t	P
	Core area (n = 134)	Secondary area (n = 114)		
Elevation (m)	2802.47 ± 175.01	2630.79 ± 250.98	−6.155	0.000*
Slope	35.02 ± 9.44	35.40 ± 11.09	0.292	0.771
Distance to animal path	265.47 ± 321.11	449.28 ± 357.55	4.231	0.000*
Distance to water	184.02 ± 195.21	190.41 ± 156.44	0.286	0.775
Vegetation coverage (%)	0.55 ± 0.19	0.59 ± 0.18	1.872	0.062
Number of trees	16.26 ± 6.99	15.45 ± 7.08	−0.905	0.366
Height of trees (m)	11.85 ± 3.56	13.95 ± 3.68	4.562	0.000*
Tree diameter at breast height (cm)	23.67 ± 8.02	27.83 ± 8.85	3.852	0.000*
Height under tree branches (m)	3.84 ± 1.83	4.73 ± 1.81	3.845	0.000*
Tree crown diameter (m)	3.32 ± 1.04	3.37 ± 0.92	0.407	0.684
Shrub coverage (%)	34.41 ± 19.85	28.22 ± 18.50	−2.539	0.012*
Number of shrubs	11.34 ± 4.52	10.31 ± 5.47	−1.605	0.110
Height of shrub (m)	2.60 ± 0.98	3.01 ± 1.27	2.812	0.005*
Shrub diameter at breast height (cm)	3.29 ± 1.63	3.42 ± 1.73	0.602	0.547
Bamboo coverage (%)	80.36 ± 14.85	74.62 ± 17.25	−2.787	0.006
Number of bamboo shoots	14.26 ± 6.95	8.05 ± 6.48	−7.279	0.000*
Basal diameter of bamboo shoots (mm)	4.66 ± 2.20	5.91 ± 2.97	3.724	0.000*
Height of bamboo shoots (cm)	92.87 ± 42.02	96.97 ± 56.48	0.641	0.523
Number of young bamboos	12.46 ± 6.43	9.59 ± 7.96	−3.095	0.002*
Basal diameter of young bamboo (mm)	4.50 ± 2.16	5.98 ± 3.30	4.125	0.000*
Height of young bamboo (cm)	108.73 ± 50.62	120.21 ± 64.81	1.536	0.126
Number of adult bamboos	58.84 ± 26.62	33.95 ± 23.42	−7.834	0.000*
Basal diameter of adult bamboo (mm)	4.67 ± 2.37	5.88 ± 3.09	3.419	0.001*
Height of adult bamboo (cm)	107.09 ± 45.91	120.14 ± 59.45	1.911	0.057
Number of dead bamboos	29.09 ± 13.44	18.15 ± 121.21	−6.715	0.000*

* Significant differences ($P < 0.05$).

Table 5

Parameter estimates of the optimal model ordered by importance value.

Factors	Importance	Estimate	Std. error	z value	Pr(> |z|)
Number of adult bamboos	1.00	0.738	0.226	3.262	0.001[a]
Distance to animal path	1.00	−0.481	0.178	−2.702	0.007[a]
Height of trees	0.98	−0.709	0.193	−3.674	0.000[a]
Number of dead bamboos	0.97	0.591	0.246	2.403	0.016[a]
Elevation	0.86	0.444	0.222	1.996	0.046[a]
Number of young bamboos	0.84	−0.401	0.204	−1.964	0.049[a]
Height of bamboo shoots	0.65	0.304	0.169	1.804	0.071
Forest age	0.47	−0.838	0.524	−1.598	0.110

[a] Significant contribution to the model.

the study area, and the fact that our field survey was conducted on a finer spatial scale (with respect to both grain and extent) compared with other studies. Our results suggest that giant pandas can adapt to steeper sloped habitat, and utilize more steep terrain than what has been commonly believed (Liu et al., 1999). This pattern is also supported by several recent studies conducted at broader spatial (Xu, 2006). This conclusion has profound significance for evaluating habitat suitability for giant pandas, as it suggests that the range of potentially suitable habitats considered in ecological modeling giant pandas should be expanded to include steeper areas in the future.

The significance of giant pandas selecting areas near animal paths was also interesting, particularly with respect to its high importance in the habitat selection model, as this variable is not often included in panda habitat selection analyses. This finding fits with what is known about giant panda ecology, as pandas have a tight energy budget as obligate bamboo foragers and should seek out opportunities to travel and forage along least-cost pathways in the dense vegetation and steep slopes (Hu and Schaller, 1985; Liu et al., 1999). The significance of elevation in our results was expected, as pandas spend more of their time at higher elevations throughout the year in Wolong due to foraging on the higher elevation arrow bamboo (Bai et al., 2017).

The study area where we tracked our 5 giant pandas has widespread bamboo understory. Therefore, we decided to omit the presence and

absence of bamboo as a variable and focus our effort on measuring the fine-scale characteristics of the bamboo structure. After accounting for other environmental variables, the average number of adult and dead bamboos was positively correlated with core home range selection, whereas the average number of young bamboos showed negative correlations with core area selection. The results might seem counter-intuitive but in fact are expected since giant pandas heavily use dense bamboo forests characterized by a large number of adult and dead bamboo (Hu, 2001). The significance of the number of bamboo culms in the models is also in line with previous research on giant panda habitat selection (Bai et al., 2018; Z. Zhang et al., 2011). However, we did not find significant effects for bamboo cover, a variable that is often used in coarse-scale studies on panda habitat selection. We attribute this to the fact that most of our study area (and giant panda home ranges) has high bamboo cover. Some studies have pointed out that giant pandas prefer moderate bamboo density to obtain greater energy gains, as sparse bamboo forest is not conducive to the food collection of giant pandas, and dense bamboo understory hinders movements of giant pandas (Hu, 2001). However, we did not observe this effect in our study area, possibly because there are more established wildlife paths distributed in the core home range area, which offsets the low accessibility associated with high bamboo density.

Our findings also support the observation that forest structure,
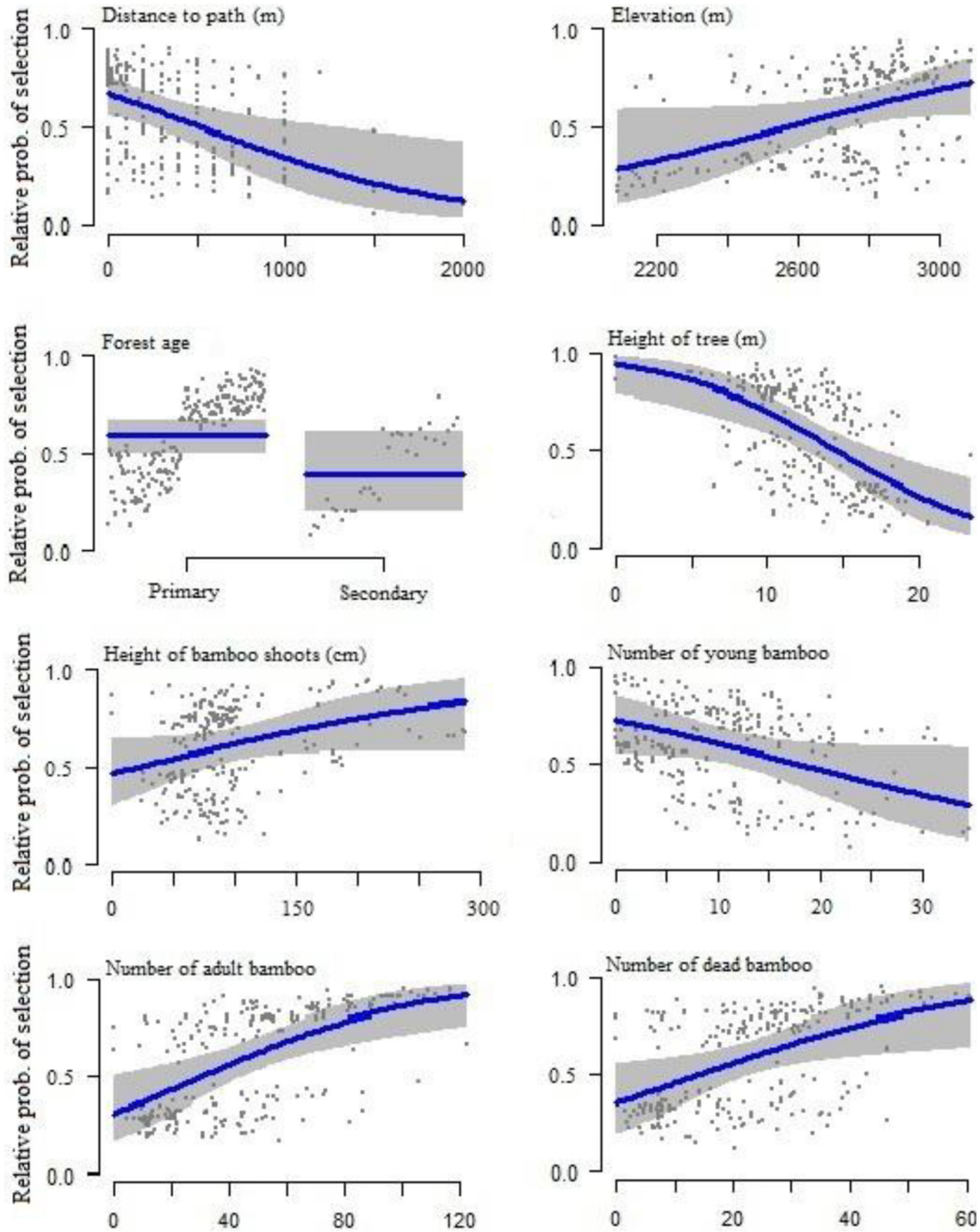
Fig. 3. Relative probability of selection for the factors in the optimal model.

particularly forest successional stage, are important factors in the habitat selection of giant pandas (Hull et al., 2014; Yang et al., 2006). Results showing that core areas had lower tree height and diameter than secondary areas, particularly with respect to tree height that had high importance in the models. We suspect that this finding is related to the fact that mixed forest was selected more strongly than coniferous forest (Z. Zhang et al., 2011) and coniferous trees in our study area are on average higher in height. Core areas also had higher primary (old-growth) forest, although the effect was not significant. This finding supports previous research conducted at larger scales, showing affinity towards the old-growth forest in Sichuan Province (Z. Zhang et al.,

2011).

It was also surprising that giant panda's core area had a higher shrub cover than the secondary area used less often by pandas. The distribution of shrubs is generally considered to have a negative impact on the habitat selection of giant pandas, as dense shrubs can compete with bamboo for resources and impede the passage of giant pandas (Hu, 2001). This finding could be related to the fact that core areas had better overall native vegetation structure including tall trees, shrubs, and lush bamboo compared to secondary areas in our study region. It appears that the shrub structure itself was not as important in influencing panda selection compared to other interrelated habitat

characteristics. Our findings highlight the complexity of these relationships and suggest that more research is needed in the future to better understand the local factors that contribute to competition in the forest understory across heterogeneous space in panda habitat.

Our findings highlight the importance of considering the relative significance of various habitat characteristics that may collectively impact giant panda habitat selection, and also illustrate the need to distinguish among variables that may be acting at different spatial scales. For instance, coarse-scale variables such as distance to paved road, forest cover, or bamboo cover, have been shown to be useful for identifying suitable panda habitat in past research, but finer scale variables, such as access to animal paths or bamboo density, maybe more important for managers to consider at the local scale when they are prioritizing areas to conserve because they support more frequent use by individual giant pandas. Future work should focus on distinguishing among the complex interactions among forest structure, bamboo growing patterns, and giant panda habitat selection by assessing larger cohorts of tracked individuals over longer time frames to further our understanding of habitat selection by this elusive species.

Our study has strong management implications for conservation planning for giant pandas. We recommend that areas that have steep slopes should not be excluded from new protected area planning and corridor designs simply because of this one feature, especially if the forest structure is sound and bamboo density is moderate to high. We also recommend that areas containing animal paths could be particularly important for corridor planning and should be prioritized in such efforts. Our study also supports the value of research on microhabitat selection patterns that can provide novel information to inform wildlife conservation and management, an approach that can also be valuable for other species worldwide.

Author contribution

Wenke Bai: Investigation, Data curation, Writing – original draft. **Qiongyu Huang**: Writing - review & editing. **Jindong Zhang**: Conceptualization, Writing - review & editing. **Jared Stabach**: Methodology, Software. **Jinyan Huang**: Investigation. **Hongbo Yang**: Methodology. **Melissa Songer**: Writing - review & editing. **Thomas Connor**: Investigation. **Jianguo Liu**: Writing - review & editing. **Shiqiang Zhou**: Resources. **Hemin Zhang**: Resources. **Caiquan Zhou**: Conceptualization, Writing - review & editing. **Vanessa Hull**: Conceptualization, Writing - review & editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 1. Model construction of the top logistic regression model sets (ΔAIC < 1)

Model number	Model construction	K	AIC	ΔAIC
46440	Elevation, distance to path, forest origin, height of tree, height of bamboo shoot, number of young bamboo, number of adult bamboo, number of dead bamboo	9	262.80	0.00
48488	Elevation, distance to path, forest origin, height of tree, height of branches, height of bamboo shoot, number of adult bamboo, number of dead bamboo, number of young bamboo	10	263.28	0.48
46376	Elevation, distance to path, height of tree, height of bamboo shoot, number of adult bamboo, number of dead bamboo, number of young bamboo	8	263.35	0.55
48424	Elevation, distance to path, height of tree, height of branches, height of bamboo shoot, number of adult bamboo, number of dead bamboo, number of young bamboo	9	263.49	0.69
111976	Elevation, distance to path, forest origin, height of tree, shrub coverage, height of bamboo shoot, number of young bamboo, number of adult bamboo, number of dead bamboo	10	263.77	0.97

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