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Hunting bamboo: Foraging patch selection and utilization by giant pandas and implications for conservation

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ABSTRACT

Food resources are patchily distributed in the environment and carnivores and herbivores have adopted different foraging strategies to maximize feeding efficiency. One interesting strategy is that of the giant panda, a member of the Carnivora that has evolved into a bamboo specialist. Giant pandas forage discriminately, but it remains unknown how nutritional hierarchical levels and landscape configuration heterogeneity affect foraging patch selection. Here, we used global positioning system collars to track wild giant pandas at high resolution (<10 m) and sampled foraging patches for nutritional hierarchical level analysis. We predicted that giant pandas select foraging patches with microhabitat characteristics that decrease energy expenditure during foraging according to optimal search theory. We introduce the concept of nutrient load as the product of local patch nutrient concentration and predicted that relatively efficient nutrients in fluctuating nutritional environments may determine foraging patch selection in giant pandas. This is the first time that microhabitat characteristics, key nutrients and foraging behavior have been studied in combination in giant pandas. We used random forest (RF) and generalized linear mixed-effects models (GLMMs) to infer habitat and nutritional factors that may influence foraging patch selection and utilization. Our results reveal that giant pandas select foraging patches with a topography that likely decreases energy expenditure. Giant pandas also favor protein-rich foraging patches, probably because protein can be digested and assimilated faster than cellulose and this maximizes net energy gains. These data provide a new perspective on foraging patch selection strategies in heterogeneous habitats of diet-specialized species under constant nutritional challenge. Improved conservation planning can be undertaken according to our findings.

1. Introduction

The food resources foraged by most animals are patchy and dispersed (Kohler, 1984; Kotliar and Wiens, 1990) and animals need to adopt distinct foraging strategies that maximize feeding efficiency in patchy habitats (Illius et al., 1999; Wilmshurst et al., 2000; Weimerskirch et al., 2007). For example, predators generally seek spatially scattered prey of high nutritional value; prefer particular trophic level prey if it is more profitable; exploit prey in a more efficient body mass range; and maximize handling efficiency and capture success (Robinson and Wilson, 1998; Svanback and Bolnick, 2005; Brose, 2010; Schneider et al., 2012; Tim Tinker et al., 2012). Large herbivores face entirely different nutritional challenges since nutritive quality of their food resources varies so much in heterogeneous environments (Sterner, 1993; Sterner and Hessen, 1994; Elser et al., 2000). Therefore, herbivores should forage in patches with relatively high harvestable food biomass, digestible energy and nutrient content, digestion rate, and low plant secondary metabolites (Robbins, 1983; Lima and Valone, 1986; Spalinger and Hobbs, 1992; Gross et al., 1993; Terry et al., 2000; Fryxell, 2008; Pretorius et al., 2011).

The giant panda (*Ailuropoda melanoleuca*) is an endangered species in the order Carnivora with a highly specialized bamboo diet and long evolutionary history (Zhao et al., 2013). Bamboo is a poor quality food source with low nutrients and high fiber content (Schaller et al., 1985; Wei et al., 1999); however, the giant panda lacks the long digestive tract of typical herbivores and extensive gut-based fermentation of bamboo is impossible (Dierenfeld et al., 1982; Wei et al., 2012). Giant pandas must therefore solve this nutritional limitation and net energy deficit through foraging strategy. For example, the giant panda is known to select more

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nutritious bamboo species and parts such as shoots and young leaves to maximize feeding efficiency (Schaller et al., 1985; Wei et al., 2015). Giant pandas also possess cellulose-digesting microbes to aid in the digestion of cellulose in bamboo (Zhu et al., 2011).

Bamboo is an abundant food resource but is distributed patchily. The abundance and quality of understory bamboo are critical components affecting the spatial distribution and survival of giant pandas (Linderman et al., 2005; Zhang et al., 2011). Some bamboo patches are used by giant pandas for several days or repeatedly used in different months, some are used for 1–2 days, and some patches are never used (Zhang et al., 2009). While we have some understanding of giant panda habitat use, we have been unable to accurately locate key foraging patches or understand differences in foraging patch selection and utilization because of technological limitations. However, with rapid advances in the functionality and operability of global positioning system (GPS) telemetry, it is now possible to precisely and quantitatively analyze spatial behavior and patch selection of free-ranging wildlife at fine spatial scales (Tomkiewicz et al., 2010; Middleton et al., 2013; Hays et al., 2014). Here we used high frequency GPS/VHF radio collars, and extensive habitat sampling, to determine aspects of giant panda foraging patch utilization at the individual level and at a fine spatial scale. We conducted diet nutritional analysis and measured microhabitat variables to explore potential factors affecting foraging patch selection by giant pandas. We then used these data to address the following two questions: (1) whether giant pandas are able to select foraging patches with microhabitat characteristics that decrease energy expenditure during foraging, and (2) whether giant pandas are able to select high nutritional quality patches in heterogeneous environment. This study aimed to explore the mechanisms behind foraging patch selection and utilization of a highly specialized species and aid its management and conservation, particularly since climate change is likely to shift bamboo distribution patterns (Tuanmu et al., 2013). This work will also contribute to our understanding of herbivore foraging optimization and adaptation to a nutritionally-challenged life history. Consequently, these data will improve conservation planning for giant pandas.

2. Material and methods

2.1. Study site

We conducted this study within Foping Nature Reserve, Shaanxi, China. The reserve was established for the preservation of giant pandas and contains the highest density of giant pandas in the word (SFA, 2006). The reserve is 293 km^2 and ranges 980–2904 m above sea level; the annual mean temperature is 11.5 °C. Within the reserve we focused on a 13 km^2 study area (Fig. 1).

The two bamboos *Bashania fargesii* and *Fargesia qinlingensis* grow at 1600–2400 m above sea level in the reserve. Giant pandas feed on *B. fargesii* at low elevations from September to May and *F. qinlingensis* at higher elevations from June to August in summer (Nie et al., 2015).

2.2. Giant panda monitoring

With approval from the State Forestry Administration in China, five wild giant pandas (three males and two females) were fitted with high frequency GPS/VHF radio collars (Lotek Wireless Inc., Ontario, Canada) (Table 1). These radio collars make it possible to locate giant pandas in bamboo patches and also recorded longitude, latitude and altitude.

Giant pandas spend approximately nine months feeding on *B. fargesii* at low elevations (hereafter termed 'winter habitat') and only move to higher elevations in summer (hereafter termed 'summer habitat') (Zhang et al., 2014; Nie et al., 2015). Our research focused on giant panda foraging patch selection strategies when feeding on *B. fargesii* at lower elevations from September to May. Each individual was collared and tracked for a different amount of time from 2010 to 2013 (Table 1). GPS locations used in this study are those at low elevations only, representing winter forage. This means we excluded GPS data from higher elevations recorded in summer and only considered the winter habitat foraging patch selection strategies of giant pandas.

The GPS collars were programed to collect location data every 3 h and we used a handheld command unit (Lotek Wireless Inc., Ontario, Canada) to download GPS data when within 100 m of a collared animal.

2.3. Habitat monitoring and foraging patch utilization

To assess foraging patch selection in giant pandas we compared the overall number of GPS data points for all individuals to a grid of 278 200 $\times$ 200 m foraging patches we established over the study area using the Spatial Analyst extension in ArcGIS v10.0 (Environmental Systems Research Institute Inc., Redlands, USA) (Fig. 1). We sampled all foraging patches on the ground from November to December 2011 and recorded 25 environmental variables in each foraging patch (definition and description of environmental variables provided in Supplementary Table A1) across five, equally distributed 1 $\times$ 1 m plots (Fig. 1). The sampling methods and selected variables followed Wei et al. (2000), which are often used to measure habitat selection in giant pandas. The recorded 25 variables represent and reflect almost all factors of microhabitat, forest-floor, vegetation, shrub, bamboo, food distribution and forage nutrient characteristics likely to affect selection of foraging patches by giant pandas. These measurements provide foraging patch information of greater detail and how giant pandas select favorable topography and optimal food resources in heterogeneous environments. Data across the five 1 $\times$ 1 m plots were averaged to provide a single value for each variable for each 200 $\times$ 200 m foraging patch. To determine bamboo nutritional quality we collected bamboo samples for nutritional analysis (Fig. 1) (Wei et al., 1999). We determined the content of crude protein and crude fat using Kjeldahl Nitrogen Determination and the Soxhlet Extraction Method, respectively (AOAC, 1980). For celluloses, hemi-celluloses and lignin analysis, we used the P. Van Soest detergent fiber method (Van Soest et al., 1991). We conducted soluble-carbohydrate determination using the Anthrone colorimetry method (Rondel et al., 2013).

To accurately characterize foraging patch utilization intensity of giant pandas within the study area, we compiled a new GIS landscape map by overlaying telemetry data and the environmental feature layer with 200 $\times$ 200 m sample grid cells across 278 points. This map shows total GPS location fixes for all tracked individuals occupied within each grid cell. The more location fixes in one grid cell, the more intensely this grid cell is utilized by giant pandas. All data were entered and mapped in ArcGIS 10.0.

Because a GPS location fix represents 3 h of giant panda activity, we assumed that the more GPS locations in a foraging patch, the more time the giant panda spent in that foraging patch (Table 1) and so 200 $\times$ 200 m foraging patches were divided into four categories (Table 2). Category 1 foraging patches were avoided entirely by giant pandas (no GPS location fix, giant panda do not utilize these); category 2 foraging patches were used rarely (1–10 GPS location fixes, giant panda utilized these for 3–30 h); category 3 foraging patches were used infrequently (10–100 GPS location fixes, giant panda utilized these for 30–300 h); and category 4 foraging patches were used frequently (more than 100 GPS location fixes, giant panda utilized these for more than 300 h).

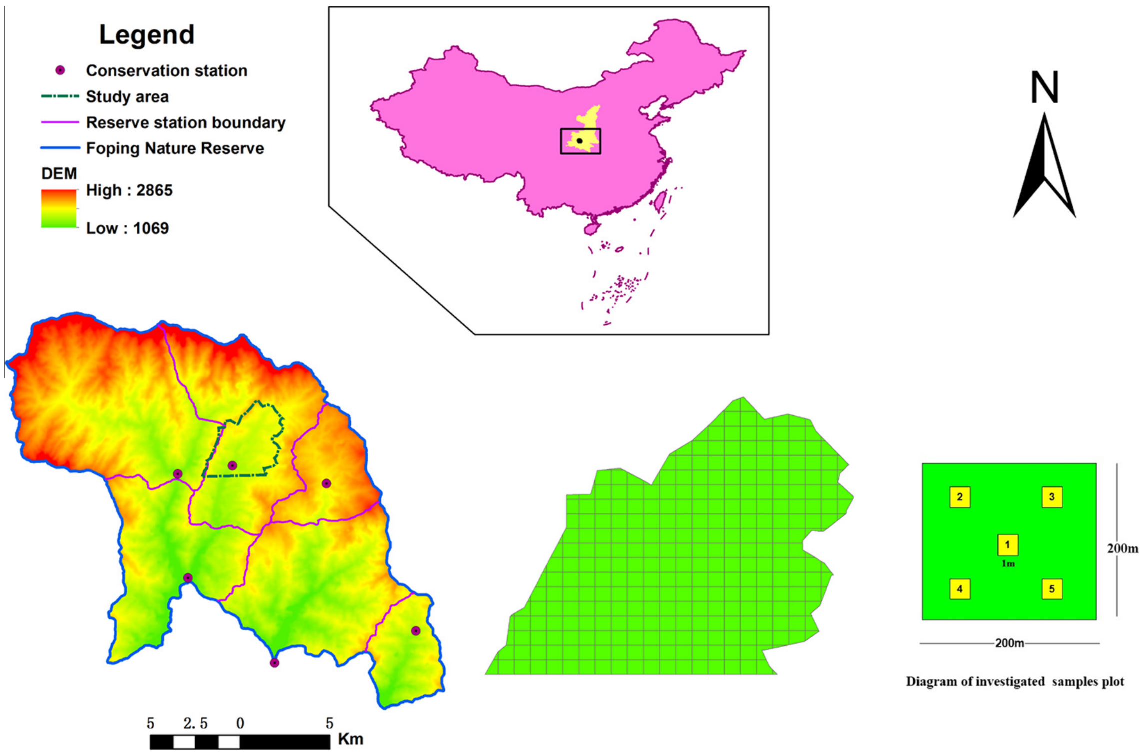

Fig. 1. Foping Nature Reserve, Shaanxi, China and our grid patch sampling design. Each 200 × 200 m patch contained five 1 × 1 m sample plots.

Table 1
Attributes of the five pandas tracked by GPS in Foping Reserve, China from 2010 to 2013.

Individual	Sex	Age	Tracked time	Tracked days	Total accurate GPS locations	Exclude error GPS locations	GPS fix rate (%)	Locations/Day
XY	Male	Adult	Nov 25 2010–Mar 3 2012	388	2535	569	81.67	6.5
XM	Female	Adult	Dec 25 2010–Mar 31 2012	326	2181	427	83.63	6.7
CC	Male	Adult	Mar 6 2011–Jan 31 2012	273	2001	183	91.62	7.3
NN	Female	Adult	Feb 26 2011–Mar 31 2012	254	772	1260	37.99	3.0
CY	Male	Adult	Apr 8 2012–Mar 14 2013	81	494	154	76.23	6.1

Table 2
Definition of patch use intensity and classification of hierarchical level.

Hierarchical level	1	2	3	4
Definition	No use	Low use	Use	High use
Number of GPS data points	0	1–10	11–100	101–585
Time (hours)	0	3–30	33–300	>303
Number of patches	47	105	109	17

2.4. Foraging patch selection modeling

Random forest (RF), a complex model of machine learning (Breiman, 2001a), was used to study the relationship between environment variables and patch utilization intensity. RF is an ensemble machine learning method for classification and regression that operates by constructing a multitude of decision trees. Decision tree is a popular method among various machine learning techniques. It is robust to inclusion of irrelevant features, and produces inspectable models (Hastie et al., 2008). Decision trees tend to learn highly irregular patterns, i.e. they overfit their training datasets. Random forest is a way of averaging multiple decision trees, trained on different parts of the same training dataset, with the goal of reducing the variance (Hastie et al., 2008). Random forest is appropriate for illustrating the nonlinear effect of variables, can handle complex interactions among variables, and is not affected by multicollinearity (Breiman, 2001b). RF provides all explanatory variable importance by measuring how much model performance declines if the variable is randomly permuted. The partial plot of the explanatory variables provided by the R package randomForest can give valuable information about the effect of explanatory variables. When the dependent variable is a continuous variable or count variable, the partial plot actually shows the predicted values (of the dependent variable) along the gradient of the explanatory variable. The plot is robust when there is no dominant interactions with this specific variable. We used all 25 explanatory variables in the RF model to explain utilization intensity of giant pandas in each grid cell, ranked the importance of these variables, and demonstrated the partial effects of these variables on patch selection intensity. In order to select the most representative variables in the next model analysis step, we used the following two criteria. (1) RF model is responsible for screening out more important variables within all explanatory variables; (2) for the remaining variables with correlation coefficients >0.5 we only retained those variables with a clear biological meaning. The specific process is that firstly we imported all 25 explanatory variables into the RF model, ranked the importance of these variables, and demonstrated the partial effects of these variables on foraging patch utilization intensity. Following this, we used Pearson's correlation (for normally distributed variables) or Spearman's correlation (for non-normally distributed variables) analyses to test the relevance between predictor variables. We rejected unimportant variables among foraging patches of different utilization intensity through RF screening and only retained variables of importance and clear biological meaning in subsequent analysis for those variables with a correlation coefficient above 0.5. We used a generalized linear mixed-effects models (GLMM) with an identity link and a Gaussian-error distribution to identify the effect of slope, slope aspect, canopy coverage, shrub cover, bamboo cover, bamboo density, open land proportion, crude protein, cellulose and nutritional quality ratio (crude protein/(celluloses + lignin)), represent quality of bamboo resources; Schaller et al., 1985) on foraging patch utilization intensity. To account for autocorrelation of vegetation type and bamboo succession state (old bamboo stands are replaced by new shoots and young bamboo stands), various vegetation types and bamboo succession states were included as single random effects and the rest of the variables were treated as fixed effects. Multimodel inference based on Akaike's information criterion (AIC) was used to evaluate the relative importance of each predictor variable (Burnham and Anderson, 2002). The global model set had all possible combinations of the ten predictor variables (total: $2^{10} - 1 = 1023$ models), and these models were ranked. We estimated the relative importance of each explanatory variable by calculating AIC weights across all of the candidate models that included the variable under consideration. We listed the top 10 models (with the lowest AICc values) and retained models that were within 2 AIC units ($\Delta AIC \leqslant 2$) of the top models to be highly supported. We performed all statistical analyses in R v3.0.3 (R Development Core Team, 2012) and required the libraries *lme4* and *MuMIn* (Bartón, 2013; Bates et al., 2013).

2.5. Spatial 3D-analysis and multiply layer overlay

3D spatial analysis was performed by Kriging interpolating layers of microhabitat into a two-dimensional raster surface using the sampling grid microhabitat variance dataset in ArcGIS v10.0 (Environmental Systems Research Institute Inc., Redlands, USA). Bamboo nutritional quality profiles of each foraging patch were calculated by crude protein/cellulose + lignin, and were Kriging interpolated into a raster surface. The utilization intensity of each foraging patch by giant pandas was transformed into a three-dimensional vector surface through point density analysis, contour line analysis and smooth line processing in ArcGIS v10.0. Finally, we overlapped these layers to generate a three-dimensional synthesis maps of foraging patch selection mechanism for giant pandas using ArcScene v10.0 (Environmental Systems Research Institute Inc., Redlands, USA).

3. Results

Our giant pandas were tracked for an average of 264 days (±51.4 SE). Each tracked giant panda had a mean of 1597 (±405 SE) GPS locations; the mean number of excluded error GPS locations was 519 (±201 SE). The mean GPS fix rate was 74.3% (± 9.4% SE). The GPS fix rate of individual NN is a little low due to the use of an older series collar, but this would not affect subsequent results because its home range is more stable than others and most of its GPS locations were focused on the same grid cells (Table 1). Seventeen high use foraging patches where giant pandas spent more than 300 h were identified (more than 100 GPS location fixes), accounting for 6.12% of the total forage area; 109 normal use foraging patches were classified (10–30 GPS location fixes, 30–300 h spent here; 39.2% of the area foraged); 105 low use foraging patches where giant pandas spent less than 30 h were identified (1–10 GPS location fixes), accounting for 37.77% of the area foraged; and 47 foraging patches were not visited by giant pandas at all (no GPS location was found here), accounting for 16.91% of the study area (Fig. 2, Table 2).

According to RF analysis, cellulose and nutritional quality ratio were the most important variables and had a negative and positive

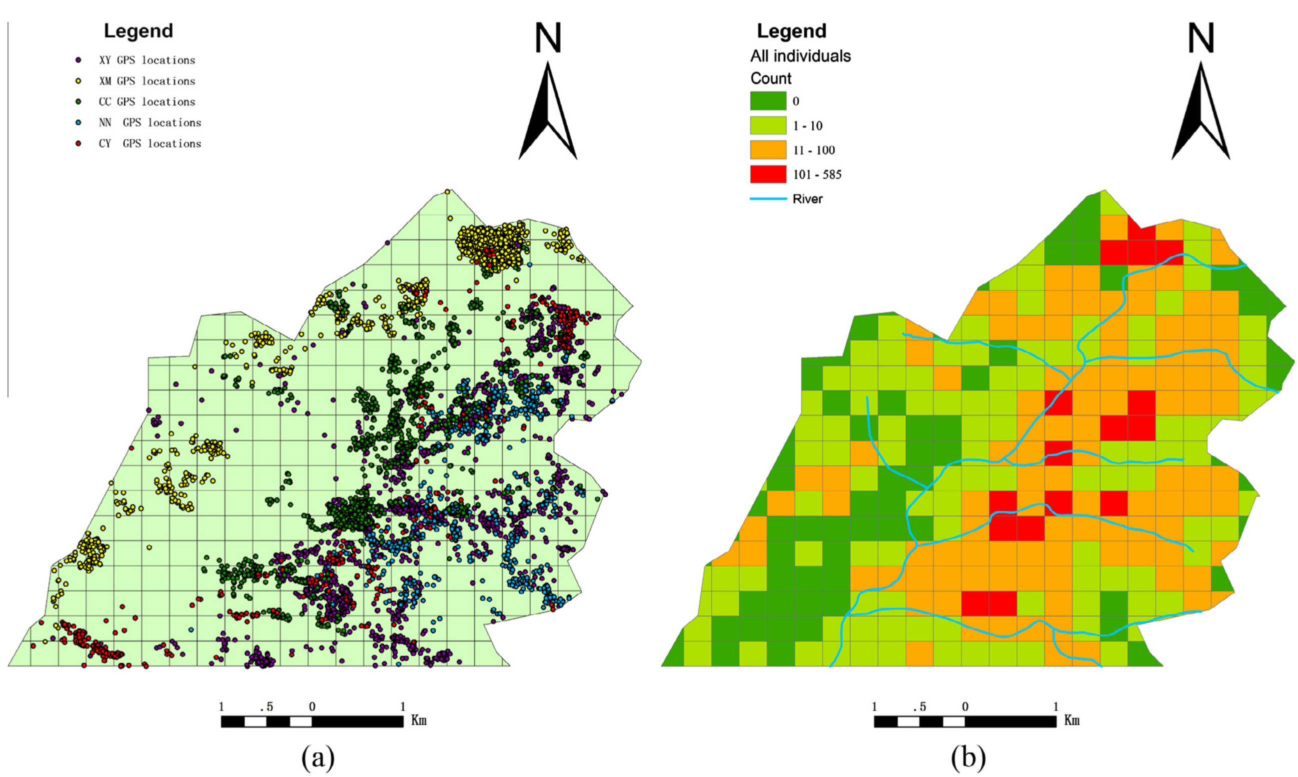

Fig. 2. (a) GPS collar locations of five giant pandas. (b) Utilization rate of all patches used by giant pandas.

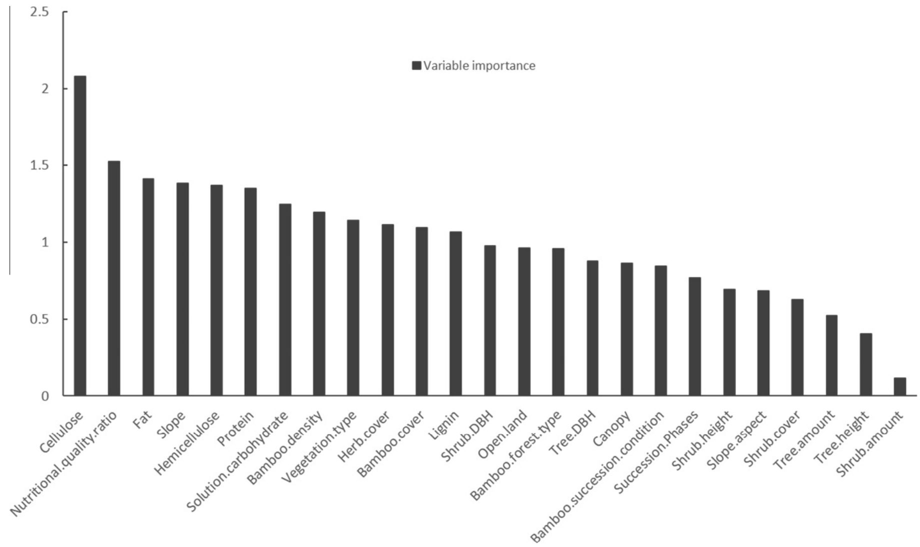

Fig. 3. Ranking variable importance associated with patch selection based on random forest analysis.

Table 3
The top ten generalized linear mixed-effects models (GLMM) for the effect of biotic and abiotic characteristics on selection intensity of various patches by giant pandas.

	1	2	3	4	5	6	7	8	9	10
Bamboo cover										
Bamboo density										
Canopy										
Cellulose	*	*	*	*	*	*	*	*	*	*
Crude protein	*	*	*	*	*	*			*	*
Nutritional quality ratio		*		*		*	*	*		
Slope	*	*			*	*	*			*
Open land										*
Slope aspect										
Shrub cover					*	*			*	
K	3	4	2	3	4	5	3	2	3	8
ΔAIC	0.00	0.28	1.39	1.44	2.13	2.65	3.28	4.67	4.75	4.80
AICc	538.6	538.9	540.0	540.0	540.7	541.2	541.9	543.3	543.3	543.4
Wi	0.21	0.18	0.10	0.10	0.07	0.05	0.04	0.02	0.02	0.02
R^2 marginal	0.45	0.45	0.44	0.44	0.46	0.46	0.45	0.44	0.45	0.45
R^2 conditional	0.45	0.45	0.44	0.44	0.46	0.46	0.46	0.44	0.45	0.46

Note: $*$, Indicates that a variable is included in the model; *K*, number of predictors in the model; ΔAIC, the difference between each model and the highest ranked model; AICc, Akaike's information criterion adjusted for small sample sizes; *Wi* (Akaike weights), the probability that a model is best given the particular set of models considered; R^2 marginal, amount of variation that is explained by fixed factors (covariates); R^2 conditional, amount of variation that is explained by both fixed and random factors. Models include vegetation type and bamboo succession condition as a random effect. Models are ranked in order of decreasing ΔAIC.

association respectively with foraging patch selection intensity. Fat, slope, crude protein and bamboo density followed in importance (Fig. 3, Supplementary material Table A4). Clear response curves for the correlation between the response variable and explanatory variables were obtained (Supplementary material, Figs. S1–S3).

According to GLMM analysis, the top 10 models included combinations of ten predictor variables. However, the top four models were the most supported (i.e. $\Delta AICc \leqslant 2$) and contained the four variables slope, crude protein, cellulose and nutritional quality ratio. In these four models, fixed factors (R^2 marginal) and random effects (R^2 conditional) both explained 45% of the variation in foraging patch utilization intensity. There was moderate model selection fit across the multi models set (*Wi* = 0.21, 0.18, 0.10 and 0.10 for the four top models) (Table 3).

The cellulose (relative importance value = 1.00), crude protein (0.91), slope (0.67) and nutritional quality ratio (0.52) were the most important predictors of foraging patch utilization intensity (Table 4); the 95% confidence intervals for cellulose, crude protein and slope only excluded zero. Foraging patch utilization intensity was positively related to nutritional quality ratio and crude protein

Table 4
Model averaging based on GLMMs (1024 models) using ten investigated variables, protein, cellulose, slope and nutritional quality ratio to explain patch selection intensity by giant pandas.

	β	SE	95% CI (lower, upper)	Relative important
Cellulose	**−10.48**	**0.81**	**−12.07, −8.90**	**1**
Crude protein	**2.38**	**0.83**	**0.75, 4.01**	**0.91**
Slope	**−0.48**	**0.22**	**−0.91, −0.04**	**0.67**
Nutritional quality ratio	**0.83**	**0.90**	**−0.93, 2.60**	**0.52**
Shrub cover	0.11	0.06	−0.01, 0.22	0.21
Open land	−0.06	0.04	−0.13, 0.01	0.1
Bamboo cover	0.04	0.04	−0.03, 0.11	0.05
Canopy	0	0.03	−0.07, 0.07	0.03
Bamboo density	0	0.01	−0.02, 0.01	0.01
Slope aspect	0	0.02	−0.04, 0.05	0

Note: Bold character indicate the best important variables through GLMMs screen in patch selection by giant pandas. β: model-averaged regression coefficients.

and negatively related to slope and cellulose (Table 4, Fig. 4). Our model results demonstrate that the nutritional quality of food resources is more important than quantity of food resources

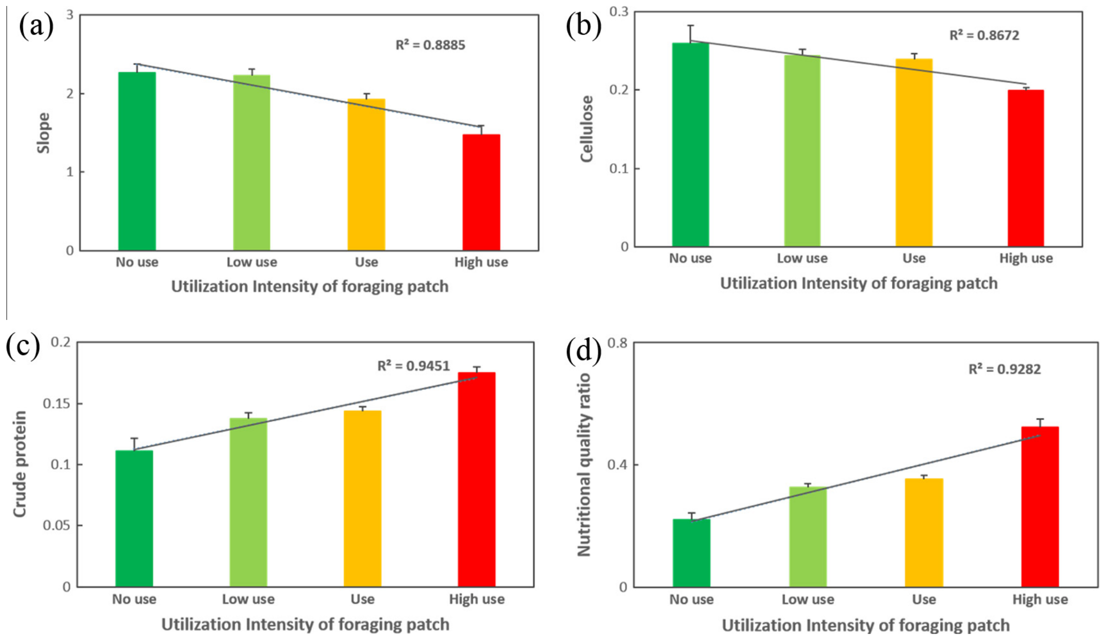

Fig. 4. The most important variables among all patches used by panda based on GLMMs analysis. (a) Slope; and (b) cellulose negatively correlated with all patches; (c) crude protein; and (d) nutritional quality ratio positively correlated with all patches.

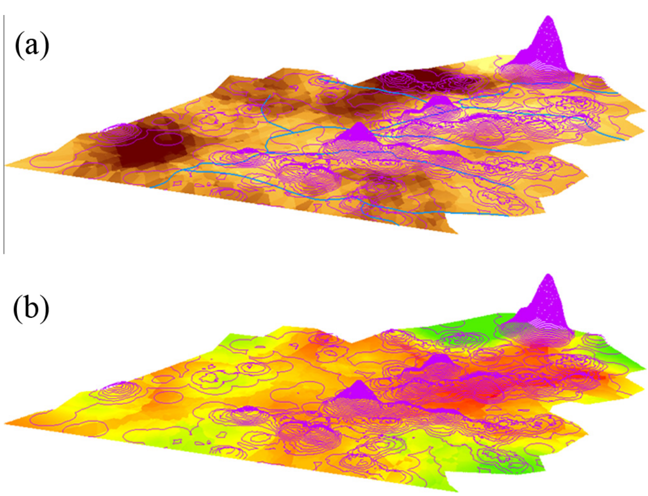

Fig. 5. 3D synthesis maps of patch selection mechanisms. Utilization intensity of each patch by giant pandas was transformed into a three-dimensional contour vector surface, thereby higher peaks indicate greater intensity of patch use. Layers of slope and nutritional quality profile (crude protein/cellulose + lignin) were Kriging interpolated into a two-dimensional raster surface. (a) Light gray areas have gentler slopes, are closer to a river or stream, and are more intensively utilized by giant pandas. (b) Crimson areas have a higher ratio of nutritional quality and are more intensively utilized by giant pandas.

(higher bamboo density and higher bamboo cover) and other microhabitat factors on foraging patch utilization by giant pandas (Fig. 3). The multiple layer overlapped GPS telemetry data, microhabitat landscape and nutritional profile and 3D-analysis also revealed that giant pandas select foraging patches which a higher nutritional quality and gentle slope based on analysis and calculation of RF and GLMMs (Fig. 5).

4. Discussion

As an obligate bamboo specialist, giant pandas must overcome nutritional challenges because of the poor quality of their primary food source. Giant pandas should forage in areas that optimize the benefits of resource harvesting and feeding and minimize nutritional and foraging barriers similar to other herbivores facing nutritional challenges (Bailey et al., 1996; Morris and Davidson, 2000; Ramp and Coulson, 2002; Zhang et al., 2004). Here, we found that giant pandas choose foraging patches with a gentle slope and that are close to water. Consistent with our prediction, a preference for gentle slopes by giant pandas has been widely regarded to reduce energy expenditure during searching, foraging and moving and free its fore-limbs to grasp bamboo culms when feeding (Schaller et al., 1985; Reid and Hu, 1991; Wei et al., 2000). This result supports the optimal search theory that giant pandas are able to select foraging patches with microhabitat characteristics that decrease energy expenditure during foraging. According to field observations, giant pandas drink water at least once a day (Schaller et al., 1985). Hence, a preference for proximity to a river or stream is likely because giant pandas must drink water in order to digest high fiber bamboo tissue that has a low water content and reduce energy expenditure during drinking (Zhang et al., 2014).

When selecting foraging patches, large herbivores face a tradeoff between food resource quality and abundance. For example, some species select foraging patches with the highest nutritional quality but low abundance (Distel et al., 1995; Olff et al., 2002; Durant et al., 2004). Our results also demonstrate that the nutritional quality of food resources is more important than the quantity of food resources. We found that utilized foraging patches by giant panda increased with increasing crude protein and nutritional quality and decreased with increasing cellulose (Table 4, Fig. 5b), indicative of a tradeoff when selecting foraging patches between protein and cellulose. Primary bamboo diet macronutrients are crude protein (15.69% DM) and total cellulose (celluloses, hemi-celluloses and lignin, 79.68% DM) and looking at foraging patch selection by giant pandas at a fine scale requires that available nutrients be expressed as total nutrient load per foraging patch grain. Crude protein and cellulose are the most abundant nutrient load for giant pandas and they can digest 90% of the crude protein in bamboo; however, the giant panda lacks the organs for digesting or fermenting cellulose like other typical herbivores or ruminants, and cellulose metabolism by them relies on their gut microbiome, hence they only can digest a little cytoderm (21% hemicellulose and 7% cellulose) (Dierenfeld et al., 1982; Schaller et al., 1985). Consequently, giant pandas actively seek more plant protein and avoid cellulose as crude protein is a more useful nutrition load than cellulose. Previous studies have demonstrated that giant pandas favor younger bamboo rather than old bamboo in the wild (Schaller et al., 1985; Zhang et al., 2009; Nie et al., 2015). Preferences for young bamboo are associated with high nutritional quality as younger bamboo has higher protein and lower cellulose than old bamboo (Schaller et al., 1985; Sun et al., 2010). This pattern is expected given that foraging efficiency relies on a greater benefit nutrition load from minimal foraging effort (time and/or energy expenditure) (Langvatn and Hanley, 1993) and that local nutrient load between patches can vary widely (Fryxell, 2008). For example, plant protein (N) content plays the most predominant role in the food preferences of many herbivores (Wallisdevries, 1996; Ritchie, 2000; Sheppard et al., 2007). In response to selection pressures, herbivore performance is generally positively related to increasing high-N plant food or the supplementation of a plant diet with N-rich foods so as to maximize the average rate of resource harvest and feeding efficiency (Mutanga et al., 2004; Sheppard et al., 2010; Rothman et al., 2011; Raubenheimer et al., 2012). Given that bamboo is a low protein and high fiber food we believe that giant pandas select protein-rich foraging patches over cellulose-rich foraging patches in order to gain maximum nitrogen. This finding also supports the hypotheses that giant pandas are able to select high nutritional quality patches in a complex environment where food resources are distributed heterogeneously and nutritional quality levels are fluctuating.

However, previous work did not concentrate upon a fine spatial scale, and instead focused on a relatively larger spatial scale (Feng et al., 2009; Qi et al., 2012) or over a limited microhabitat scale (Zhang et al., 2009). Studies of habitat selection based on these scales put more emphasis on the landscape and topographic effects on foraging and movement of giant pandas, but did not clearly identify a strong association between nutritional hierarchical levels and heterogeneity of foraging landscape configuration with foraging patch selection by giant pandas. Because variation in the quality and quantity of forage resources is a prime driver of giant panda foraging behavior and habitat use, research lacking nutrient and energy measurements cannot reflect intrinsic mechanisms underlying foraging patch selection. In our approach, our aim was to construct a more comprehensive understanding of exactly how this large herbivore utilizes foraging habitat and so we explored giant panda behavior using nutrition load and optimal search theory. For the first time, we show that nutritional hierarchical levels and landscape configuration heterogeneity affect foraging patch selection in giant pandas and that they select foraging patches that decrease energy expenditure during foraging. These data contribute to herbivore forage patch selection mechanisms in heterogeneous habitats and have further specific implications for the management of giant pandas in the wild.

Small sample sizes are a persistent problem in ecology studies, the results of which often affect final inferences. The issue of small sample sizes is unavoidable in our research and we cannot eliminate this limitation by expanding the sample of wild giant pandas due to strict State Forestry Administration approval to fit five GPS/VHF radio collars only. However, we did use statistical methods suitable for small sample sizes as much as possible. Population censuses through molecular census and camera trapping techniques indicate about 13–15 individuals residing in our study area (Hu, Zheng, unpublished data). Although our GPS location data covers only five individuals, results based on this sample size can provide a relatively robust and reliable inference for foraging patch selection strategy by giant pandas.

With the development of GIS and GPS techniques, the approach adopted here demonstrates the efficacy of using these techniques to accurately quantify the distribution of bamboo resources, nutrient heterogeneity and foraging patch structure in giant pandas. The nutritional selection patterns revealed using these integrative methods will improve conservation programs by ensuring that key habitat is protected and managed from a foraging perspective. We now have a much better understanding of foraging patch selection spatially and temporally in this highly endangered species and conservation managers can use this information to re-design measures aimed at protecting high-quality habitat with high protein and low cellulose content.

Climate change is threatening understory bamboo and in turn the survival and health of giant pandas. For example, almost all of the bamboo forest in the study region may disappear by the end of the twenty-first century (Tuanmu et al., 2013). Given the importance of nutritional quality to giant panda foraging behavior and the role of understory bamboo, wildlife managers need to begin taking steps to ensure this crucial resource remains available under a changing climate.

Last, our findings have implications for habitat connectivity projects and translocations. For example, plans to establish corridors, new habitat and sites for relocations and translocations must consider high protein content, nutritional quality, gentle slopes, and proximity to water. In particular, the release of captive-reared animals should consider the feed supply ratio of high protein and low fiber.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.03.023.

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