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What determines selection and abandonment of a foraging patch by wild giant pandas (*Ailuropoda melanoleuca*) in winter?

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Abstract
Background, aim, and scope Foraging patches can be described as a nested hierarchy of aggregated resources, implying that study of foraging by wild animals should be directed across different spatial scales. However, almost all previous research on habitat selection by the giant panda has concentrated upon one scale. In this research, we carried out a field study to understand foraging patch selection by giant pandas in winter at both microhabitat and feeding site scales and, for the first time, attempted to understand how long it would stay at the feeding sites before moving on.
Materials and methods The field survey was conducted from November 2002 to March 2003 at Fengtongzhai Nature Reserve (102°48′–103°00′ E, 30°19′–30°47′ N), Baoxing County of Sichuan Province, China, to collect data in both microhabitat and control plots. The microhabitat plots were located by fresh feces or foraging traces left by giant pandas, and the control plots were established to reflect the environment. Within each microhabitat plot, one 1×1 m^2 plot was centralized at the center of each feeding site, in which numbers of old bamboos and old shoots, including eaten and uneaten, were counted, respectively.
Results The results showed that winter microhabitats selected by this species were characteristic of gentle slopes and high old-shoot proportions and that the latter was even higher at feeding sites. Two selection processes, namely, from the environment to microhabitats and from the latter to feeding sites, were found during this species' foraging patch utilization. Giant pandas preferred to eat old shoots to old bamboo at feeding sites in winter and did not leave unless old-shoot density fell to lower than the average in the environment.
Discussion Both microhabitats and feeding sites selected by giant pandas were characteristic of high old-shoot density, indicating that the preferred food item had a significant influence upon its foraging patch selection. The preference for gentle slopes by giant pandas was presumed to save energy in movement or reflect the need to sit and free its fore-limbs to grasp bamboo culms when feeding but also seemed to be correlated with an easier access to old shoots. The utilization of old shoots at feeding sites was assumed to help maximize energy or nutrient intake during their foraging.
Conclusions The difference between microhabitat plots and control plots and between microhabitats and feeding sites uncovered a continuous selection process from the environment via microhabitats to feeding sites. The utilization of old shoots at feeding sites was parallel to the marginal value theorem. The selection and abandonment of foraging patches by giant pandas was an optimal behavioral strategy adapted to their peculiar food with high cellulose and low protein.
Recommendations and perspectives Our results uncovered the importance of multiple scales in habitat selection research. To further understand the process of habitat selection, future research should pay more attention to resolve the question of how to locate foraging patches under dense bamboo forests by the giant panda, which was

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traditionally considered to have poor eyesight, although our research has answered what type of habitats the giant panda prefers and when to leave.

Keywords Feeding site · Fengtongzhai Nature Reserve · Giant panda (*Ailuropoda melanoleuca*) · Giving-up density · Marginal value theorem · Microhabitat · Old shoot · Winter

1 Background, aim, and scope

For most animals, food resources are not distributed evenly in the environment but patchily. A patch can be functionally defined as a discrete spatial unit differing from its surroundings in nature or appearance (Kotliar and Wiens 1990; Wiens 1976) or by a change in the rate of a process or behavior (Bailey et al. 1996; Senft et al. 1987; Sih 1980). For large herbivores, the foraging patches can usefully be described as a nested hierarchy of aggregated resources (Schaefer and Messier 1995; Senft et al. 1987), and the hierarchy theory provides a conceptual framework to direct the study of foraging by large herbivores across different spatial scales (O'Neill et al. 1986), for example, habitat selection, which was often cited as a spatial scale-dependent ecological process (Eloy et al. 2000; Gordon and Wittenberger 1991; Johnson 1980; Morris 1987, 1992).

Belonging to the order Carnivora, the giant panda (*Ailuropoda melanoleuca*) has been known for its vegetarian diet, for bamboo ingredients constitute more than 99% of its annual diet (Hu et al. 1985). Although little is known of its behavior and ecology in the wild, much effort has been made to learn about its habitat selection (Lindburg and Baragona 2004). However, most previous studies were only concentrated upon one spatial scale, either at microhabitat (Wei et al. 2000; Zhang et al. 2006) or at feeding site (Wei et al. 1996a, b, 1999). Here, we studied foraging patch selection by wild giant pandas in winter at both microhabitat and feeding site scales. Giant pandas have widely been considered to prefer to move on gentle slopes, and old shoots constitute their primary food source in winter (Hu et al. 1985; Reid and Hu 1991; Wei et al. 2000; Zhang et al. 2006). Thus, we predicted (1) that slopes and old shoots are both limiting factors significantly affecting their foraging patch selection in winter and (2) giant pandas would prefer to eat old shoots than old bamboos at feeding sites.

One of the central challenges in classical foraging theory is to attempt to explain how foragers respond to food distributed in patches, and patch departure decision is one of the components to this response, where foragers determine the amount of time to spend in a patch before moving on (Kate et al. 2005). The prevailing approach to predict departure decisions at the patch scale invokes the marginal value theorem, which predicts that foragers will depart from a single patch when their instantaneous rate of intake drops below the average rate of intake attainable in all patches (Charnov 1976; Kate et al. 2005). If giant pandas prefer to eat old shoots at feeding sites, we can predict (3) they will leave feeding sites when old-shoot density falls below the average in the environment.

2 Materials and methods

2.1 Study area

Our fieldwork occurred from November 2002 to March 2003 at Fengtongzhai Nature Reserve (102°48′–103°00′ E, 30°19′–30°47′ N), Baoxing County of Sichuan Province, China, with the approval of the wildlife authority, Sichuan Forestry Department. The reserve covers about 390 km^2 of rugged ridges and narrow valleys at elevations of 1,000–4,896 m. Our field research base was located in the core region (102°53′27.5″ E, 30°37′02.9″ N), with an area of about 20 km^2. Mean annual temperature, humidity, and rainfall are 5.9–7.2°C, 79–83%, and 730–1,300 mm, respectively. The highest mean daily temperature occurs in July, ranging from 15.1°C to 16.3°C, and the lowest in January, ranging from −4.0°C to 2.7°C (from Baoxing Weather Station, unpublished data).

As altitude increases, vegetation transitions occur from subtropical evergreen deciduous broad-leaved mixed forest to coniferous forest, then to shrub and grasslands at the highest elevation. Two bamboo species, *Yushania brevipaniculata* and *Bashania faberi* are dominant in the reserve, while the former occurs on the middle-lower part (about 1,500–2,600 m), and the latter on the middle-upper part (about 2,400–3,300 m) of the hillside. Some variables (bamboo density, canopy, etc.) vary greatly among bamboo species during different seasons and, since giant pandas spend most of their time in *B. faberi* bamboo forests, we focused our fieldwork in this bamboo forest in winter.

2.2 Foraging patch selection at microhabitat scale

Giant pandas live in mountainous terrain covered by dense forests, making direct observations difficult. Their microhabitats were usually identified through feces left in the environment, which has been confirmed to be an effective index (Reid and Hu 1991; Wei et al. 2000; Zhang et al. 2004, 2006).

We compared microhabitat plots (20×20 m^2) and control plots (20×20 m^2), reflecting the environment at large, to investigate foraging patch selection at the microhabitat scale. Microhabitat plots were centered on fresh fecal deposits randomly found in the field (Wei et al.

2000; Zhang et al. 2006), with an average distance not less than 100 m between them. To establish control plots, we first randomly located points on the ridges in our study area which were equally distant from each other and then established eight transects from these points. Transects were oriented downslope, and control plots were established at about every 80-m loss in elevation and sampled similarly to microhabitat plots. In each 20×20 m^2 plot, another two independent sampling units were built, including one 1×1 m^2 plot and two 20 m^2 rectangular transects (each 2×10 m^2; Wei et al. 2000), and both were centralized on the fecal location (for microhabitat plots) or the center (for control plots). In addition, at the center of each 100 m^2 square plot, an additional 1×1 m^2 plot was sampled in a 20×20 m^2 plot. Fifteen variables were measured (Table 1).

2.3 Selection and utilization at feeding sites

Shoots of *B. faberi* in their first year of growth, from autumn to spring of the next year, are called old shoots (Hu et al. 1985). Old shoots have some features making them easily distinguishable from old bamboo (more than 1 year old), including (1) usually no branches on the culm, (2) only one to three leaves on top of each culm, and (3) sheaths on the basal node intact and not stained.

Within each microhabitat plot, we carefully searched for feeding sites where the giant panda took in food. A feeding site is defined as a small area where the giant panda is assumed to reach its food items without moving on. One 1×1 m^2 plot was centralized at the center of each feeding site in which the numbers of old bamboos and old shoots, including eaten and uneaten, were counted respectively. When giant pandas eat old shoots, only middle parts are ingested, leaving rooted stems from several to tens of centimeters in length and the upper parts abandoned in the environment (Hu et al. 1985), allowing us to count old shoots eaten at feeding sites.

2.4 Data analysis

We conducted independent samples *t* tests to compare variables between microhabitat and control plots when data were normally distributed and Mann–Whitney *U* tests when the distributional assumptions were not met. Only variables with significant difference between these two types of plots were involved in subsequent analyses. Because multicollinearity will either inflate or reduce the contribution of predictor variables (Liang and Thomson 1994), only the variable with clear biological meaning was entered into subsequent logistic regression analysis for those with a correlation coefficient above 0.50 (Fabrizio et al. 2003; Sebastien et al. 2003). The χ^2 test was adopted to test whether giant pandas preferred to eat old shoots rather than old bamboos at feeding sites. In the end, we compared the paired difference of old-shoot density in control plots, microhabitat plots, and feeding sites before and after foraging through independent samples *t* tests.

The significance level was set at 0.05.

Table 1 Description and definition of variables in research

Variables	Description
Vegetation type	Six categories: mixed evergreen and deciduous broad-leaved forest, mixed coniferous and broad-leaved forest, coniferous forest, shrub, grassland, and open land
Slope	Eight grades, including 0–10°, 10–20°, 20–30°, 30–40°, 40–50°, 50–60°, 60–70°, and ≥70°
Slope aspect	Aspect of each 20×20 m^2 plot, defined by four categories: eastern slope (45–135°), southern slope (135–225°), western slope (225–315°), and northern slope (315–45°)
Canopy	Canopy of overstory in each 20×20 m^2 plot, divided into four categories: <25%, 25–50%, 50–75%, and ≥75%
Bamboo density (culms/m^2)	Average number of culms in five 1.0-m^2 bamboo plots
Bamboo height (cm)	Average height of culms in five 1.0-m^2 bamboo plots (five culms are measured randomly at each plot)
Old-shoot proportion (%)	Average proportion of old shoots in five 1.0-m^2 bamboo plots
Tree density	Average number of trees in two 20-m^2 rectangular transects in 20×20 m^2 plot
Tree size (cm)	Average breast height diameter (DBH) of trees in each 100-m^2 square plot nearest to the center of 400-m^2 plot
Tree dispersion (m)	Average distance of the nearest tree to the center in each 100-m^2 square plot
Shrub density	Average number of shrubs in two 20-m^2 rectangular transects in 20×20 m^2 plot
Shrub size (cm)	Average DBH of shrubs in each 100-m^2 square plot nearest to the center of 400-m^2 plot
Shrub dispersion (m)	Average distance of the nearest shrub to the center in each 100-m^2 square plot
Tree stump density	Average number of tree stumps (>15 cm in diameter) in each 100-m^2 square plot
Fallen log density	Average number of fallen logs (>15 cm in diameter) in each 100-m^2 square plot

3 Results

Fifty microhabitat plots, 50 control plots, and 105 feeding sites were sampled in the field. The mean for each variable differed to some extent between microhabitat and control plots (Table 2). However, only six variables were significantly different. Compared with control plots, the slope was flatter, and bamboo density, bamboo height, old-shoot proportion, tree size, and shrub size were larger in microhabitat plots (see Table 2).

Among these six variables, with a significant difference between microhabitat and control plots, no correlation coefficient exceeded 0.5, and thus, all of them were entered into the logistic regression analysis. Only slope and old-shoot proportion made a significantly greater contribution to differentiating microhabitat plots from control plots (G^2= 73.37, df=6, P=0.00; Table 3), with an overall correct prediction rate of 80.4%.

Compared with microhabitat plots, old-shoot density at feeding sites was significantly higher (10.82±4.45 vs. 18.13± 8.96 culm/m^2, t=−6.76, P=0.00; Fig. 1). Although giant pandas ate a small amount of old bamboos at feeding sites, they preferred old shoots significantly (χ^2=41.09, P=0.00; Fig. 2).

Old-shoot density was decreased to 4.09±3.74 culm/m^2 after foraging at the feeding sites, significantly lower than that before foraging (t=14.75, P=0.00), indicating the excessive foraging by the giant panda found there (see Figs. 1 and 2). Old-shoot density at the feeding sites after foraging was also significantly lower than that in control plots (4.09±3.74 vs. 5.62±4.74 culm/m^2, t=2.01, P=0.048; see Fig. 1).

4 Discussions

Six variables were significantly different between microhabitat and control plots (see Table 2), and old-shoot proportion at feeding sites was higher than that in microhabitat plots, indicating that both microhabitats and feeding sites were distinctive foraging patches selected by giant pandas functionally in our study area. However, once eliminating the potential collinearity among variables, microhabitats selected by the giant panda in winter were only characteristic of gentle slope and high old-shoot proportions, parallel to what was found in Wolong Nature Reserve where feces left by giant pandas were more often found on gentle slopes and primarily composed of stem fragments of old shoots (Hu et al. 1985; Reid and Hu 1991). Interestingly, slope gradient is also an important determinant of grazing distribution of large herbivores; for example, cattle generally avoid grazing slopes over 10% (Bailey et al. 1996; Cook 1966; Mueggler 1965).

Habitat selection is a continuum that was segregated into hierarchical levels, and analyzing habitat selection at multiple scales can allow for observation of influences that may be masked within a single-level analysis (Andrea et al. 2003; Johnson 1980). This research, different from most previous studies, concentrated on one spatial scale and uncovered two continuous processes during this species' foraging patch utilization: in the environment, the giant panda prefers microhabitats with gentle slopes and high old-shoot densities and, in microhabitats, it usually selects feeding sites with higher old shoots to forage.

Many factors can affect selection of foraging patches by wild animals, such as food distribution, intraspecific and

Table 2 Pair-wise comparisons for variables between microhabitat and control plots

Variables	Mean±SD		t or U	P
	Habitat plot	Control plot		
Vegetation type	2.14±0.88	2.38±0.92	1,067.50	0.17
Slope	2.34±1.04	4.14±1.60	448.00	0.00
Slope aspect	1.74±0.73	1.70±0.81	998.00	0.66
Canopy	1.98±0.89	2.26±1.05	1,070.00	0.19
Bamboo density	74.69±21.02	56.30±41.49	2.80	0.007
Bamboo height	96.65±18.58	75.80±24.45	4.59	0.00
Old-shoot proportion	14.97±6.20	8.80±4.81	5.56	0.00
Tree density	0.52±0.57	0.49±0.54	1,176.00	0.85
Tree size	48.33±16.65	37.85±14.80	3.24	0.002
Tree dispersion	6.28±2.15	6.46±1.85	−0.46	0.65
Shrub density	1.37±1.00	2.19±2.13	963.00	0.089
Shrub size	11.08±6.84	8.38±7.61	780.00	0.001
Shrub dispersion	4.42±1.54	4.44±1.81	−0.068	0.95
Tree stump density	0.30±0.30	0.38±0.36	1,110.50	0.32
Fallen log density	1.13±0.63	1.33±0.79	1,088.00	0.26

Table 3 Variables to distinguish microhabitat from control plots through logistic regression analysis

Variables	*B*	SE	Wald	Sig.
Slope	0.97	0.30	10.49	0.001
Old-shoot proportion	−0.22	0.077	8.48	0.004
Bamboo density	−0.016	0.011	2.13	0.15
Bamboo height	−0.013	0.014	0.81	0.37
Tree size	−0.023	0.02	1.37	0.24
Shrub size	0.015	0.038	0.16	0.69
Constant	2.76	2.02	1.85	0.17

B regression coefficient; *Sig.* significance value

interspecific competition, predation, body size, and so on (Daniel and Coulson 2002; Dave et al. 2003; Hemani et al. 2004; Zhang et al. 2004). At both microhabitat and feeding site scales, foraging patches selected by giant pandas were characteristic of high old-shoot densities (see Fig. 1), implying the influence of a preferred food item upon their foraging patch selection. A preference for gentle slopes by giant pandas is widely considered to correlate with energy saving in movement (Hu et al. 1985; Wei et al. 2000) or reflects the need to sit and free its fore-limbs to grasp bamboo culms when feeding (Reid and Hu 1991). This preference also seemed to be correlated with easier access to old shoots, for slope was significantly negatively correlated with old-shoot proportions below 70° (r=−0.94, P=0.005, unpublished data), and giant pandas significantly preferred old shoots than old bamboos at feeding sites (χ^2= 41.09, P=0.00; see Fig. 1).

Optimal foragers should leave a patch when the benefit obtained from foraging is balanced by the summed energetic costs, the risk of predation, and the cost associated with opportunities lost from other fitness-enhancing activities if they have evolved to maximize the

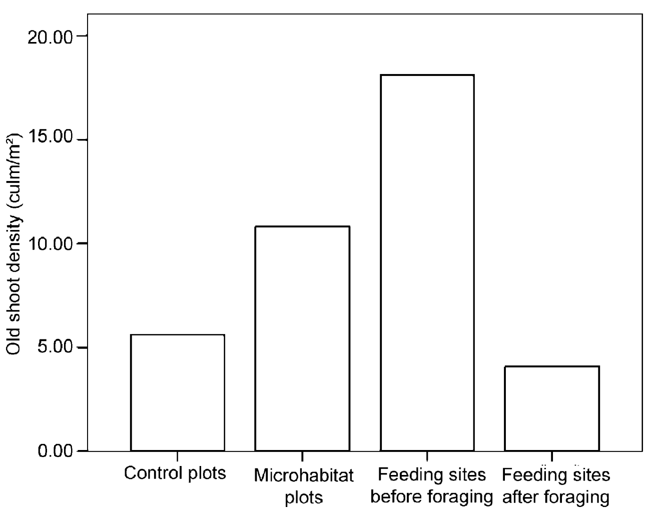

Fig. 1 Variation in old-shoot density during the process of foraging patch utilization

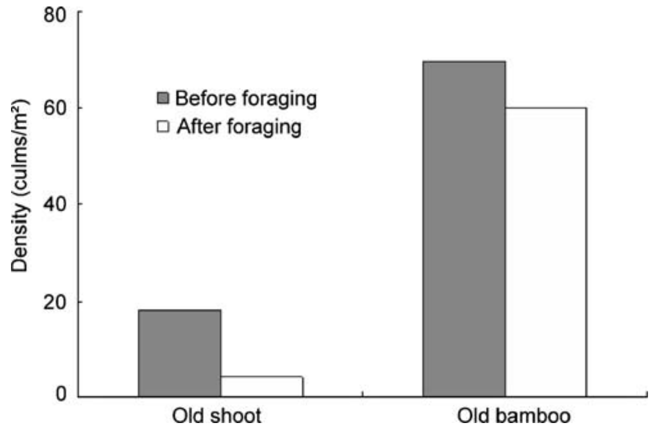

Fig. 2 Variation in density of old shoots and old bamboos before and after foraging at feeding sites (χ^2=41.09, P=0.00)

average rate of resource harvest (Brown 1988; Morris and Douglas 2000). Giving-up densities provides an accurate assessment of the quality of adjacent habitats and of the location within which the patch occurs (Morris and Douglas 2000). This research, for the first time, tried to determine when the giant panda would depart a feeding site through the giving-up density of old shoots, which was lower than the average in the environment (4.09±3.74 vs. 5.62±4.74 culm/m^2, P=0.048, see Fig. 1). As for foraging strategies, the giant panda seems to maximize the ingestion rate to meet its nutrient and energy demands from bamboo, which is widely considered low quality because of its low protein and high cellulose content (Hu et al. 1985). As such, a panda can eat 10–18 kg of fresh leaves or stems or about 40 kg of new shoots per day and spends more that 50% of the day foraging (Hu et al. 1985). During the process of foraging, old shoots will be depleted, and the density will be gradually decreased to approach the average in the environment. Giant pandas need not move to search for a new foraging patch unless the old-shoot density has decreased to below the average in the environment. This behavioral strategy can help avoid energy expenditure during movement and maximize energy or nutrient intake at feeding sites. The results described above were roughly in agreement with the prediction from the marginal value theorem.

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