NORTH-WESTERN JOURNAL OF ZOOLOGY 13 (1): 109-117
Article No.: e161701
©NwjZ, Oradea, Romania, 2017
http://biozoojournals.ro/nwjz/index.html

Microhabitat separation between giant panda and golden takin in the Qinling Mountains and implications for conservation

Wei WEI[1,2], You-You HUANG[1,2], Hong ZHOU[1,2], Shi-Bin YUAN[1,2], Zhi-Xin ZHOU[3,4], Yong-Gang NIE[5] and Ze-Jun ZHANG[1,2]*

1. Key Laboratory of Southwest China Wildlife Resources Conservation (Ministry of Education), China West Normal University, Nanchong 637002, China.
2. Institute of Rare Animals and Plants, China West Normal University, Nanchong 637009, Sichuan, China.
3. Guangdong Entomological Institute, Guangzhou 510260, Guangdong, China.
4. Guangdong Public Laboratory of Wild Animal Conservation and Utilization.
5. Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, hinese Academy of Sciences, Beijing 100101, China.
*Corresponding author, Z.J. Zhang, E-mail: zhangzj@ioz.ac.cn

Received: 03. December 2015 / Accepted: 30. March 2016 / Available online: 26. June 2016 / Printed: June 2016

Abstract. The giant panda (*Ailuropoda melanoleuca*) and golden takin (*Budorcas taxicolor bedfordi*) are large endangered species that coexist within the southern Qinling Mountains, China. Here, we determined the coexistence mechanisms for these sympatric species by investigating microhabitat selection from May to July and from September to November 2009 in a nature reserve. Our results suggested that each species has a distinct microhabitat selection pattern. We found that abiotic factors (elevation and slope) and biotic factors (bamboo cover, density and herb-cover proportion) are simultaneously responsible for microhabitat separation between giant pandas and golden takins during the summer and the winter. We inferred that pattern of microhabitat separation is influenced by diet, migration time, the annual phenological cycle of food resources, energy expenditure and metabolic requirements. Appropriate conservation strategies should not only focus on giant panda protection, but also be extended to encompass the protection of sympatric species. Our study has significant implications for biodiversity conservation across large tracts of China.

Key words: *Ailuropoda melanoleuca*, *Budorcas taxicolor bedfordi*, sympatric species, microhabitat separation, conservation implications.

Introduction

Ecologists have long been interested in the mechanisms that allow the coexistence of sympatric species (Schoener 1974, Diamond & Case 1986). Closely related sympatric species usually share similar potential niches or have similar life history traits. For example, how species compete for similar resources when distributed in overlapping areas or how they avoid competition remain challenging questions. Previously, researchers have attempted to explain the coexistence mechanisms of species through the measurement of abiotic and biotic factors (Werner 1977, Gotelli 1997, Qi et al. 2009).

Giant pandas (*Ailuropoda melanoleuca*) and golden takins (*Budorcas taxicolor bedfordi*) are endangered species and sympatric within the southern part of the Qinling Mountains in China (Wu et al. 1990, IUCN 2007, Wang et al. 2010, Zhang et al. 2011, Li et al. 2017). Previous studies have indicated that these species suffer similar environmental pressures and barriers to genetic flow because of habitat loss and fragmentation, poaching and inbreeding depression (Wei et al. 1999, Zeng et al. 2003, Wei et al. 2015b, Hong et al. 2015, Hong et al. 2016). The giant panda is a highly endangered species in the order Carnivora and with a highly specialized bamboo diet for which it has low digestive efficiency (Zhu et al. 2011, Zhao et al. 2013, Lei et al. 2015, Nie et al. 2015a, Wei et al. 2015a, Wei et al. 2015c). The golden takin is herbivorous with a broad diet that also includes bamboo leaves and shoots (Zeng et al. 2010). These two species may compete for similar food resources during some stages of their life histories. Further, both species engage in seasonal vertical movement in mixed bamboo forest landscapes. Thus, there should be overlapping niches (Wang et al. 2010). Distribution and diet overlap between these species raise the question of whether they share niches and resources via microhabitat partitioning. Previous studies have reported habitat selection and microhabitat utilization for these species in the Qinling Mountains (Song et al. 1995, Liu et al. 2005, Feng et al. 2009, Zhang et al. 2009). However, these studies failed to determine a relationship explaining microhabitat utilization between the two species and factors responsible for microhabitat separation at the microhabitat scale.

To improve our understanding of observed patterns of microhabitat separation between giant pandas and golden takins we investigated patterns of microhabitat preferences in these animals. We aimed to (1) verify whether each species has special microhabitat-selection patterns; (2) describe which factors are responsible for microhabitat separation; and (3) generate an effective strategy for protection of sympatric species and regional biodiversity.

Materials and methods

Study site

We conducted this study in Foping Nature Reserve, Shaanxi, China (Fig. 1). This reserve was established primarily for preserving giant pandas. This region contains the highest density of wild giant pandas in the world (population density = 76) (Administration 2006). The reserve covers 293 km² and the elevation ranges from 980 to 2,904 m above sea level. The annual mean temperature is 11.5°C. Annual mean rainfall is 930 mm and the first snowfall occurs in November on high ridges and about a month later descends to lower altitudes (< 1,500 m). Snow begins to melt in early March and is completely melted at higher ranges by late March. The population of golden takin was estimated at 435–527 individuals in 1996 (Zeng et al. 1998).

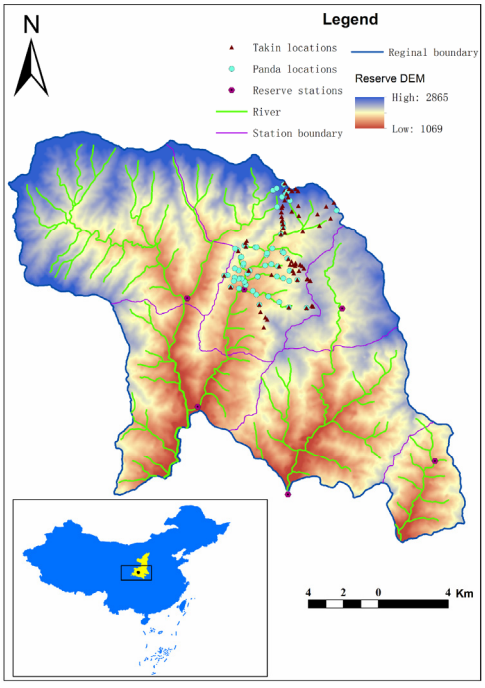

Figure 1. Giant panda and golden takin distribution locations acquired from feces in Foping Nature Reserve, DEM shown corresponds with elevation range in the study area

The distribution of vegetation in the study area shows characteristic vertical zonation, with four major forest types: broadleaf deciduous (below 2,000 m), mixed coniferous and deciduous (2,000–2,500 m), coniferous forests (above 2,500 m), and some interspersed subalpine shrubs and meadows at the top of the mountains (above 2,600 m) (Ren et al. 1998). Two bamboo species, *Bashania fargesii* (mean elevation 1,600 m) and *Fargesia qinlingensis* (mean 2,400 m), dominate the forest understory and are the main food resources for giant pandas.

Microhabitat identification

Both species are difficult to observe directly in the field, so feces can be used as an indicator of microhabitat utilization (Wei et al. 2000, Zhang et al. 2004, 2009). Giant panda feces are spindle-shaped (average length by width 14.5 cm × 5.0 cm) and blackish green; golden takin feces are black and resemble large shelled peanuts or fecal mound similar to cattle. Both species' feces are easy to identify and distinguish in the field.

Sampling design and variable measurement

A detailed sampling method firstly used by Dueser and Shugart (1978) considers diverse sizes and shapes and small transects together; which has been proved to be suitable for most terrestrial mammals (Morrison et al. 1992). This sampling method was later developed and modified by Wei et al. (2000) and applied to the research of microhabitat separation of giant pandas and red pandas (*Ailurus fulgens*).

We walked randomly through the habitats with different vegetation types within the reserve to search for signs of each species and fresh feces in 2009. The presence of giant panda and golden takin were determined primarily by fresh feces. Once a fresh fecal group was found, the following were established: a 20 m × 20 m sampling plot was built and centred on the fecal location; one 1.0 m² bamboo plot at the centre of each 20 m × 20 m plot; and two 20 m² rectangular transects (each 2 m × 10 m) were set within the 20 m × 20 m plot. The two 20 m² rectangular transects were perpendicular to each other, and their diagonals crossed at the location of the feces. Each side of the rectangular transect was parallel to the corresponding side of the 400 m² square plot (Wei et al. 2000, Zhang et al. 2004). The minimum distance among microhabitat plots was not less than 100 m. To establish control plots, we randomly located points on slopes in our study area, which were equally distant from each other, and established 15 transects from these points. Twenty-two microhabitat variables were measured (Table 1). In total, we had sampled 44 habitat plots of giant panda, 46 habitat plots of golden takin and 80 control plots, respectively, in the summer. Moreover, we had sampled 17 habitat plots of giant panda, 27 habitat plots of golden takin and 58 control plots in the winter.

Data analysis

We used the Kruskal-Wallis test to compare means for all 22 variables among the two species and control group.

Table 1. The variables used in this research.

Variables	Description
Altitude	Altitude of each 20 × 20 m plot
Slope	Slope of the 20 × 20 m plot range from 0° to 90°; divide into 6 categories: every 15° is a category; measured with a gradiometer
Slope aspect	Aspect of the each 20 × 20 m plot; divide into categories: towards east (45–135°), towards south (135–225°), towards west (225–315°), and towards north (315–45°)
Vegetation type	Six type: shrub, deciduous broadleaf forest, mixed conifer and broadleaf forest, conifer forest, grassland, and others
Canopy	Canopy of overstory in each 20 × 20 m plot, defined as 5 categories: <20%, 21–40%, 41–60%, 61–80% and >81%
Tree density (no./m2)	Total tree amount of each 20 × 20 m plot
Tree height (m)	Average height of trees in two 2 × 10 m rectangular transects plots; defined as 5 categories: 5–10 m, 11–15 m, 16–20 m, 21–25 m and >25 m
Tree diameter at breast height (DBH) (cm)	Average DBH of the trees nearest the center in each 10×10 m square plot
Succession phases	Successional changes in plant communities; five type: immature forest, bushwood, secondary forest, mature forest and old forest.
Shrub cover (%)	Coverage of shrub in each 20 × 20 m plot, divided into 5 categories: 0–20%, 21–40%, 41–60%, 61–80% and >81%
Shrub density (no./m2)	Total shrub amount of each 20 × 20 m plot
Shrub height (m)	Average height of shrubs in two 2 × 10 m rectangular transects plots; defined as 6 categories: <1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m and 5–6 m
Shrub DBH (cm)	Average DBH of the shrubs nearest the center in each 10 × 10 m square plot
Bamboo forest	Whether have large dense tracts of bamboo forest or not in the 20 × 20 m plot
Bamboo type	The species of bamboo in each 20 × 20 m plot, including B. fargesii and F. qinlingensis
Bamboo cover (%)	Average coverage of bamboo in five 1 × 1 m plot, divided into 5 categories: 0–20%, 21–40%, 41–60%, 61–80% and >81%
Bamboo density (no./m2)	Average number of culms in five 1 × 1 m bamboo plots
Bamboo height (m)	Average height of culms in five 1 × 1 m bamboo plots; defined as 6 categories: <1 m, 1–2 m, 2–3 m, 3–4 m, 4–5 m and 5–6 m
Herb-cover (%)	Proportion of herb-cover area in each 20 × 20 m plot; five categories: <20%, 21–40%, 41–60%, 61–80%, and >81%
Open-land proportion (%)	Proportion of vacant land area without any plant in each 20 × 20 m plot; five categories: <20%, 21%–40%,41%–60%, 61–80%, and >81%
Water-source dispersion (m)	Estimated straight-line distance from the sampling plot to the nearest water source; five categories: 0–100, 101–200, 201–300, 301–400 and >400
Road-path dispersion (m)	Estimated straight-line distance from the sampling plot to the nearest road; five categories: 0–100, 101–200, 201–300, 301–400 and >400

We retained for further analysis only those variables that showed significant differences using this nonparametric test, to provide us with a conservative basis for detecting microhabitat separation.

For those variables showing significant differences, Mann-Whitney U tests were used to compare whether or not significant differences existed among microhabitat plots of giant panda, golden takin and controls. Stepwise discriminant function analysis was used to further analyse microhabitat separation between the two species and to detect the variables primarily responsible. We used Spearman Correlation Analysis to compare correlation coefficients for each two variables. If correlation coefficients exceeded 0.7 we only retained more biological meaningful variables entered for subsequent logistic regression analysis as this eliminates multicollinearity effects (Wei et al. 2000; Zhang et al. 2009). All test were conducted using SPSS v21 (SPSS Inc., Chicago, USA), and the significance level of all analyses was set at 0.05.

Results

Summer habitat separation

The Kruskal-Wallis tests showed that six of 22 variables differed significantly ($P < 0.05$) (Table 2). Mann-Whitney U tests demonstrated that nine variables (elevation, shrub density, bamboo forest, bamboo type, bamboo cover, bamboo height, herb cover, water-source dispersion and road-path dispersion) differed between giant panda and golden takin plots. Giant panda microhabitat plots were at a lower elevation than control plots and golden takin plots (control plots and golden takin plots were at the similar elevation) (Table 3). Similarly, giant pandas preferred habitats with fewer shrubs, taller bamboo, less herb cover and closer to a water source. When comparing giant panda and

Table 2. Means, SE and Kruskal-Wallis tests for each variable among different plot groups.

Summer habitat separation				
Variables	Panda Mean SE	Takin Mean SE	Control Mean SE	Kruskal-Wallis tests χ^2（P）
Altitude	1849.05(43.35)	2015(38.13)	1965.9(33.74)	12.9(0.002)
Bamboo forest	1(0.00)	1.13(0.05)	1.13(0.04)	6.14(0.046)
Bamboo cover	3.11(0.19)	2.13(0.23)	2.58(0.18)	9.14(0.01)
Bamboo height	2.66(0.15)	1.80(0.14)	2.1(0.13)	12.16(0.002)
Herb-cover proportion	1.59(0.15)	2.74(0.21)	2.11(0.14)	18.23(0.000)
Water-source dispersion	1.14(0.06)	1.63(0.14)	1.43(0.09)	9.51(0.009)
Winter habitat separation				
Variables	Panda Mean SE	Takin Mean SE	Control Mean SE	Kruskal-Wallis tests χ^2（P）
Altitude	1677.71(24.57)	2085.41(54.55)	1961.93(36.22)	25.16(0)
Slope	1.00(0.00)	1.33(0.11)	1.40(0.09)	6.87(0.032)
Slope aspect	1.65(0.17)	2.30(0.14)	2.38(0.12)	9.88(0.007)
Vegetation type	2.18(0.10)	2.89(0.18)	2.76(0.11)	9.61(0.008)
Canopy	1.24(0.11)	1.52(0.15)	1.76(0.11)	7.79(0.02)
Tree height	3.24(0.25)	2.30(0.21)	2.55(0.14)	8.91(0.012)
Bamboo type	1.00(0.00)	1.81(0.08)	1.53(0.08)	25.87(0)
Bamboo cover	4.29(0.19)	1.89(0.22)	2.57(0.20)	25.16(0)
Bamboo density	3.76(0.22)	2.48(0.29)	2.69(0.21)	8.45(0.015)
Bamboo height	2.06(0.14)	1.52(0.14)	2.09(0.15)	8.49(0.014)
Herb cover	1.12(0.08)	3.11(0.25)	2.21(0.18)	24.16(0)
Open-land proportion	1.35(0.12)	1.11(0.08)	1.50(0.11)	6.03(0.049)
Water-source dispersion	1.00(0.00)	1.70(0.19)	1.41(0.11)	9.12(0.01)

Table 3. Mann-Whitney U tests for all variables with significant differences in Table 2 ($\bar{x}1$ represents means of variables for giant panda group, $\bar{x}2$ represents that for takin group and $\bar{x}3$ represents that for control group).

Summer habitat separation									
Variables	$\bar{x}1-\bar{x}2$	U	P	$\bar{x}1-\bar{x}3$	U	P	$\bar{x}2-\bar{x}3$	U	P
Altitude	-165.95	556	0.000	-116.85	1291.5	0.014	49.1	1576.5	0.18
Shrub density	-4.31	767.5	0.048	-3.45	1343	0.029	0.86	1773	0.734
Bamboo forest	-0.13	880	0.014	-0.12	1540	0.015	0.01	1830	0.93
Bamboo type	-0.2	764	0.025	-0.08	1546	0.213	0.12	1640	0.252
Bamboo cover	0.98	632	0.002	0.53	1432.5	0.082	-0.45	1540.5	0.123
Bamboo height	0.86	604.5	0.000	0.56	1342	0.021	-0.3	1556.5	0.127
Herb cover	-1.15	533.5	0.000	-0.52	1314	0.011	0.63	1363	0.012
Water-source dispersion	-0.49	718.5	0.002	-0.28	1463	0.031	0.21	1617.5	0.17
Road-path dispersion	-0.5	765	0.019	-0.43	1467	0.066	0.07	1720.5	0.495
winter habitat separation									
Variables	$\bar{x}1-\bar{x}2$	U	P	$\bar{x}1-\bar{x}3$	U	P	$\bar{x}2-\bar{x}3$	U	P
Altitude	-407.7	22.107	0	-284.22	16.924	0	123.48	3.656	0.056
Slope	-0.33	5.99	0.014	-0.4	6.747	0.009	-0.07	0.066	0.797
Slope aspect	-0.65	7.373	0.007	-0.73	8.909	0.003	-0.08	0.05	0.822
Vegetation type	-0.71	8.027	0.005	-0.58	8.45	0.004	0.13	0.244	0.621
Canopy	-0.28	2.307	0.129	-0.52	7.688	0.006	-0.24	1.424	0.233
Tree height	0.94	7.982	0.005	0.69	6.389	0.011	-0.25	0.849	0.357
Bamboo type	-0.81	27.074	0	-0.53	14.313	0	0.28	4.521	0.033
Bamboo cover	2.4	23.777	0	1.72	15.728	0	-0.68	3.954	0.047
Bamboo density	1.28	7.806	0.005	1.07	6.413	0.011	-0.21	0.423	0.516
Bamboo height	0.54	7.377	0.007	-0.03	0.018	0.893	-0.57	6.674	0.01
Herb cover	-1.99	22.528	0	-1.09	10.513	0.001	0.9	8.242	0.004
Open-land proportion	0.24	4.82	0.028	-0.15	0.009	0.926	-0.39	5.6	0.018
Water-source dispersion	-0.7	8.816	0.003	-0.41	4.919	0.027	0.29	2.391	0.122

golden takin plots, elevation, bamboo cover, herb cover and water- source dispersion had larger absolute discriminant coefficients than other variables (Fig. 2a,b,c), indicating that microhabitat separation mainly results from these four variables (Wilk's Lambda = 0.658, $P < 0.01$; 77.8% of observations classified correctly; Table 4). Similarly, bamboo height and water-source dispersion were mainly responsible for the separation between the giant panda and control plot groups, and herb cover was mainly responsible for separation between golden takin and control plot groups (Table 4). Among variables where the correlation coefficients exceeded 0.7, we excluded biologically meaningless variables (bamboo forest, bamboo type and road-path dispersion), and thus, the remaining six variables were used in the logistic regression. Bamboo cover, bamboo height, herb cover and water-source dispersion had a greater contribution differentiating giant panda and golden takin microhabitat selection with an overall correct prediction rate of 77.8% ($\chi^2 = 42.32$, df = 6, $P < 0.01$; Table 5).

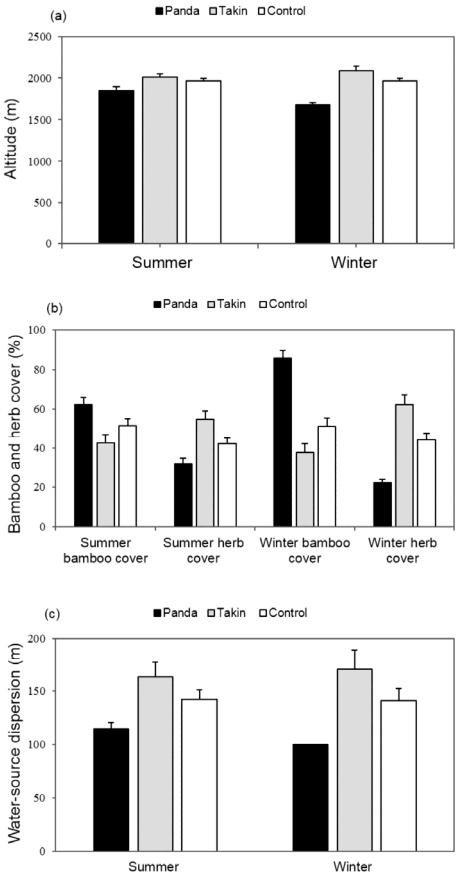

Figure 2. Seasonal microhabitat variable separation for giant pandas and golden takin: (a) elevation divergence, (b) bamboo cover and herb-cover differences and (c) water-source dispersion difference. All variables within this figure are significant ($P<0.05$).

Table 4. Discriminant coefficients between every two group plots.

Summer microhabitat separation			
Variables	Panda-takin	Panda-control	Takin-control
Altitude	**0.426**	-0.234	-0.139
Shrub density	0.088	-0.042	0.219
Bamboo forest	0.212	-0.401	0.506
Bamboo type	0.116	0.085	-0.264
Bamboo cover	**-0.446**	0.393	-0.789
Bamboo height	-0.297	0.796	-0.494
Herb cover	**0.659**	-0.322	1
Water-source dispersion	**0.48**	-0.667	-0.149
Road-path dispersion	0.144	-0.098	-0.108
Wilks' LAMBDA	0.658	0.914	0.948
P	0	0.004	0.011
Precise	77.80%	53.70%	61.40%
Winter microhabitat separation			
Variables	Panda-takin	Panda-control	Takin-control
Altitude	0.299	0.604	0.025
Slope	0.231	0.126	0.146
Slope aspect	0.208	0.25	0.288
Vegetation type	-0.001	0.315	0.149
Canopy	-0.182	0.027	-0.007
Tree height	0.015	-0.33	-0.063
Bamboo type	**0.837**	0.362	0.1
Bamboo cover	**-0.75**	-0.64	-0.756
Bamboo density	-0.333	-0.361	-0.652
Bamboo height	-0.222	0.014	-0.543
Herb cover	**0.659**	0.434	1
Open-land proportion	0.049	0.237	-0.352
Water-source dispersion	0.201	0.368	0.208
Wilks' LAMBDA	0.292	0.607	0.911
P	0	0	0.006
Precise	94.45%	85.5%	68.8%

Winter habitat separation

Kruskal-Wallis test showed that 13 of the 22 variables differed significantly (Table 2). Mann-Whitney U tests within different groups showed that the twelve variables differed between giant panda and golden takin plots: elevation, slope, slope aspect, vegetation type, tree height, bamboo

Table 5. Variables to distinguish giant panda plots from golden takin plots according to logistic regression.

Summer habitat separation					
	B	S.E.	Wald	df	P
Elevation	0.002	0.001	3.591	1	0.058
Shrub density	0.038	0.031	1.438	1	0.23
Bamboo cover	0.224	0.373	0.362	1	**0.547**
Bamboo height	-0.882	0.425	4.307	1	**0.038**
Herb cover	0.769	0.372	4.275	1	**0.039**
Water-source dispersion	1.031	0.47	4.805	1	**0.028**
Constant	-6.488	2.615	6.156	1	0.013
Winter microhabitat separation					
	B	S.E.	Wald	df	Sig.
Elevation	0.009	0.007	1.588	1	0.208
Bamboo cover	-0.784	1.112	0.497	1	**0.481**
Bamboo density	-0.563	1.1	0.262	1	**0.609**
Bamboo height	-0.245	1.563	0.025	1	0.876
Herb cover	-0.03	1.359	0.001	1	0.982
Water-source dispersion	14.091	7219.531	0	1	**0.998**
Constant	-25.242	7219.535	0	1	0.997

type, bamboo cover, bamboo density, bamboo height, herb cover, open-land, and water-source dispersion. Giant pandas prefer microhabitats that have a lower elevation, gentler slope, southern aspect, broadleaf deciduous forest, a smaller canopy, greater bamboo cover and density, less herb-cover and close to water sources (Fig. 2a,b,c). In contrast, golden takin prefer less bamboo cover, shorter bamboo, more herb-cover and less open-land (Table 3, Fig. 2b). Between microhabitat plots of giant panda and golden takin, bamboo type, bamboo cover and herb cover had larger discriminant coefficients than other variables (Table 4), indicating that microhabitat separation between the two species can be mainly explained by three variables (Wilk's Lambda = 0.292, $P < 0.01$; 94.45% of observations classified correctly). Similarly, elevation, bamboo cover and herb cover were mainly responsible for the separation between giant panda and control plot groups, and herb cover was mainly responsible for that between golden takin and control plot groups (Table 4). Logistic regression analysis showed that bamboo cover, bamboo density and water source dispersion had a greater contribution distinguishing the two species' plots ($\chi^2 = 42.48$, df = 6, $P < 0.01$; Table 5), with an overall correct prediction rate of 90.9%.

Discussion

Our results reveal different patterns of microhabitat utilization between two sympatric species in Foping Nature Reserve. Suitable microhabitats should contain abundant resources and favourable topographic conditions essential for individual survival and reproduction where animals can maximize individual fitness. Environmental heterogeneity promotes the coexistence of sympatric species by reducing interspecific competition (Stephanie 2004). Our results show that giant pandas and golden takins prefer different habitats in different seasons. From the late spring to the early summer, giant pandas and golden takins select diverse microhabitats. Unlike golden takin, giant pandas are specialized bamboo feeders, and bamboo resources play a key role in microhabitat selection whereby they prefer bamboo forest with greater cover and density (Fig. 2b). Because bamboo is a low-quality food (Hu et al. 1985, Schaller et al. 1985, Wei et al. 2000, Nie et al. 2015b, Wei et al. 2015c), a strong preference for habitats with high bamboo density can reduce giant panda energy expenditure while searching for forage (Reid & Hu 1991, Zhang et al. 2004). Conversely, the golden takin has a broader diet that includes bamboo and herbs, shrubs and young trees. Our results demonstrate that golden takin prefer habitats with more shrubs, more herb-cover and less bamboo cover (Fig. 2b), consistent with previous research (Zeng et al. 2001). In addition, the two species undergo a regular seasonal large-scale vertical movement (Zeng et al. 2008, Zhang et al. 2014, Nie et al. 2015b, Wei et al. 2015c). The migration from winter habitats (low elevation) to summer habitats (high elevation, >2,000 m) occurs in early spring in golden takins and late spring in giant pandas (Wang et al. 2010). Our results confirm the divergence in elevation between the two species (Fig. 2a), suggesting that giant pandas move to higher elevations later than golden takins. The seasonal migration of giant pandas is driven by the annual bamboo cycle. In Foping Nature Reserve there are two main bamboo species (*B. fargesii* and *F. qinlingensis*) consumed by giant pandas (Nie et al. 2015b, Wei et al. 2015c). The shooting season of *B. fargesii* occurs in early May, and peaks in late May; the shooting season of *F. qinlingensis*, occurs from the mid-June to the end of July and peaks in July (Pan et al. 1988). The shoots of *F. qinlingensis* are available when giant pandas move up to summer habitats in mid-June. In contrast, because golden takin are generalists, the phenological change in their forage is not completely influenced by the bamboo cycle. Once alpine vegetation begins to

sprout in May to July, they ascended to high altitudes at the beginning of May (Zeng et al. 2008, 2010). Thus, golden takins occupy a higher elevation niche (2,015 ± 259 m) than giant pandas (1,849 ± 288 m) from the spring to the summer. Giant pandas also prefer microhabitats closer to water than golden takin in the summer (Fig. 2c), perhaps because bamboo shoots sprout earlier and are of better quality in areas closer to rivers and streams.

The giant panda and golden takin return to winter habitats in early autumn. The migration time of giant pandas is earlier than golden takin (Wang et al. 2010). As the shoots of *F. qinlingensis* lignify seriously in August, giant pandas have to switch to eat leaves and stems of *F. qinlingensis*. And *B. fargesii* begins to sprout new leaves at low elevations later, so giant pandas gradually move down to winter habitats. Meanwhile, the weather becomes colder and the decline in forage quality and quantity at high elevations forces golden takins to move down to search for food in late autumn. Microhabitat separation of the two species is significant in winter habitats: giant pandas prefer gentler slopes and dense bamboo forests at lower elevations, whereas golden takin prefer higher herb cover and less open-land as this maximizes energy net income and reduces energy expenditure. Our data indicate that giant pandas remain close to rivers and streams during the autumn and the winter, perhaps because of the increasing requirements of water when digesting high-fibre food (Hu et al. 1985, Zhang et al. 2014).

Sympatric species show differences in at least one spatial dimension to decrease excessive interspecific competition and coexist harmoniously, including feeding sites, dietary habits, microhabitat utilization, activity rhythm and day roosts (Honer 1982, Wei et al. 2000, Siemers & Swift 2006, Campbell et al. 2007, Jacobs & Barclay 2009, Jiang et al. 2013). Microhabitat separation is regarded as the most common form of niche partitioning in sympatric mammals. Microhabitat separation is contributing to multiple-species coexistence (Schoener 1982, Marsh & Harris 2000, Sébastien et al. 2003). Our results suggest that giant pandas and golden takin display different microhabitat selection patterns although they appear to have overlapping activity ranges during part of the year. This partitioning of specific microhabitats between the two species may reflect an ecological adaptation directly related to dietary habits, annual phenological cycles of food resources, migration patterns, energy expenditure and metabolism requirements, ensuring their survival and reproduction by minimizing interspecific competition (Grether et al. 2009).

It has been generally accepted that giant panda is an umbrella for other sympatric animals and once its habitat is conserved, other species in the same habitats will be protected (Zhang et al. 2006, Li & Pimm 2015). However, our results reveal that these sympatric species have distinct microhabitat-selection patterns and that if we only consider the protection of giant panda habitats, we will fail to protect key habitats for non-targeted species such as golden takin (also see Kang et al. 2013). We think such these two significant different results were probably caused by different spatial scales. Habitat selection is a spatial scale-dependent ecological process (Morris 1992, Eloy et al. 2000). Co-occurring other species can be well protected under the conservation of giant panda in landscape scale or regional scale. By contrast, our research had concentrated upon a small microhabitat scale. Thus, based on microhabitat selection scale, we suggest that specific approaches are needed to conserve understory bamboo forests, alpine shrub and meadows related to the dietary habits, annual phenological cycle and migration patterns of sympatric species. Conservation approaches combining surrogate species protection with non-target species protection will provide a broader and stronger conservation platform to enhance biodiversity conservation.

Acknowledgements. This project was supported by the National Natural Science Foundation of China (31270570), and International Cooperation Foundation for Giant Pandas of the State Forestry Administration (CM 1425). We would like to thank X.M. Zhou for comments on this manuscript. X.L. Wang, A.X. Zhang, J.L. Pu and C.D. Li assisted in the field. Foping Nature Reserve Administration Bureau provided a great deal of assistance. We also thank the two anonymous reviewers for their constructive comments.

References

Administration, S.F. (2006): The third national survey report on giant panda in China. Science Press, Beijing.

Campbell, P., Schneider, C.J., Zubaid, A., Adnan, A.M., Kunz, T.H. (2007): Morphological and ecological correlates of coexistence in Malaysian fruit bats (Chiroptera: Pteropodidae). Journal of Mammalogy 88: 105–118.

Diamond, J., Case, T.J. (1986): Overview: introductions, extinctions, exterminations, and invasions. pp. 65–79. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York.

Dueser, R.D., Shugart, H.H. (1978): Microhabitats in forest floor small mammal fauna. Ecology 59: 89–98.

Eloy, R., Francisco, P., Miguel D. (2000): Defining key habitats for low density populations of Eurasian badgers in Mediterranean environments. Biological Conservation 95: 269–277.

Feng, T., Manen, V.F., Zhao, T.N., Li, M., Wei, F. (2009): Habitat assessment for giant pandas in the Qinling mountain region of China. Journal of Wildlife Management 73: 852–858.

Gotelli, N.J. (1997): Competition and coexistence of larval ant lions. Ecology 78: 176–1773.

Grether, G.F., Losin, N., Anderson, C.N., Okamoto, K. (2009): The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biological reviews 84: 61–635.

Hong, M.S., Yuan, S.B., Yang, Z.S., Yang, X.Y., Gu, X.D., Huang, F., Zhang, Z.J. (2015): Comparison of microhabitat selection and trace abundance of giant pandas between primary and secondary forests in Liziping Nature Reserve, China: effects of selective logging. Mammalian Biology 80: 37–379.

Hong, M.S., Wei, W., Yang, Z.S., Yuan, S.B., Yang, X.Y., Gu, X.D., Huang, F., Zhang, Z.J. (2016): Effects of timber harvesting on *Arundinaria spanostachya* bamboo and feeding-site selection by giant pandas in Liziping Nature Reserve, China. Forest Ecology Management 373: 74-80.

Horne, B.V. (1982): Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in serial stages of coniferous forests. Ecology 63: 992–1003.

Hu, J.C., Schaller, G.B., Pan, W.S., Zhu, J. (1985): The giant panda of Wolong. Sichuan Publishing House of Science and Technology, Chengdu, China.

IUCN. (2007): IUCN Red List of Threatened Species, World Conservation Union, Gland, Switzerland. <http://www.iucnredlist.org>, accessed: 2010.08.21.

Jacobs, D.S., and Barclay, R.M.R. (2009): Niche differentiation in two sympatric sibling bat species Scotophilus dinganii and Scotophilus mhlanganii. Journal of Mammalogy 90: 879–887.

Jiang, T.L., Lu, G.J., Sun, K.P., Luo, J.H., Feng, J. (2013): Coexistence of Rhinolophus affinis and Rhinolophus pearsoni revisited. Acta Theriologica 58: 47–53.

Kang, D.W., Yang, H.W., Li, J.Q., Chen, Y.P. (2013): Can conservation of single surrogate species protect co-occurring species? Environmental science and pollution research 20: 6290–6296.

Lei, M.W., Yuan, S.B., Yang, Z.S., Hong, M.S., Yang, X.Y., Gu, X.D., Huang, F., Zhang, Z.J. (2015): Comparison of microhabitats and foraging strategies between the captive-born Zhangxiang and wild giant pandas: implications for future reintroduction. Environmental Science and Pollution Research 22: 15089–15096.

Li, B.V., Pimm, S.L. (2015): China's endemic vertebrates sheltering under the protective umbrella of the giant panda. Conservation Biology 30(2): 329-339.

Liu, X., Toxopeus, A.G.A., Skidmore, K., Shao, X., Dang, G., Wang, T., Prins, H.H.T. (2005): Giant panda habitat selection in Foping Nature Reserve, China. Journal of Wildlife Management 69: 1623–1632.

Li, Y., Swaisgood, R. R., Wei, W., Nie, Y., Hu, Y., Yang, X., Gu, X., Zhang, Z. (2017): Withered on the stem: is bamboo a seasonally limiting resource for giant pandas? Environmental Science and Pollution Research 24: 10537-10546.

Marsh, A.C.W., Harris, S. (2000): Partitioning of woodland habitat resources by two sympatric species of *Apodemus: lessons* for the conservation of the yellow-necked mouse (*A. flavicollis*) in Britain. Biological Conservation 92: 275–283.

Morris, D.W. (1992): Scales and costs of habitat selection in heterogeneous landscape. Evolutionary Ecology 6: 412–432.

Morrison, M.L., Marcot, B.G., Mannan, R.W. (1992): Wildlife-habitat relationships: concepts and applications. The University of Wisconsin Press, Madison.

Nie, Y., Speakman, J.R., Wu, Q., Zhang, C., Hu, Y., Xia, M., Yan, L., Hambly, C., Wang, L., Wei, W., Zhang, J., Wei, F. (2015a): Exceptionally low daily energy expenditure in the bamboo-eating giant panda. Science 349: 171–174.

Nie, Y.G., Zhang, Z.J., Raubenheimer, D., Elser, J.J., Wei, W. Wei, F.W. (2015b) Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. Functional Ecology 29: 26–34.

Pan, W.S., Gao, Z.S., Lu, Z. (1988): The Giant Panda's Natural Refuge in the Qinling Mountains. pp. 245. Beijing University Press, Beijing, China.

Qi, D.W., Hu, Y.B., Gu, X.D., Li, M., Wei, F.W. (2009) Ecological niche modeling of the sympatric giant and red pandas on a mountain-range scale. Biodiversity Conservation 18: 2127–141.

Reid, D.G., Hu, J.C. (1991): Giant panda selection between *Bashania fabric* habitats in Wolong Reserve, Sichuan, China. Journal of Applied Ecology 28: 228–243.

Ren, Y., Wang, M.L., Yue, M., Li, Z.J. (1998): Plants of Giant Panda's habitat of Qinling Mountains. pp. 488. Shaanxi Science and Technology Press, Xi'an, China.

Schaller, G.B., Hu, J.C., Pan, W.S., Zhu, J. (1985): The giant panda of Wolong. The University of Chicago Press, Chicago.

Schoener, T.W. (1974): Resource partitioning in ecological communities. Science 185: 27–39.

Sébastien, S., Nicolas, P., Cornelis, N. (2003) Winter habitat selection by two sympatric forest grouse in western Switzerland: implications for conservation. Biological Conservation 112: 373–382.

Siemers, B.M., Swift, S.M. (2006): Differences in sensory ecology contribute to resource partitioning in the bat Myotis bechsteinii and Myotis nattereri (Chiroptera Vespertilionidae). Behavioral Ecology and Sociobiology 59: 373–380.

Song, Y., Yu, Y., Gong, H., Zhang, S. (1995): Habitat utilization of the golden takin during later autumn and early winter in Foping Nature Reserve. Chinese. Biodiversity 3 (supplement): 73–78. [In Chinese with English Abstract]

Stephanie, E.H. (2004): Habitat overlap of enemies: temporal patterns and the role of spatial complexity. Oecologia 138: 475–484.

Wang, T.J. Skidmore, A.K., Zeng, Z.G., Pieter, S.A.B., Si, Y.L., Liu, X.H., Herbert, H.T.P. (2010): Migration Patterns of Two Endangered Sympatric Species from a Remote Sensing Perspective. Photogrammetric engineering and remote sensing 76(12): 1343–1352.

Wei, F.W., Feng, Z.J., Wang, Z.W., Li, M. (1999): Feeding strategy and resource partitioning between giant and red pandas. Mammalia 63: 417–430.

Wei, F.W., Feng, Z., Wang, Z., Hu, J. (2000): Habitat use and separation between the giant panda and the red panda. Journal of Mammalogy 80: 448–455.

Wei, F., Hu, Y., Yan, L., Nie, Y., Wu, Q., Zhang, Z. (2015a): Giant pandas are not an evolutionary cul-de-sac: evidence from multidisciplinary research. Molecular Biology and Evolution 32: 4–12.

Wei, F., Swaisgood, R., Hu, Y., Nie, Y., Yan, L., Zhang, Z., Qi, D., Zhu, L. (2015b): Progress in the ecology and conservation of giant pandas. Conservation Biology 29: 1497–1507.

Wei, W., Nie, Y., Zhang, Z., Hu, Y., Yan, L., Qi, D., Li, X., Wei, F. (2015c): Hunting bamboo: Foraging patch selection and utilization by giant pandas and implications for conservation. Biological Conservation 186: 260–267.

Werner, E.E. (1977): Species packing and niche complementarity in three sunfishes. American Naturalist 111: 553–579.

Wu, J.Y., Han, Y.P., Qu, H., Liu, S.X., Zhu, X.M., Jia, J.X., Liu, J.Y., Zhang, L. (1990): The Chinese Takin. pp.192. China Forestry Publishing House, Beijing, China.

Zeng, Z.G., Song, Y.L., Gong, H.S. (1998): Population size and age structure of golden takin in Foping Nature Reserve. Acta Theriologica Sinica 18: 241–246. [in Chinese with English Abstract]

Zeng, Z.G., Song, Y., Zhong, W., Gong, H., Zhang, J., Dang, G. (2001): Food habits of golden takin Chinese. Journal of Zoology 36: 36–44.

Zeng, Z.G., Zhong, W.Q., Song, Y.L., Li, J.S., Zhao, L.G., Gong, H.S. (2003): Present Status of Studies on Eco-Biology of Takin. Acta Theriologica Sinica 23: 161–167. [in Chinese with English Abstract]

Zeng, Z.G., Skidmore, A.K., Song, Y.L., Wang, T.J., Gong, H.S. (2008): Seasonal altitudinal movements of golden takin in the Qinling Mountains of China. Journal of Wildlife Management 72: 611–617.

Zeng, Z.G., Beck, P.S.A., Wang, T.J., Skidmore, A.K., Song, Y.L., Gong, H.S., Prins, H.H.T. (2010): Effects of plant phenology and solar radiation on seasonal movement of golden takin in the Qinling Mountains, China. Journal of Mammalogy 91: 92–100.

Zhang, Z., Wei, F., Li, M., Zhang, B., Liu, X., Hu, J. (2004): Microhabitat separation during winter among sympatric giant pandas, red pandas, and tufted deer: the effects of diet, body size, and energy metabolism. Canadian Journal of Zoology-Revue Canadienne de Zoologie 82: 1451–1458.

Zhang, Z.J., Wei, F.W., Li, M., Hu, J.C. (2006): Winter microhabitat separation between giant and red pandas in Bashania faberi bamboo forest in Fengtongzhai nature reserve. Journal of Wildlife Management 70: 231–235.

Zhang, Z.J., Zhan, X.J., Yan, L., Li, M., Hu, J.C., Wei, F.W. (2009): What determines selection and abandonment of a foraging patch by wild giant pandas (*Ailuropoda melanoleuca*) in winter? Environmental Science and Pollution Research 16: 79–84.

Zhang, Z., Swaisgood, R. R., Zhang, S., Nordstrom, L. A., Wang, H., Gu, X., Hu, J., Wei, F. (2011): Old-growth forest is what giant pandas really need. Biology Letters 7: 403–406.

Zhang, Z.J., Shepperd, J.K., Swaisgood, R.R., Wang, G., Nie, Y.G., Wei, W., Zhao, N.X., Wei, F.W. (2014): Ecological scale and seasonal heterogeneity in the spatial behaviors of giant pandas. Integrative Zoology 9: 47–61.

Zhao, S., Zheng, P., Dong, S., Zhan, X., Wu, Q., Guo, X., Hu, Y., He, W., Zhang, S., Fan, W., Zhu, L., Li, D., Zhang, X., Chen, Q., Zhang, H., Zhang, Z., Jin, X., Zhang, J., Yang, H., Wang, J., Wang, J., Wei, F. (2013): Whole-genome sequencing of giant pandas provides insights into demographic history and local adaptation. Nature Genetics 45: 67–71.

Zhu, L., Wu, Q., Dai, J., Zhang, S., Wei, F. (2011): Evidence of cellulose metabolism by the giant panda gut microbiome. Proceedings of The National Academy of Sciences of The United States of America 108: 17714–17719.