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Microhabitat use and separation between giant panda (*Ailuropoda melanoleuca*), takin (*Budorcas taxicolor*), and goral (*Naemorhedus griseus*) in Tangjiahe Nature Reserve, China

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Abstract. The coexistence mechanisms of sympatric species have attracted wide attention from ecologists. The giant panda (*Ailuropoda melanoleuca*), takin (*Budorcas taxicolor*) and goral (*Naemorhedus griseus*) are species which are being seriously endangered along to the Himalayan-Hengduan Mountains. To improve the understanding of mechanism of microhabitat separation and coexistence between the giant panda and the other two sympatric species, we investigated microhabitat characteristics at Tangjiahe Nature Reserve, Qingchuan County of Sichuan Province, China during 2013 by sampling 86 fecal-site plots for giant pandas, takins and gorals as well as 80 control plots. Our results suggested that each species has their own specific microhabitat selection pattern. Furthermore, the giant pandas more often selected microhabitats with gentler slope, more bamboo, lower tree canopy and a small herb shrub while the takins and gorals preferred the microhabitats with less bamboo, but more trees and shrubs. Thus, based on our findings, food resources, dietary requirements and energy expenditure are considered as the main ecological factors which caused the microhabitat separation among these three species. Because of the narrow dietary, the giant panda's specificity to its microhabitat is higher than that of the other two animals, which results in their segmentation. This study provides a scientific evidence that conservation efforts should be under way to protect the sympatric habitat, not only the suitable habitat for giant pandas but also that of takins and gorals, which can make a great improvement to the local biodiversity.

Key words: sympatric species, microhabitat selection, coexistence, habitat partitioning, conservation implications

Introduction

Knowledge of how similar or ecologically close species coexist is crucial to understanding community diversity (Chesson 2000, HilleRisLambers et al. 2012). Sympatric species often avoid excessive interspecific competition by partitioning resource utilization along three main niche dimensions, i.e. in space (Campbell et al. 2007), food (Siemers & Swift 2006), and activity time (Jacobs & Barclay 2009, Jiang et al. 2013). Understanding the species' niche differentiation advances our understanding of the coexistence mechanism among different species and provides a deeper insight into the different ecological factors that impact on species coexistence (Zhou 1992). In addition, such knowledge also provides a reliable theoretical basis for policymakers to manage and develop effective conservation strategies (Kontoleon & Swanson 2003). A substantial body of previous research has proposed that the protection of umbrella species brings great benefits to sympatric species (Wesner & Belk 2012). In the recent years, however, some studies have shown that conservation of single surrogate species cannot guarantee the protection of other non-target species in the same habitat (Lindenmayer & Likens 2011). For example, Kang et al. (2013) found that the protection of umbrella species did not support the conservation of the entire ecosystem and that we should understand the needs of the whole ecosystem to protect sympatric species and community diversity. Thus, a better of understanding of the process by which co-occurring species evolve different forms of niche partitioning will help to

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maximize the utility of conservation strategies for the protection of community diversity.

The giant panda (*Ailuropoda melanoleuca*), takin (*Budorcas taxicolor*), and goral (*Naemorhedus griseus*) are endemic to the Himalayan-Hengduan Mountains (Ge et al. 1989, Wu & Hu 2001, Wu et al. 2002). The giant panda is an endemic species of China that belongs to the order Carnivora and has evolved to specialize (~99 %) on various species of bamboo during a long evolutionary history (Zhao et al. 2013, Wei et al. 2018). The wild population is 1864 pandas, which inhabit six highly fragmented mountain ranges in three remote provinces in southwest China (Sichuan, Shaanxi, and Gansu) (State Forestry Administration 2015). The takin is a large (250-500 kg) and endangered mountain ungulate that is distributed along the eastern edge of the Tibetan Plateau and Himalayas. They forage over 160 species of plants including bamboo leaves and shoots (IUCN 2014). The goral is a widespread species found through much of southern, southeastern, and central China. They inhabit steep areas and plateaus in mountainous areas and will sometimes use subtropical mixed forests and evergreen-deciduous forests near cliffs (Smith & Xie 2008). The three species (giant panda, takin, and goral) are sympatric in the Qinling, Minshan, Qionglai, Xiangling and Liangshan Mountains in western China, which is a unique region of sympatry for these three species. They all inevitably face similar environmental pressures, such as deforestation, habitat loss and fragmentation, poaching, and population subdivision (Wei et al. 1999c, Huang & Wang 2001, Zeng et al. 2003). Sympatric distribution and resources overlap between these species have attracted attention of ecologists, in particular, whether they compete for closed resources or, if not, how they avoid competition in the same area? However, few studies have analyzed the habitat requirements and coexistence strategies of these three species. Thus, there a comparative study of the habitat selection is required to establish a more comprehensive conservation strategy for these three species. In order to address the possibility of interspecific competition between these three species and to improve our understanding of observed patterns of habitat partitioning, our research aimed to answer these questions: (1) whether each species evolved its own microhabitat selection strategy based on their relative overall distribution; (2) which ecological factors affect the microhabitat separation of these species; and (3) how can we develop more appropriate management and conservation strategies for species co-coexistence and community diversity?

Material and Methods

Study area

Our study site was located at Tangjiahe Nature Reserve, Qingchuan County of Sichuan Province, China (104°36′-104°52′ E, 32°30′-32°41′ N). The reserve area is about 400 km^2 (Fig. 1). The montane broad-leaved evergreen forests occur at elevations below 1600 m and are mainly hardy plants. Because this area was logged in the 1970s, the typical evergreen broad-leaved forest shows only patchy distribution on the two sides of a small river and evergreen and deciduous broad-leaved mixed forests occur at elevations of 1600-2000 m. This area has also been logged and the typical mixed forest only appears in some local sites around the ditch. The coniferous and broad-leaved mixed forest occurs at elevations of 2000-2300 m. The subalpine coniferous forest occurs at elevations of 2300-2500 m. At more than 2500 m, there is alpine bush and meadow (Ge et al. 1989). The study area has a subtropical monsoon climate with a mean annual temperature of 12 °C. The lowest mean daily temperature occurs in January with average temperatures of −1.2 °C and the highest is in July with average temperatures of 19.7 °C and a temperature difference of 20.9 °C. Within the reserve, three species of bamboo (*Fargesia denudate Yi*, *F. scabrida Yi*, and *F. rufa Yi*), which are the dominant forest understory in the middle altitude (1900 m) to the edge of the forest line (Hu 2005), are the staple food resource for giant pandas. While takins and gorals feed primarily on tender herbs, as well as young branches and leaves of various trees and shrubs, sometimes they also feed on young bamboo leaves (Schaller et al. 1986). As there are no human settlements within the reserve boundary and only some settlement sites located on the lower elevations before reserve establishment, its ecological

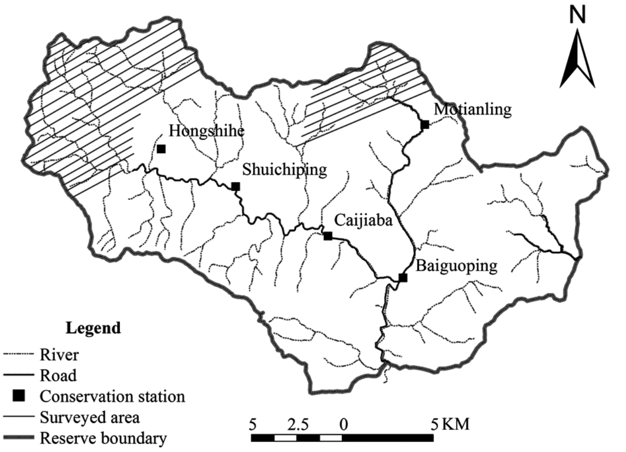

Fig. 1. Distribution of surveyed area in Tangjiahe Nature Reserve, China.

Table 1. Description and definitions of variables in the research.

Variables	Description and definitions
Elevation (m)	Elevation at the center of 20 × 20 m plots
Slope (°)	Slope of the 20 × 20 m plots, five categories: 0-15°, 16-30°, 31-45°, 46-60°, and > 60°
Slope aspect (°)	Eight categories: east (67.5-112.5°), southeast (112.5-157.5°), south (157.5-202.5°), southwest (202.5-247.5°), west (247.5-292.5°), northwest (292.5-337.5°), north (337.5-22.5°), northeast (22.5-67.5°)
Vegetation type	Six categories: shrub, deciduous broadleaf forest, deciduous broadleaf and coniferous mixed forest, coniferous forest, grassland, and others
Tree canopy (%)	Canopy of the overstorey in 20 × 20 m plots, five categories: 0-20 %, 21-40 %, 41-60 %, 61-80 %, and > 80 %
Number of trees	Number of trees (> 5 m in height) counted in two 2 × 20 m rectangles of 20 × 20 m plots
Height of trees (m)	Estimated average height of trees in the four 10 × 10 m square plots nearest to the center of the 20 × 20 m plots, five categories: 5-10 m, 11-15 m, 16-20 m, 21-25 m, and > 25 m
Tree DBH[a] (cm)	Average diameter of trees at the breast height nearest to the center of the 20 × 20 m plots in the four 10 × 10 m square plots
Shrub cover (%)	Canopy of the understorey in 20 × 20 m plots, five categories: 0-20 %, 21-40 %, 41-60 %, 61-80 %, and > 80 %
Number of shrubs	Number of shrubs (0-5m in height) counted in two 2 × 20 m rectangle of 20 × 20 m plots
Shrub height (m)	Estimated average height of shrubs in the four 10 × 10 m square plots nearest to the center of the 20 × 20 m plots, five categories: 0-1 m, 1-2 m, 2-3 m, 3-45 m, and 4-5 m
Shrub DBH[a] (cm)	Average diameter of shrubs at the breast height nearest to the center of the 20 × 20 m plots in the four 10 × 10 m square plots
Bamboo cover (%)	Cover of bamboos in 20 × 20 m plots, five categories: 0-20 %, 21-40 %, 41-60 %, 61-80 %, and > 80 %
Bamboo density (culms/m^2)	Estimated average culms of bamboos in five 1 × 1 m square plots in the 20 × 20 m plot, five categories: 0-5 culms/m^2, 6-10 culms/m^2, 11-15 culms/m^2, 16-20 culms/m^2, and > 20 culms/m^2
Bamboo height (m)	Estimated average height of bamboos in five 1 × 1 m square plots in the 20 × 20 m plot, five categories: 0-1 m, 1-2 m, 2-3 m, 3-4 m, 4-5 m, > 5 m
Herb cover (%)	Cover of herbs in 20 × 20 m plots, five categories: 0-20 %, 21-40 %, 41-60 %, 61-80 %, and > 80 %
Proportion of open land (%)	Proportion of area of open land in 20 × 20 m plots, five categories: 0-20 %, 21-40 %, 41-60 %, 61-80 %, and > 80 %
Distance to water (m)	Direct distance to the nearest water source, six categories: 0-100 m, 101-200 m, 201-300 m, 301-400 m, 401-500 m, > 500 m

[a] Diameter at breast height.

systems are well preserved and it provides favourable conditions for the survival and reproduction for giant pandas, takins, and gorals. The three species in the region are widely distributed and the region is the ideal base for animal ecology research (Wu et al. 2002).

Field investigation method

The giant panda, takin, and goral all inhabit the mountainous terrain covered by dense forests, which make direct observations difficult (Zhang et al. 2009). We identified their microhabitat through feces trace, which has been confirmed to be an effective index (Reid & Hu 1991, Wei et al. 2000, Zhang et al. 2009). We systematically set 20 survey transects with each length from 2 to 4 km, and each transect covered an area of about 4 km^2 within the nature reserve. A buffer of 2 m either side was included in each survey transect to minimize bias due to differences in the detectability of giant pandas, takins, and gorals in dense forests (Qi et al. 2011). Transects were oriented along the elevation gradient and traversed all the habitat types of these three species. Then we made sampling plots once we found feces traces left by the three species by walking along transects (Reid & Hu 1991, Wei et al. 2000). The sampling plot followed the method of Wei et al. (2000) as follows: plots were centralized on the fecal or other trace locations. Three independent kinds of microhabitat plots, including one 1 × 1 m^2 plot, two 10 × 2 m^2 rectangular transects, and one 20 × 20 m^2 plot were set on these center of signs (Wei et al. 2000). In each 20 × 20 m^2 plot, another two independent sampling units were set, including two 20-m^2 rectangular

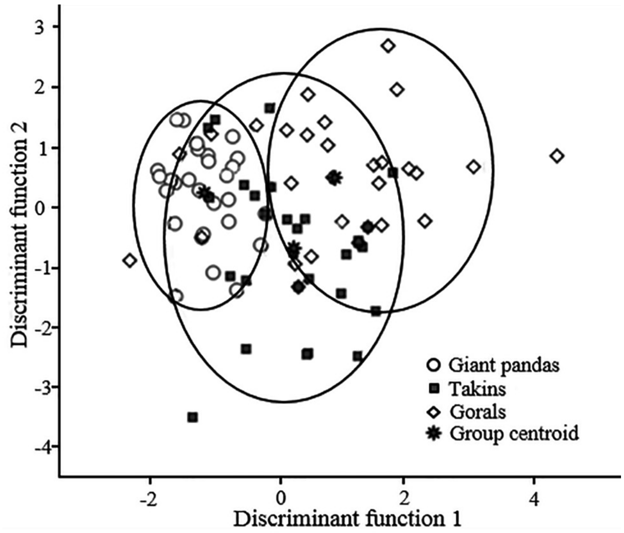

Fig. 2. Scatterplot of habitat plots for giant pandas, takins, and gorals through discriminant function analysis.

transects were set perpendicular to each other and four 1 × 1 m^2 small plots were placed at the center of each 100 m^2 quadrant (Wei et al. 2000, 2015). The minimum distance between microhabitat plots was not less than 100 m. All habitat features were studied in 20 × 20 m sampling plots. Control plots were established at the start and end of each survey transect and every 100-m change in elevation along transect gradient and following transitions between the forest types to ensure that all habitat types were sampled. Control plots were sampled similarly to microhabitat plots (Wei et al. 2000, 2018, Zhang et al. 2011). Within the sampling plot, we measured 18 ecological factors, including tree, shrub, bamboo, herb, and forest-floor characteristics (Table 1).

Data analysis

The normality of the 18 variables was tested using the Kolmogorov-Smirnov test. We conducted an independent sample one-way ANOVA test to compare variable differences among three species microhabitats and control plots when data were normally distributed and the Kruskal-Wallis H test was used when the distribution assumptions were not met (Du 1984, Lu et al. 1997). We used different variables for correlation analysis (Pearson's test for continuous variables or Kendall's test for discrete variables). When the correlation coefficient was > 0.5 in the group variables (Fabrizio et al. 2003, Sebastien et al. 2003), we only retained the variables that were most biologically meaningful for logistic regression analysis in order to reveal the main ecological factors

Table 2. Comparison of means of variables among different groups.

Variables	Mean (±SD)			
	Control plots	Giant pandas	Takins	Gorals
Elevation (m)*	2291 (±269)	2405 (±179)	2308 (±234)	2360 (±229)
Slope (°)	3.18 (±1.31)$^{a, b}$	2.69 (±0.38)^{a}	3.00 (±1.26)^{a}	3.55 (±1.18)^{b}
Slope aspect (°)	4.67 (±2.31)	5.00 (±2.40)	4.24 (±2.28)	4.14 (2.23)
Vegetation type	2.85 (±0.76)	2.57 (±0.74)	2.62 (0.68)	2.93 (0.80)
Tree canopy (%)	2.88 (±1.19)^{a}	2.00 (±0.82)^{b}	2.31 (±1.28)$^{a, b}$	2.47 (±1.21)$^{a, b}$
Number of trees*	3.21 (±2.19)	1.84 (±1.06)	2.38 (±1.89)	3.17 (±2.49)
Height of trees (m)	3.03 (±1.19)	2.54 (±1.10)	2.45 (±1.21)	2.97 (±1.38)
Tree DBH (cm)	26.34 (±6.82)	26.04 (±5.64)	23.34 (±6.58)	27.67 (±15.51)
Shrub cover (%)	1.48 (±0.71)	1.25 (±0.65)	1.38 (±0.56)	1.24 (±0.51)
Number of shrubs*	3.86 (±6.00)	2.20 (±2.68)	3.78 (±3.43)	2.88 (±2.39)
Shrub height (m)	4.30 (±1.42)	4.21 (±1.26)	4.03 (±1.61)	4.03 (±1.40)
Shrub DBH (cm)	5.17 (±2.07)	5.37 (±2.29)	4.81 (±2.12)	4.96 (±1.97)
Bamboo cover (%)	3.30 (±1.45)^{a}	4.71 (±0.53)^{b}	2.90 (±1.72)^{a}	2.83 (±1.61)^{a}
Bamboo density (culms/m^2)	3.67 (±1.43)^{a}	4.86 (±0.45)^{b}	3.00 (±1.73)^{a}	3.10 (±1.59)^{a}
Bamboo height (m)	2.52 (±0.57)^{a}	3.07 (±0.47)^{b}	2.52 (±0.63)^{a}	2.34 (±0.77)^{a}
Herb cover (%)	2.42 (±1.23)^{a}	1.64 (±0.91)^{b}	2.93 (±1.41)^{a}	2.48 (±1.33)^{a}
Proportion of open land (%)	1.67 (±0.89)	1.75 (±0.75)	1.55 (±0.78)	1.90 (±0.98)
Distance to water (m)	2.45 (±2.05)	3.29 (±2.06)	2.34 (±2.00)	3.03 (±1.99)

*Variables compared through one-way ANOVA and others through Kruskal-Wallis H test. Note: for variables with a significant difference among groups, values with one or two of the same superscript letters indicate no significant difference. Values without the same superscript letters indicate that the difference was significant.

Table 3. Variables to distinguish habitat from control plots through logistic regression analysis (not included those with Wald's values below 1.0).

Species	Variables	B	Wald	Sig.
Giant pandas	Bamboo density	43.48	6.98	0.01
	Bamboo height	25.64	5.37	0.02
	Slope	–18.74	4.61	0.03
	Number of trees	–8.73	3.94	0.05
	Herb cover	–6.89	2.16	0.14
	Number of shrubs	3.82	2.10	0.15
Takins	Bamboo density	–7.64	5.11	0.02
	Tree DBH	–7.09	4.74	0.03
	Elevation	15.60	2.04	0.15
	Number of trees	–1.91	1.85	0.17
	Slope aspect	–1.99	1.63	0.20
	Bamboo height	6.42	1.39	0.24
Gorals	Bamboo density	–11.16	7.92	0.01
	Slope	7.13	3.39	0.07
	Elevation	20.56	2.96	0.09
	Distance to water	2.27	1.57	0.21
	Proportion of open land	3.50	1.21	0.27

Table 4. Pooled within-groups correlation between discriminating variables and standardized canonical discriminant functions.

Variables	Function 1	Function 2
Bamboo cover	–0.66*	0.37
Bamboo density	–0.62*	0.46
Bamboo height	–0.55*	0.05
Slope	0.08	0.66*
Herb cover	0.40	–0.53*
Number of shrubs	0.24	–0.42*

* Largest absolute correlation between each variable and the discriminant function.

Table 5. Classification results for habitat plots among species through discriminant function analysis.

Species	Predicted group membership			Total plots
	Giant pandas	Takins	Gorals	
Giant pandas	24 (85.7)	4 (14.3)	0 (0.0)	28
Takins	5 (17.2)	20 (69.0)	4 (13.8)	29
Gorals	5 (17.2)	4 (13.8)	20 (69.0)	29

for selection of the microhabitat by the three animals (Zhang et al. 2009, Wei et al. 2017). On this basis, we screened the main variables that significantly influence the microhabitat separation of the three species through a standardized canonical discriminant functions analysis (Fan et al. 2010). We identified the differences in the preferred microhabitat of these three species and detected the main ecological variables responsible for these differences. The above analyses were completed using statistical analysis software SPSS13.0. The significance level of all analyses was set at 0.05.

Results

In total, we sampled 28 habitat plots of giant pandas, 29 habitat plots of golden takins, 29 habitat plots of gorals and 80 control plots, respectively, during our research period. The one-way ANOVA and Kruskal-Wallis H test results indicated that among the 18 ecological factors, there was a significant difference in slope (U = 9.84, *P* = 0.02), tree canopy (U = 8.83, *P* = 0.03), bamboo cover (U = 26.29, *P* = 0.00), bamboo density (U = 26.60, *P* = 0.00), bamboo height (U = 20.21, *P* = 0.00), and herb cover (U = 14.45, *P* = 0.00) (Table 2). However, there was no significant difference in elevation (F = 1.62, *P* = 0.19), slope aspect (U = 2.54, *P* = 0.47), vegetation type (U = 5.35, *P* = 0.15), number of trees (F = 2.23, *P* = 0.09), height of trees (U = 5.27, *P* = 0.15), tree DBH (U = 4.24, *P* = 0.24), shrub cover (U = 3.42, *P* = 0.33), number of shrubs (F = 2.25, *P* = 0.00), shrub height (U = 0.87, *P* = 0.83), shrub DBH (U = 0.97, *P* = 0.81), proportion of open land (U = 2.54, *P* = 0.47), or distance to water (U = 5.54, *P* = 0.14) (Table 2). The giant panda and takin plots were on gentler slopes than the control plots, whereas goral plots were on steeper slopes. All three species preferred plots with a lower tree canopy than the control plots. For bamboo cover, bamboo density, and bamboo height, microhabitat plots selected by giant panda have higher coverage and abundance than control plots while takin and goral plots have lower bamboo cover, density, and height. Compared with the other two species, the giant panda preferred microhabitats with gentler slopes, lower tree canopy, more bamboo, and a smaller herb canopy. The above differences clearly indicate that each species have their own microhabitat selection pattern. Logistic regression analysis showed that bamboo density, bamboo height, slope, and tree DBH had a greater contribution to distinguishing the three species' plots and each habitat factor at the significant level of 0.05 both have variance homogeneity (Table 3).

However, only six variables (bamboo cover, bamboo density, bamboo height, slope, herb cover, and number of shrubs) were entered as discriminant functions (Table 4). As the criterion to retain variables in the discriminant functions, we used the eigenvalues set to a threshold (> 3.84 for entry and < 2.71 for removal). Stepwise discriminant analysis demonstrated that the variables with a significantly greater contribution could remain in the discriminant functions. Thus, these six variables clearly had the highest discriminant power to identify the microhabitat separation for the three species. Two discriminant functions were set at the same time and the total correct classification rate was 74.57 % for the 86 sampling microhabitat plots (Table 5).

In addition, the scatterplot for the microhabitat plots visually illustrates the microhabitat separation among the three species (Fig. 2). The microhabitat plots of the giant panda deviated from the other two species along the x-axis, implying that there is a significant difference (ANOVA, F = 101.63, *P* < 0.01). The larger absolute value of the standardized canonical discriminant function coefficient, the greater the discriminating ability. Thus, bamboo cover, bamboo density, and bamboo height were mainly responsible for the microhabitat separation between the giant panda, takin, and goral along the x-axis. Similarly, it also had a significant difference in the y-axis, implying that slope, herb cover, and number of shrubs were mainly responsible for the microhabitat separation of these three species along the y-axis (ANOVA, F = 89.15, *P* < 0.01).

Discussion

Habitat separation is often considered to be responsible for multispecies coexistence (Qi et al. 2009). Our study revealed that each species has its own distinct microhabitat selection pattern. The utilization of specific microhabitats by animals reflects an ecological behaviour adaptation related to its diet composition, body size, energy strategy, and other factors, so as to ensure its successful survival and reproduction by minimizing competition (Zhang et al. 2004, Qi et al. 2009). Suitable habitat should comprise different resources and various environment configurations to meet the survival and reproduction requirements for sympatric animals. Thus, environmental heterogeneity can promote the co-occurrence of species by reducing interspecific competition (Stephanie 2004). Among the 18 variables that were surveyed in our study, six differed significantly between the three species plots, which indicates that giant panda, takin, and goral prefer different habitats in Tangjiahe Nature Reserve. However, the patterns of the microhabitats varied with species. The giant panda prefers microhabitats with a gentler slope than those of takin and goral. It is plausible that by using gentler slopes, giant pandas may reduce energy expenditure during searching, foraging, and moving, and may free its forelimbs to grasp bamboo culms when feeding (Hu et al. 1985, Wei et al. 2000). However, we found that takin and goral often dwell on steeper cliffs and ridges. We speculate that takin and goral occupying a steeper niche than the giant panda is related to the topography, which prevents poachers or predators from hunting and allows escape. Such differences in the slope selection indicate that the giant pandas, takins, and gorals follow different strategies of energy expenditure and avoiding predators.

For the other five different variables, our results revealed that giant pandas select microhabitats with high bamboo cover, density, and height, but takin and goral did not. As a specialist bamboo feeder, bamboo resources are essential for giant panda survival and reproduction. The life of the giant panda is directly influenced by bamboo as a panda will consume a large amount of bamboo each day, and thus their demands for bamboo cover, density, and height are obviously higher than those of the other two species due to the high specificity in the panda's forage patterns (Nie et al. 2015, Li et al. 2017). Besides, such microhabitats with denser and higher bamboo have better concealment conditions than microhabitats with a sparse bamboo forest. In addition, bamboo is a low-quality food (Hu et al. 1985, Wei et al. 2000), and pandas have a strong preference toward habitats with high bamboo density, which reduces the pandas' energy expenditure while foraging (Reid & Hu 1991, Wei et al. 2015, Wei et al. 2017). Unlike the giant panda, takin and goral are not specialist feeders and they not only forage bamboo but also feed on herbs, shrubs, and tender tree leaves. Hence, they usually occur in habitats with more shrubs, a greater proportion of herb cover, and with a lower bamboo cover (Wu & Hu 2001, Zeng et al. 2001). The giant panda's preference for a lower tree canopy was directly correlated with bamboo growth. Due to the growth of the understorey bamboo requiring sufficient light, bamboo leaves from forests with a low canopy were the most nutritious. By contrast, the microhabitats selected by takins and gorals have greater tree canopy and more trees and shrubs than pandas' microhabitats, and such microhabitats can supply better concealment conditions.

Although many of the previous investigations found that the conservation *in situ* of giant pandas guaranteed long-term adaptation with other species in the same distribution area (Fleishman et al. 2000, Zhang et al. 2004), our research found that, although the three syntopic species exist in overlapping microhabitats, the habitat utilization patterns are significantly different. It explains why the giant pandas have the higher specificity in habitat utilization than the other two species with the smallest variation coefficient for the giant panda (Hu et al. 1985) (Table 2). A suitable microhabitat is the main factor for the survival of wildlife and different microhabitat demand reflects their different physiological and ecological needs. Part of the reason is to reduce the competition between species (Launer & Murphy 1994) rather than competition leading to ecological adjustment (Caro 2003, Stephanie 2004). For sympatric species, environmental heterogeneity can reduce competition to promote their coexistence (Berger 1997, Zhang et al. 2009). The existence of these differences may have led to mutual adaptation of the three species and allowed long-term coexistence.

Here we show that the three species differ significantly in their microhabitat selection, and the discriminant function analysis showed how different species in similar habitats use separated. The scatterplot for the microhabitat plots visually illustrates microhabitat separation (Fig. 2). Although the three species ecologically overlap, they have different group centroids (Wang et al. 2005), illustrating that the activity centers and hence microhabitats are different (Zhang et al. 2004). Along the x-axis, the microhabitats of the gorals are far from the giant pandas and the takins. Variables with the largest absolute value of the standardized canonical discriminant function coefficient make the strongest contribution to the power of the corresponding function (Du 1984, Wei et al. 2000). Therefore, we conclude that bamboo cover, bamboo density, and bamboo height were mainly responsible for the microhabitat separation between the gorals, the giant pandas, and the takins along the x-axis. Similarly, slope, herb cover, and number of shrubs were mainly responsible for the microhabitat separation between the gorals, the giant pandas, and the takins along the y-axis. In summary, although the three species have a similar distribution area, their niches did not completely overlap.

If sympatric animals want to coexist harmoniously in similar overlapping distribution areas, they need to show some niche differences in at least one spatial dimension to decrease excessive interspecific competition, e.g. in dietary differentiation, feeding sites, microhabitat selection. It has been generally accepted that microhabitat separation is the most basic form of niche partitioning in sympatric mammals as it contributes to multiple-species coexistence (Wei et al. 2017). Our results reveal that these three sympatric species have distinct microhabitat-selection patterns. This separation of specific microhabitats among the three species may reflect an ecological adaptation directly related to their own dietary, energy strategy and nutrition requirements. Thus, based on our results, different habitat conservation measures should be implemented respectively for these three species. The giant pandas prefer habitat with a gentle slope. However, such an area might have serious human disturbance through logging, hunting and infrastructure construction. Thus a specific management approach should occur to conserve such areas. The giant pandas also prefer habitat with a high density of bamboo forest, but takins and gorals do not; they prefer habitat with abundant trees and herbs. Thus, it is necessary that conservation efforts should not only pay attention to conserve understory bamboo, but also provide more focus on protecting overstory and meadows closely related to dietary habits of other herbivores, in order to reinforce local biodiversity conservation.

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Literature

Berger J. 1997: Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. *Conserv. Biol. 11: 69–78.*

Campbell P., Schneider C.J., Zubaid A. et al. 2007: Morphological and ecological correlates of coexistence in Malaysian fruit bats (Chiroptera: Pteropodidae). *J. Mammal. 88: 105–118.*

Caro T.M. 2003: Umbrella species: critique and lessons from East Africa. *Anim. Conserv. 6: 171–181.*

Chesson P. 2000: Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst. 31: 343–366.*

Du Y. 1984: Biological statistics. *Higher Education Publishing House, Beijing. (in Chinese)*

Fabrizio S., Pedrini P. & Marchesi L. 2003: Adaptive selection of foraging and nesting habitats by black kites (*Milvus migrants*) and its implications for conservation: a multi-scale approach. *Biol. Conserv. 112: 351–362.*

Fan Z., Zhang Z.J., Wei W. et al. 2010: Comparison of skull morphology among Chinese white-bellied rat (*Niviventer confucianus*) populations from five mountains in China. *Acta Theriol. Sin. 30: 171–176.*

Fleishman E., Murphy D.D. & Brussard P.F. 2000: A new method for selection of umbrella species for conservation planning. *Ecol. Appl. 10: 569–579.*

Ge T.A., Hu J.C. & Jiang M.D. 1989: The herd compositions, numbers and distribution of Sichuan takin (*Budorcas taxicolor tibetana*) in Tangjiahe Nature Reserve. *Acta Theriol. Sin. 9: 262–268.*

HilleRisLambers J., Adler P.B., Harpole W.S. et al. 2012: Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst. 43: 227–248.*

Hu J.C. 2005: A report of the comprehensive survey on Tangjiahe Nature Reserve in Sichuan. *Sichuan Publishing House of Science and Technology, Chengdu*.

Hu J.C., Schaller G.B., Pan W.S. & Zhu J. 1985: The giant panda of Wolong. *Sichuan Science and Technology Press, Chengdu.*

Huang F.X. & Wang Y.S. 2001: Difficulties and counter-measures for biodiversity conservation. *Biodiv. Sci. 9: 399–406.*

IUCN 2014: The IUCN Red List of Threatened Species, version 2014.1. *Accessed 15.06.18. http://www.iucnredlist.org*

Jacobs D.S. & Barclay R.M.R. 2009: Niche differentiation in two sympatric sibling bat species *Scotophilus dinganii* and *Scotophilus mhlanganii*. *J. Mammal. 90: 879–887.*

Jiang T.L., Lu G.J., Sun K.P. et al. 2013: Coexistence of *Rhinolophus affinis* and *Rhinolophus pearsoni* revisited. *Acta Theriol. 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? *Environ. Sci. Pollut. Res. 20: 6290–6296.*

Kontoleon A. & Swanson T. 2003: The willingness to pay for property rights for the giant panda: can a charismatic species be an instrument for nature conservation? *Land Econ. 79: 483–499.*

Launer A.E. & Murphy D.D. 1994: Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. *Biol. Conserv. 69: 145–153.*

Li Y., Swaisgood R.R., Wei W. et al. 2017: Withered on the stem: is bamboo a seasonally limiting resource for giant pandas? *Environ. Sci. Pollut. Res. 24: 10537–10546.*

Lindenmayer D.B. & Likens G.E. 2011: Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss. *Ecosystems 14: 47–59.*

Lu W., Zhu Y., Sha J. & Zhu H. 1997: SPSS for Windows. *Publishing House of Electronics Industry, Beijing. (in Chinese)*

Nie Y.G., Zhang Z.J., Raubenheimer D. et al. 2015: Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. *Funct. Ecol. 29: 26–34.*

Qi D.W., Hu Y.B., Gu X.D. et al. 2009: Ecological niche modeling of the sympatric giant and red pandas on a mountain-range scale. *Biodivers. Conserv. 18: 2127–2141.*

Qi D.W., Zhang S.N., Zhang Z.J. et al. 2011: Different habitat preferences of male and female giant pandas. *J. Zool. Lond. 285: 205–214.*

Reid D.G. & Hu J.C. 1991: Giant panda selection between *Bashania faberi* habitats in Wolong Nature Reserve, Sichuan, China. *J. Appl. Ecol. 28: 228–243.*

Schaller G.B., Teng Q., Pan W. et al. 1986: Feeding behavior of Sichuan takin (*Budorcas taxicolor*). *Mammalia 50: 311–322.*

Sebastien S., Perrin N. & Neet C. 2003: Winter habitat selection by two sympatric forest grouse in Western Switzerland: implications for conservation. *Biol. Conserv. 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). *Behav. Ecol. Sociobiol. 59: 373–380.*

Smith A.T. & Xie Y. 2008: A guide to the mammals of China. *Princeton University Press, Princeton, New Jersey.*

State Forestry Administration (SFA) 2015: The fourth national giant panda survey. *State Forestry Administration of China Press.*

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

Wang Y.N., Zhou C.Q., Zhang J. et al. 2005: Spatial niche of the rodents in summer in Tangjiahe Nature Reserve. *Acta Theriol. Sin. 25: 39–44.*

Wei F., Costanza R., Dai Q. et al. 2018: The value of ecosystem services from giant panda reserves. *Curr. Biol. 21: 2174–2180.*

Wei F.W., Feng Z.W., Wang Z.W. & Hu J.C. 1999c: Current distribution, status and conservation of wild red pandas *Ailurus fulgens* in China. *Biol. Conserv. 89: 285–291.*

Wei F.W., Wang Z.W. & Hu J.C. 2000: Habitat use and separation between the giant panda and the red panda. *J. Mammal. 80: 448–455.*

Wei W., Han H., Zeng J. et al. 2017: Diet and foraging-site selection by giant pandas in a National Nature Reserve in China. *Anim. Biol. 67: 53–67.*

Wei W., Huang Y., Zhou H. et al. 2017: Microhabitat separation between giant panda and golden takin in the Qinling Mountains and implications for conservation. *North-West. J. Zool. 13: 109–117.*

Wei W., Nie Y., Zhang Z. et al. 2015: Hunting bamboo: foraging patch selection and utilization by giant pandas and implications for conservation. *Biol. Conserv. 186: 260–267.*

Wei W., Swaisgood R.R., Dai Q. et al. 2018: Giant panda distributional and habitat-use shifts in a changing landscape. *Conserv. Lett.: doi: org/10.1111/conl.12575.*

Wesner J.S. & Belk M.C. 2012: Habitat relationships among biodiversity indicators and co-occurring species in a freshwater fish community. *Anim. Conserv. 15: 445–456.*

Wu H. & Hu J.C. 2001: A comparison in spring and winter habitat selection of takin, serow and goral in Tangjiahe, Sichuan. *Acta Ecol. Sin. 21: 1628–1633.*

Wu H., Zhang Z.J., Hu J. & Hu J.C. 2002: A preliminary study on habitat use of Sichuan takin in spring and winter. *Chin. J. Zool. 37: 23–27.*

Zeng Z.G., Song Y., Zhong W. et al. 2001: Food habits of Chinese golden takin. *J. Zool. Lond. 36: 36–44.*

Zeng Z.G., Zhong W.Q., Song Y.L. et al. 2003: Present status of studies on eco-biology of takin. *Acta Theriol. Sin. 23: 161–167.*

Zhang Z., Swaisgood R.R., Zhang S. et al. 2011: Old-growth forest is what giant pandas really need. *Biol. Lett. 7: 403–406.*

Zhang Z.J., Wei F.W., Li M. et al. 2004: Microhabitat separation during winter among sympatric giant pandas, red pandas, and tufted deer: the effects of diet, body size, and energy metabolism. *Can. J. Zool. 82: 1451–1458.*

Zhang Z.J., Zhan X.J., Yan L. et al. 2009: What determines selection and abandonment of a foraging patch by wild giant pandas (*Ailuropoda melanoleuca*) in winter? *Environ. Sci. Pollut. Res. 16: 79–84.*

Zhao S., Zheng P., Dong S. et al. 2013: Whole-genome sequencing of giant pandas provides insights into demographic history and local adaptation. *Nat. Genet. 45: 67–71.*

Zhou K.Y. 1992: Development tendency on conservative biology and current development strategy in China. *Chin. J. Zool. 27: 42–48.*