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Implications of habitat overlap between giant panda and sambar for sympatric multi-species conservation

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ABSTRACT

Context. Studies of distribution and habitat utilisation of sympatric animals, especially those experiencing population increases, are useful for understanding their specialised habitat niches and interspecies relationships, in addition to developing effective protection strategies. **Aims.** As a species that lives within the range of the giant panda, the sambar population has been increasing in the past few decades in Southwest China. In this paper, we aimed to analyse the overlap in habitat area and habitat suitability between giant panda and sambar in Wolong National Nature Reserve to examine potential sympatric species competition in the context of wildlife conservation. **Methods.** We ran MaxEnt models based on giant panda occurrence sign locations (n = 316) and sambar presence locations (n = 598). In addition, we predicted the core and secondary habitat for the two species to assess the degree of competition across a gradient of habitat conditions. **Key results.** Our analysis detected significant habitat overlap between the two species – up to 75.96% in their potential habitat, with suitability overlap indices reaching 0.74. **Conclusions.** These results indicate that the similarity of habitat requirements of the two species is high in our study area. In addition, the competition over space utilisation between the two species' populations could intensify in the future as the sambar population increases. **Implications.** Our results suggest that habitat restoration and corridor construction could be recommended as conservation strategies for future wildlife conservation in China's Giant Panda National Park. Moreover, future wildlife conservation should pay greater attention to the niche overlap and interspecific competition among sympatric species. We suggest strengthening habitat restoration and corridors for all key species in the region, not just giant pandas, to alleviate the increased competition associated with niche overlap among sympatric species.

Keywords: ecological niche, habitat overlap, interspecific competition, panda, population increases, potential habitat, sambar, space utilisation, sympatric animals.

Introduction

Coexistence mechanisms among sympatric species is an important topic in the study of wildlife ecology, and understanding interspecific relationships is of great significance for improving sympatric multi-species conservation efforts. However, ecologists usually study the interspecies relationships among sympatric animals by differentiating their microhabitat selection strategies while sometimes ignoring the impacts of niche overlap at a broad scale (Qi *et al.* 2009; Wei *et al.* 2017; Wang *et al.* 2018*a*). In particular, the competition brought on by population increase of one species in a short period could be detrimental to sympatric species survival.

This phenomenon is prominent in the six mountains where wild giant pandas are distributed. The giant panda (*Ailuropoda melanoleuca*), as an icon of global wildlife conservation, has received effective protection in the past few decades (Swaisgood *et al.* 2018; State Forestry and Grassland Administration 2021). The population increased from 1114 in 1987 to 1864 in 2014 (State Forestry and Grassland Administration 2021).

However, their habitat range (~25 800 km^2) is only part of six isolated mountains in southwest China (State Forestry and Grassland Administration 2021). In the same region, China's wildlife conservation effort has led to a rapid increase in populations of many sympatric species, including some of the large ungulates with high population growth rates (due to lack of natural predators and the absence of human poaching; Li and Pimm 2016; Li *et al*. 2020). However, such rapid population growth might pose significant threats to charismatic species such as giant pandas, because the long-term viability of species is usually limited by the carrying capacity of the habitat.

Moreover, habitat utilisation is a fundamental concept for understanding niche overlap and interspecific competition. Niche overlap and competition among sympatric species may negatively impact their habitat utilisation and conservation status. Some studies in giant panda habitat, for example, have revealed that a significant increase in the number of livestock has led to the relocation of wildlife habitats due to niche overlap, including for giant pandas (Li *et al*. 2017; Zhang *et al*. 2017; Wang *et al*. 2019). This finding revealed that the rapid increase in overlap among species may affect spatial distribution and habitat selection. However, such exclusionary effects vary among different species. For example, sambar (*Rusa unicolor*) can make use of habitats where livestock exists, whereas giant pandas, red pandas (*Ailurus fulgens*), and Sichuan snub-nosed monkeys (*Rhinopithecus roxellanae*) cannot (Zhang *et al*. 2017). Niche overlap and competition among species have a significant impact on the survival and resources availability for wildlife. Generally, the suitability of habitats for secondary competitors is reduced by primary competitors to the extent that the occurrence of secondary competitors are suppressed by the presence of primary competitors (Mondal *et al*. 2012). For example, in South Asia, tigers (*Panthera tigris*) occupy advantageous habitat with rich prey resources, in turn causing dispersal of leopards (*Panthera pardus*) into less suitable habitats around them (Odden *et al*. 2010; Harihar *et al*. 2011). In another example, takin (*Budorcas taxicolor*) has an obvious advantage over sambar in the utilisation of salt wells due to its size (Liu *et al*. 2019). Therefore, an in-depth understanding of the overlap in the spatial distribution and habitat suitability of sympatric species is essential for effective wildlife protection and management.

A previous study based on infrared camera monitoring showed that the sambar is a key ungulate with extensive distribution and the highest encounter rate in the core habitat of the giant panda in Wolong National Nature Reserve (Zhang *et al*. 2017). The average population density of sambar in Wolong Nature Reserve was 0.25/km^2, and the maximum density of the survey transect is 0.76/km^2 (Yao *et al*. 2017). In fact, the population distribution area of sambar in Wolong Nature Reserve accounts for 39.67% (793.41 km^2) of the total area (Luo 2021), so the population density of sambar may be much larger than the aforementioned value. In addition, the elevation range of sambar is 1600–3600 m (Yao *et al*. 2017), which is consistent with the elevation distribution of giant pandas (Bai *et al*. 2018). A survey based on wildlife signs showed that the coincident rate of sambar and giant panda occurrence reached 66.58% within the primary forest in the Wolong National Nature Reserve (Wang *et al*. 2018*b*). Moreover, sambar feeds on arrow bamboo (*Bashania fangiana*), a staple bamboo for wild giant pandas in Wolong National Nature Reserve (Bai *et al*. 2020). The content of the arrow bamboo residue in sambar's manure is as high as 91.82% during the season with forage shortage (Guan *et al*. 2020). These results indicate that there may be significant interspecific competition between giant panda and sambar for food resources. In addition, since the dispersal of sambar is restricted by rugged terrain, as well as by the human land use and fragmentation of habitat, interspecific competition with giant pandas may intensify as the sambar population grows. The situation may negatively affect species' fitness and complicate the management of both species in protected areas (Wang *et al*. 2015).

In this paper, we quantify habitat overlap between the giant panda and sambar to assess the degree of competition among these sympatric animals and implications for multi-species conservation at a landscape level. We integrated species occurrence records and a wide range of environmental variables to predict current potential suitable habitat and suitability indices for giant pandas and sambar using species distribution models. The aim was to quantify the degree of overlap in terms of their spatial distribution of suitable area and degree of similarity in the respective suitability indices. The overlap of suitable areas only examines the presence and absence of habitat over space between two species, whereas the comparison of suitability quantifies the differences in habitat characteristics. This study provides new insight for multi-species conservation by understanding the spatial competition between giant pandas and one ungulate species with an overlapping range. Additionally, it is our hope that this study will be able to provide insight into the wildlife conservation strategies that manage the rapid population growth of ungulates within giant panda habitat.

Materials and methods

Data collection

Both species' occurrence data were derived from records of the 4th National Giant Panda Survey, which was carried out from 2012 to 2013 (Sichuan Forestry Department 2015), and from the routine background survey of Wolong National Nature Reserve in 2016. The transects (750–3500 m) in the surveys were set up in every 2 km^2 survey plot ($n = 173$), which were required to pass through various habitats of giant pandas and sambar to record their activity signs, including species entities, footprints, feeding traces, faeces, etc. (Tang *et al.* 2015). In total, we obtained 317 occurrence records of giant pandas and 598 occurrence records of sambars.

Because giant panda and sambar are forest dwelling animals, the survey area of this study has covered forests with elevations of 1600 m to 3600 m throughout the reserve. Nine environmental variables were used in our models: (1) elevation; (2) slope; (3) aspect; (4) vegetation type; (5) bamboo distribution; (6) distance to road; (7) distance to stream; (8) distance to resident; and (9) distance to livestock. The data of elevation, slope, and aspect at 30-m resolution were derived from DEM provided by NASA's Shuttle Radar Topography Mission (Farr *et al.* 2007). The vegetation type layer (including grassland, shrubland, woodland, cultivated land, construction land, bare land, and water area) was derived from a supervised classification of Landsat-8 Operational Land Imager (OLI) imagery (30-m resolution) acquired in August 2015 (Bai *et al.* 2018). The bamboo distribution layer (absent and present of bamboo) was produced by the 3rd National Giant Panda Survey (State Forestry Administration 2006). All distance layers were based on Euclidean distance to points/lines (road, stream, resident and livestock) outlined by the 4th National Giant Panda Survey (Sichuan Forestry Department 2015). To be consistent, bamboo distribution and all distance layers were resampled to 30-m resolution.

Model procedure

In order to analyse overlap in suitable habitat between the two sympatric animals, we predicted their habitat suitability using the Maximum Entropy (MaxEnt) model. It uses presence-only data and environmental predictor variables to predict habitat suitability of species (Phillips *et al.* 2006; Elith *et al.* 2006). We ran MaxEnt models based on giant panda occurrence sign locations (n = 316) and sambar presence locations (n = 598). We randomly divided the presence data into training (80% of the locations) and evaluation (20% of the locations) data, and ran the models five times (Bai *et al.* 2018). The five model predictions were averaged to produce aggregated habitat suitability of two species across Wolong Nature Reserve. Area under the receiver operator curve (AUC) was used to evaluate the predictive power of the model and to verify the precision of the model forecast (Hijmans *et al.* 2017). The output of the models was habitat suitability index (HSI), which reflects the suitability of habitat. We chose threshold that maximises the sum of the sensitivity (true positive rate) and specificity (true negative rate), and then converted the suitability map to binary presence and absence maps (Hijmans *et al.* 2017).

Habitat overlap analysis

In order to assess overlap between giant panda and sambar, we estimated the core and secondary habitat for the two species. The core and secondary habitats were defined as the areas above (and equal to) and below the average suitability value of their suitable habitats. The percentage contribution of predictor variables produced by the Maxent model were used to analyse the relative importance for each species' habitat suitability (Wang *et al.* 2017). To quantify and visualise the degree of overlap of different types of habitats of giant pandas and sambar at a fine scale, we set an overlap index of area (OI_a) and suitability (OI_s) based on binary (presence and absence maps) and continuous (raw suitability index maps) output of MaxEnt models. The total potential habitat was calculated by the union of both species' habitats. Finally, the OI_a and OI_s were calculated according to the following formulas:

i. The formula to calculate OI_a:

$$OI_a = O_{ij}/(O_i \times O_j)^{1/2}$$

where OI_a is the overlap index of area, O_{ij} is the area of spatially overlapped habitat of interest (core/secondary) between giant panda and sambar, O_i is total area of habitat of interest (and core/secondary) of giant panda, and O_j is total area of suitable habitat of interest area (and core/secondary) of sambar.

ii. The formula to calculate OI_s:

$$OI_s = \frac{\sum (1 - |S_i - S_j|)}{n}$$

where OI_s is the overlap index of suitability, n is the amount of grid cells in the collection of their suitable habitat, S_i is habitat suitability index of giant panda, and S_j is habitat suitability index of sambar. OI_s values range from 0 (least degree of overlap) to 1 (highest degree of overlap).

Results

In our models, the average AUC values are 0.8889 (giant panda) and 0.8876 (sambar) respectively, indicating that the model results have a certain degree of credibility (Swets 1988). Finally, the giant panda models predicted approximately 592.05 km^2 suitable habitat (HSI ≥ 0.26) and 310.73 km^2 core habitat (HSI > 0.59), and the sambar models predicted approximately 656.04 km^2 suitable habitat (HSI ≥ 0.31) and 311.72 km^2 core habitats (HSI > 0.57). The total potential habitat of giant pandas and sambar was distributed in the southeastern part of the reserve, accounting for around 30% of the area of Wolong Nature Reserve.

There is 75.96% of area overlap in the suitable habitat, and 46.67% of area overlap in the core suitable habitat (Table 1). Among them, more than half of the area (60.04% and 55.66%) of the core habitat of one species was in the habitat of the other species (Table 1). The OI_s value of

Table 1. The OI_a of giant panda and sambar in Wolong Nature Reserve, China.

OI_a (%)	Core suitable area of giant panda	Secondary suitable area of giant panda	Suitable habitat area of giant panda
Core suitable area of sambar	46.67	32.49	55.66
Secondary suitable area of sambar	39.21	35.71	51.98
Suitable habitat area of sambar	60.04	47.67	75.96

Note that this includes OI_a between core, secondary and whole suitable habitat.

potential habitat reached 0.74, indicating that most of the two species' habitats have a high level of the suitability overlap, except for the region in the southwest of the reserve (Fig. 1).

Evaluation of the percentage contribution of each variable to the models illustrated that bamboo distribution and elevation were the most important variables for the habitat suitability of two species (Fig. 2). Both species were distributed in bamboo forests below 3600 m with high habitat overlap. In addition, all other variables have a low contribution (<10), except for the predictor of vegetation type, which had up to 16.08% relative contribution to the habitat suitability of sambar (Fig. 2).

Discussion

In mountain forests of southwest China, topographic factors play a decisive role in the distribution of the available resources, including vegetation and bamboo forest (Bai *et al.* 2018). Therefore, elevation, bamboo, and vegetation were the most important variables for habitat suitability evaluation in our models. They determined the spatial distribution of giant pandas and sambar. In our study, the OI_a of core habitat (46.67%) and entire habitat (75.96%) reflected that there is a high overlap of habitat use between giant panda and sambar.

It is critical that wildlife conservation takes into account the relationships with other species (Jiang 2004), especially when the populations of sympatric animals are increasing rapidly in an isolated region. In our study, the OI_s was up to 0.74, reflecting that there was potential resource

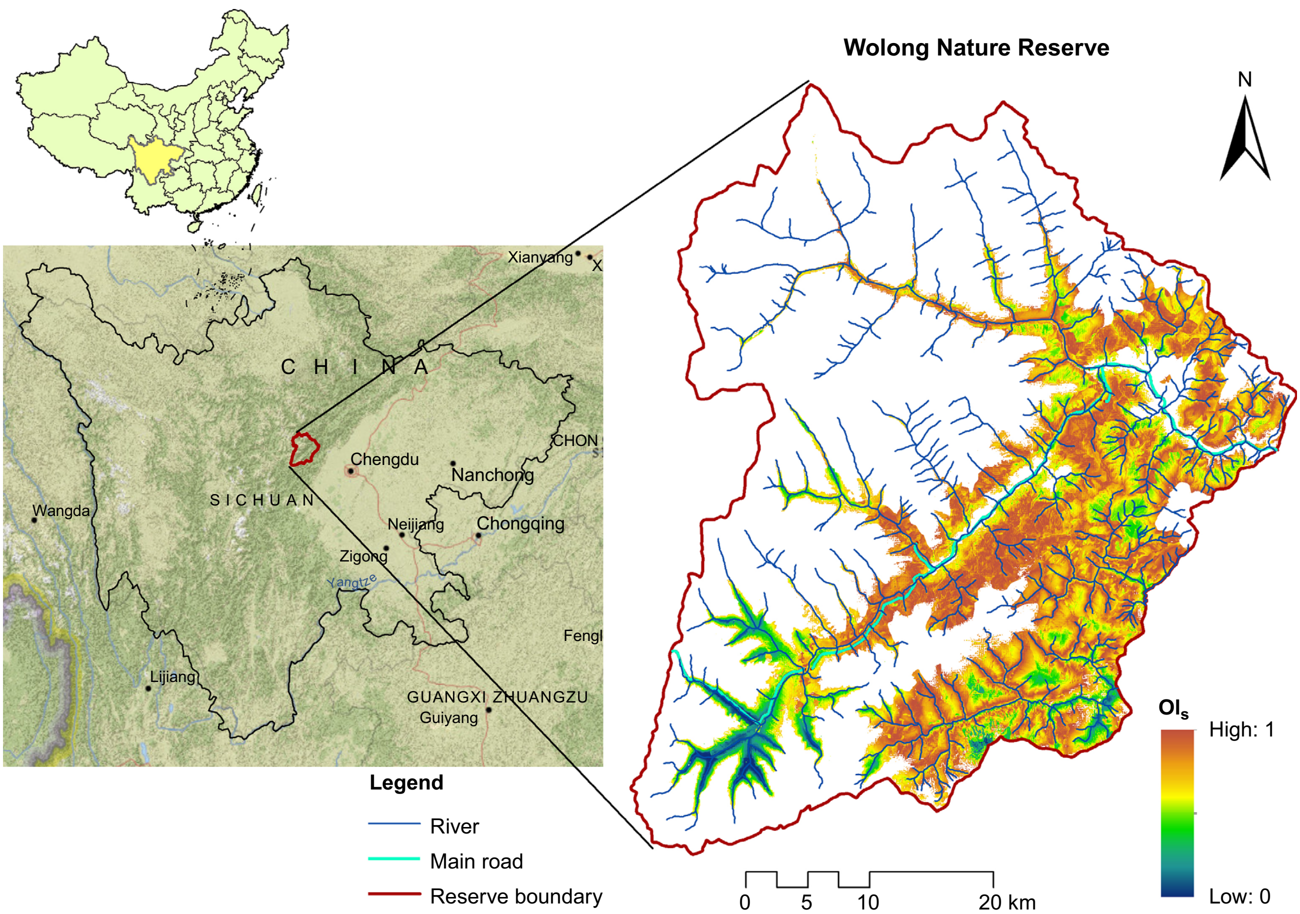

Fig. 1. The location of study area, and the OI_s of giant panda and sambar in Wolong Nature Reserve, China.

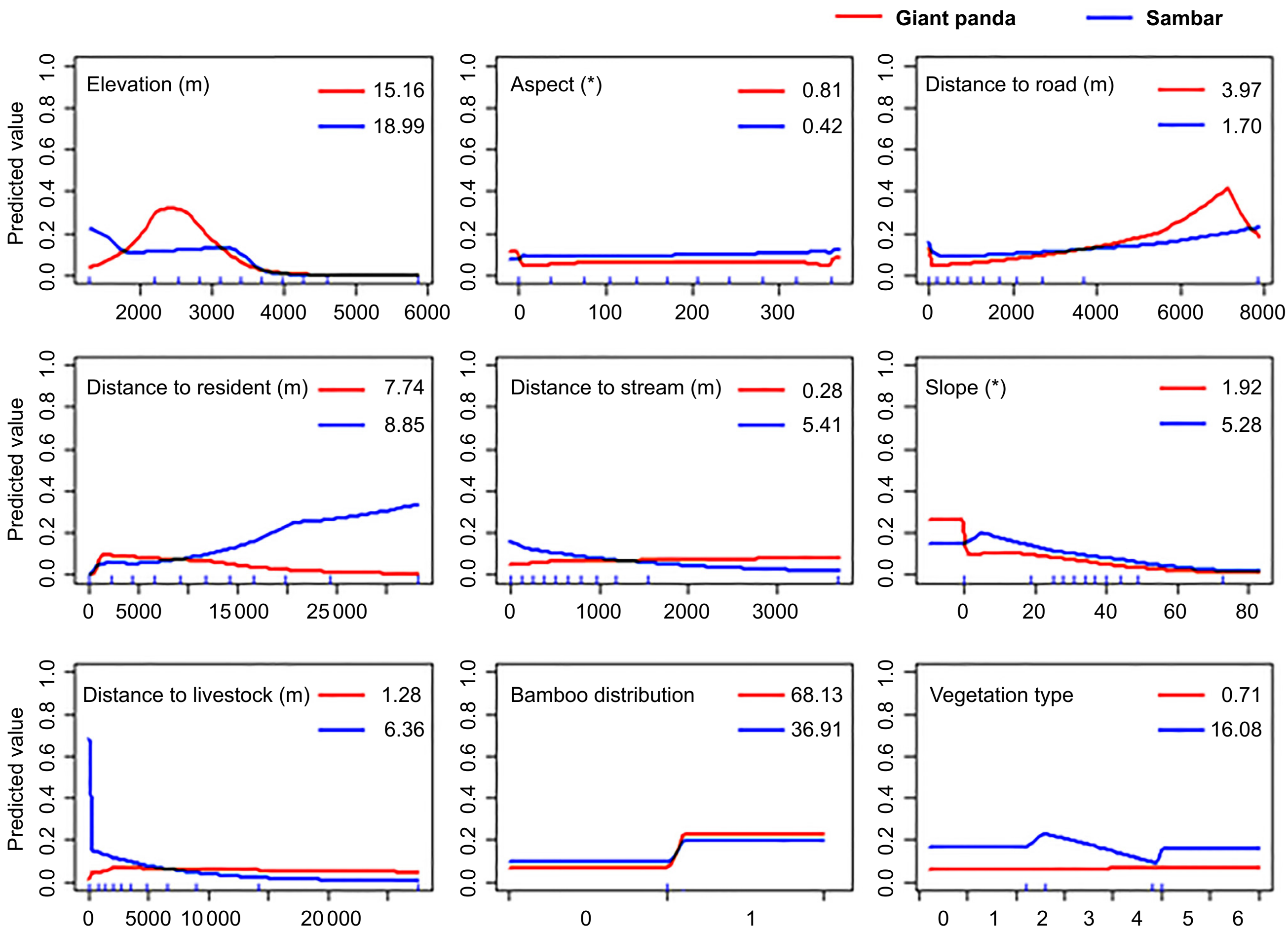

Fig. 2. The response curves of environmental variables of giant panda (red line) and sambar (blue line); the mean relative contribution of environmental variables, quantifying the variable importance, are shown in the upper right corner of their response curves chart, and the numbers on the *x*-axis of the last two pictures indicate their different categories in orders with data resources.

competition between giant panda and sambar. A previous study documented (based on wildlife sign surveys) that 18 of the total 27 habitat factors had consistent selectivity in the habitat selection between giant panda and sambar (Wang *et al.* 2018*a*). This competition has often been ignored in previous studies of species occupancy. For instance, a previous study showed that sympatric animals (including wild boar) were not limiting the distribution of giant pandas, despite having significant habitat overlap (Wang *et al.* 2015). However, the seasonal food (bamboo shoots) competition between giant pandas and wild boars may have negative impacts on giant panda populations, particularly as a result of the substantial increase of the wild boar (Nie *et al.* 2019). Moreover, sambar are known to compete with giant panda. They mainly feed on bamboo in winter (bamboo makes up 91.82% of their diet in February) (Guan *et al.* 2020). Further study is required to quantify the degree of competition for bamboo resources between these species in areas where sambar have increased in recent years. Future studies should not only pay attention to the spatial overlap, but also the degree of habitat suitability overlap among sympatric species. In addition, we recommend that the OI_s, based on habitat suitability, is an easy-to-understand indicator to characterise the degree of interspecific competition for habitat resources.

Recent increases in livestock have seriously limited the population distribution of giant pandas (Wang *et al.* 2015, 2019; Zhang *et al.* 2017). The issue of livestock encroachment has been studied by many scholars as a major issue in and around protected areas. Similarly, in the isolated region with low habitat suitability, the resources of giant panda might be reduced and degraded by the population growth of sympatric species like sambar. So far, the population of giant panda and their sympatric species (especially ungulates) seems to be increasing rapidly thanks to the expanding protected area network and lack of carnivores in the giant panda habitat (Li and Pimm 2016; Li *et al.* 2020). For example, in addition to the growth of the sambar population, takin population in the Tangjiahe National Nature Reserve has increased from ~500 in 1986 to ~1324 in 2014

(Wu *et al.* 1998; Guan *et al.* 2015). As the local population continues to increase, this may lead to overgrazing pressure in some meadow areas of the nature reserve. Compared with giant pandas, the utilisation rate of bamboo shoots by wild boar has also significantly increased from 2008 to 2016 in the Foping National Nature Reserve (Nie *et al.* 2019). In isolated habitat patches with relatively low carrying capacity, a high density of sympatric ungulate species could be even more detrimental to endangered or vulnerable herbivore species conservation, particularly during extreme environmental events such as earthquakes, bamboo flowering, or extreme drought (Hu and Schaller 1985; Zhang *et al.* 2011).

Animals choose the best quality habitat, including shelter, water and food resources, and living space, in line with their resource needs (Hu and Schaller 1985). However, some studies have revealed that giant pandas are using some less suitable habitats, such as habitat with higher slopes, and abandoning habitat with high-quality bamboo shoots for food (Hull *et al.* 2016; Nie *et al.* 2019). Therefore, both landscape-scale habitat utilisation studies and resource availability studies at the microhabitat scale are important to inform the conservation of giant pandas. Moreover, the impact of interspecies population interactions on the survival of giant panda has received some attention (Wang *et al.* 2015, 2018*a*; Nie *et al.* 2019). We suggest long-term monitoring of population growth and interspecific competition of major sympatric animals, including their spatial distribution, habitat range and connectivity, population estimates, and habitat carrying capacity, as well as dispersal mechanisms to determine when and where management intervention is needed.

Our study made contributions to developing biodiversity conservation strategies, including understanding interspecific interactions and habitat use of sympatric species at the landscape level. It is crucial for habitat management of large mammals that reside in highly fragmented habitats, especially when the population increases rapidly under 'umbrella protection effects'. Habitat expansion is the optimal condition for alleviating interspecific competitive pressure. The latest national giant panda survey report reveals that habitat fragmentation is currently the main limiting factor for giant panda population recovery (State Forestry and Grassland Administration 2021). Therefore, habitat restoration and ecological corridor establishment have been put forth via the China Giant Panda National Park as an important way to efficiently rejuvenate the wild giant panda population (Huang *et al.* 2020; State Forestry and Grassland Administration 2021). So far, although conservationists had conducted a great deal of research on the potential design of giant panda corridors, most of the plans had been created based on species occurrence data and habitat conditions of giant panda to mitigate the risk of reduced genetic diversity and local extinction (Wang *et al.* 2014; Wei *et al.* 2018). Those corridor plans, however, are far from enough to ensure sympatric species migration (Wang *et al.* 2018*c*; Li *et al.* 2021), which could in turn alleviate increased competition among sympatric species. We believe that an effective wildlife conservation strategy will not focus on just one species, but should comprehensively consider all species of the region. For instance, strengthening the construction of multi-species migration corridors could be a mechanism for density-dependent dispersal to mitigate interspecies competition.

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Data availability. Dataset and analyses reported in this article will be archived using the data provided in Dryad Digital Repository (https://datadryad.org/stash/share/ehk5Y7-PglMg5FGPXhJ8g7eFY5lGByQ08XqAs2Czfw8) (Bai *et al.* 2022).

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