

Shared resources between giant panda and sympatric wild and domestic mammals



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ABSTRACT

Interactions between sympatric species may negatively affect a species' fitness, and complicate management of species assemblages in protected areas. An example of the need to quantify the strength and direction of the species interactions is giant panda conservation in newly established reserves. Although the habitat requirements of giant panda have been broadly studied, the degree of its interactions with sympatric large mammals remains unclear. In this paper, we systematically surveyed for species occurrence in the southwestern China during 2008–2013, to better understand the interactions between giant panda and four sympatric large mammal species. We constructed species-specific occupancy models based on camera-trapping data using both environmental and detection variables. We then used the important predictor variables for each species to construct pairwise species co-occurrence models following a Bayesian framework. Our analysis detected significant habitat overlap between giant panda and its sympatric species. However, there was no evidence of native species limiting the distribution of giant pandas despite their extensive use of the same forests. The only evidence for negative interactions was between the distributions of giant panda and domestic cattle within bamboo forest, the primary habitat of giant pandas. The co-occurrence model has value for any conservation planning that benefits from knowledge of inter-species interactions. Our study suggests that, in southwestern China, strict grazing control of domestic cattle in protected areas is warranted until the nature of its interactions with native large mammals can be determined.

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1. Introduction

The interactions between species, either within or between taxonomic groups, play a significant role in structuring animal communities and can range from mutually beneficial (Arnan et al., 2011; Ovaskainen et al., 2010) through neutral (Arnan et al., 2011) to mutually harmful (Pollock et al., 2014). For species of similar body size and foraging strategies, interactions may lower the fitness of at least one species in the dyad (Acebes et al., 2012; Waddle et al., 2010). For example, in the deserts of Argentina, the increased density of domestic donkeys (*Equus asinus*) had a negative impact on the distribution and abundance of guanacos (*Lama guanicoe*), a finding which led to recommended management policies for controlling domestic equids (Acebes et al., 2012). Sites occupied by invasive tree frogs (*Osteopilus septentrionalis*) in Florida reduced the probability of occupancy for 2 native species, *Hyla cinerea* (9 times less likely) and *Hyla*

Squirella (15 times less likely), indicating these species interactions influenced the community assemblage (Waddle et al., 2010). By measuring the proportion of species' pairs that do not co-occur in sets of communities, Kamilar and Ledogar (2011) found that primate communities are not randomly structured and may be the result of interspecific competition. If endangered animals interact with sympatric species, knowledge on the strength and direction of these interactions is important for conservation planning (Acebes et al., 2012; Angelini et al., 2011).

The giant panda (*Ailuropoda melanoleuca*) is an endangered species distributed in approximately 24 habitat patches among six mountain ranges in China (State Forestry Administration, 2006). Giant pandas share distribution with multiple large mammal species whose ranges are broader and often whose local populations are higher in numbers, such as takin (*Budorcas taxicolor*), Asiatic black bear (*Ursus thibetanus*), wild boar (*Sus scrofa*), and domestic cattle (*Bos taurus*) (IUCN, 2000). While the habitat requirements of giant panda have been well studied during the past decades (Liu et al., 2005; Wei et al., 1995; Zhang et al., 2011), the degree to which other large mammal impact giant panda remains unclear.

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The annual giant panda monitoring conducted by nature reserves has revealed several dramatic population declines or distribution shifts in some reserves; some of which were speculated to be the consequences of species' interactions. For example, the avoidance of takin was given as the most probable explanation for the reduced abundance of giant pandas in Tangjiahe Nature Reserve (Wan et al., 2005). Takin and goral (*Naemorhedus griseus*) have been considered "competitive species" due to their heavy consumption of bamboo leaves, while Asiatic black bear and wild boar are believed to alter giant panda habitat selection through their foraging on bamboo shoots (Gong et al., 2006). Ran et al. (2002a) speculated that resource competition and habitat overlap caused livestock to negatively affect giant panda distribution in both the Xiangling and Liangshan Mountains. Hull et al. (2014b) reported domestic horse distributions overlap with suitable giant panda habitat, and speculated that bamboo consumption by horses may have caused observed population declines of giant panda. However, most discussions are speculative (Gong et al., 2006; Wan et al., 2005), or based on indirect evidence from each species' habitat selection (Hull et al., 2014b; Ran et al., 2002a,b).

Quantifying the strength and direction of the interactions between giant panda and sympatric species (both inter- and intra-guild) requires co-occurrence analysis (MacKenzie et al., 2004; Pollock et al., 2014). The presence-absence matrices of any two species inevitably involve multiple factors (e.g., habitat preferences, physiological tolerances, and detection probabilities), some of which are likely to create non-random patterns of species co-occurrence that merely reflect dissimilar habitat preferences instead of actual interactions between the species (MacKenzie et al., 2004; Miller et al., 2012). To differentiate between similar covariate responses and species avoidance or attraction, co-occurrence models provide a powerful tool for constructing interaction models by accounting for species-specific detection probabilities and habitat preferences, as well as species interactions (Gotelli and Ulrich, 2010).

The purpose of this study was to examine the interactions between giant pandas and sympatric large-bodied herbivores (takin, wild boar, and domestic cattle) and the only other ursid species sharing the same habitat (Asiatic black bears). As the reserve system in this region of China was established to conserve giant pandas, which remain at low population densities, our focus was the impact of the more abundant species on giant panda distribution, and not on how the presence of giant panda might impact other species. Our objectives were to use the knowledge on species associations to guide conservation planning for giant panda by: (1) quantify associations in forest landscapes for select sympatric species in southwestern China, and (2) introduce a Bayesian framework for species co-occurrence models. Using this large mammal community as an example, we present a hierarchical approach for modelling interactions between species with variable landscape affinities and detection probabilities.

2. Material and method

2.1. Study area

We used portions of forest habitat among three mountain ranges (Qinling, Minshan, and Qionglai Mountains) as our study area (Fig. 1). These three mountain ranges harbor approximately 89% of the wild giant panda population (State Forestry Administration, 2006), and are within a biodiversity hotspot of global significance (Myers et al., 2000). The study area has a rugged terrain with a broad elevation range varying from 1190 to 4450 m. The original forest composition along the elevation gradient (from low to high) is early successional fields, broadleaf forest,

conifer-deciduous mixed forest, and conifer forest (Tang and Ohsawa, 2002; Zhang, 2001). The landscapes have been significantly altered by agriculture, commercial logging, highway construction, and other human activities in the past decades (Loucks et al., 2001).

2.2. Sampling design and data collection

Our field investigations were conducted in and around eight nature reserves (Wanglang, Wolong, Tangjiahe, Changqing, Huangbaiyuan, Niuweihe, Xiaohegou, and Laohegou Nature Reserves) in Sichuan and Shaanxi Province (102.89°–107.67° E, 30.81°–33.82° N, Fig. 1) from March 2008 through March 2013. We created 1 × 1 km² sampling grids in and around these eight reserves, and conducted camera-trapping surveys in selected cells (see Li et al., 2010a, 2012, and Wang et al., 2014 for details). At the beginning of each sampling period, we randomly selected grid cells and placed one survey location in each selected grid cell at the best location that was identified by field staff. Cameras (CamTrakker™ Digital Ranger or Reconyx™ PC800/900) were mounted on trees at 40 cm height and operated 24 h per day with a 20 s delay between sequential photographs. Most camera stations were baited with commercial carnivore scent lure (Carman's Magna-Glan Lure, Montgomery Fur Company, UT, USA) upon deployment to slow animal movement around the camera to ensure sufficient reaction time for the camera sensor (Barea-Azcón et al., 2007; Crooks, 2002). At the end of each survey period (30–50 days, mean 36 days), the digital flash cards were collected, and the cameras were moved to the next survey locations (Li et al., 2012).

For environmental variables, we reviewed previous habitat studies for each target species (Li et al., 2007; Ran et al., 2002b; Schaller et al., 1989), and identified six variables that may affect their occupancy probabilities (Table S1). We used a 30-m resolution DEM (ASTER, 2009) to delineate the elevation and slope raster. During camera deployment, field staff recorded the presence or absence of bamboo understorey at each survey location, and identified the forest age (primary or secondary forest) and composition (broad-leafed, mixed, or coniferous forest). Geo-referenced data of human residences were obtained from the Shaanxi and Sichuan Forestry Departments. GIS layers were standardized to 100 × 100 m spatial resolution, and the mean value of elevation and slope, and the distance from each survey location to residences was calculated using ArcToolbox in ArcGIS 10.2 (ESRI, 2013).

We identified three variables that may affect the detection probabilities of our target species: monthly mean temperature, scent lure persistence, and camera trap model (Table S1). We obtained monthly mean temperatures from WorldClim Data (Hijmans et al., 2004), and categorized the temperature during each survey period into low (<5 °C), medium (5–15 °C), or high (>15 °C) accordingly (Winchell and Doherty, 2008). We divided the time since scent lure application during each survey into short (within 10 days), long (11–20 days), and none (>20 days or not applied) (Li et al., 2010a,b), and categorized the trigger delay of our camera models at each survey location into short (≤1 s), or long (>1 s).

2.3. Data analysis

2.3.1. Occupancy modelling

We measured our survey effort by the number of 24 h periods (Tobler et al., 2008), and divided the camera-trapping duration at each survey location into 5-day segments (Li et al., 2010a). For each segment a species was considered "detected" if any detection was made during the 5 days, and "not-detected" otherwise. Prior to model construction, we examined the collinearity of variables

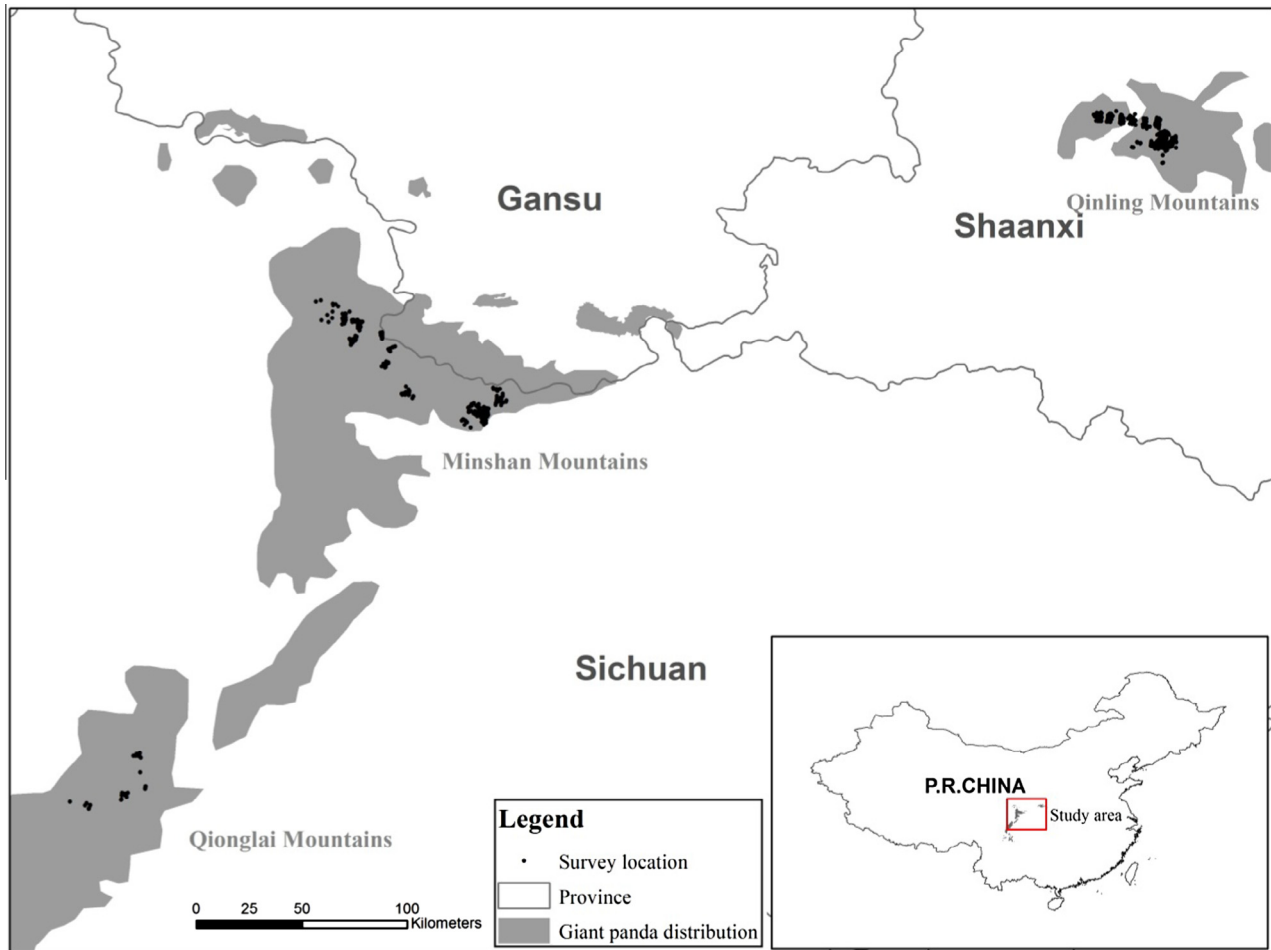


Fig. 1. Map of region and study design. 953 survey locations were investigated using camera-trapping in the three mountain ranges during 2008–2013 in Qinling Mountains, Minshan Mountains, and Qionglai Mountains.

and excluded the variables that have a pairwise correlation >0.5 for subsequent analyses.

We randomly selected 100 sample locations for model validation, and used the remaining locations to construct the occupancy models for each species. Prior to occupancy modelling, we examined the collinearity using Spearman's rho, and selected covariates that have a pairwise correlation <0.5 for subsequent analyses (Dormann et al., 2013). To select significant detection variables, we first constructed a general occupancy model that included all occupancy variables, and then investigated all combinations of the 3 possible detection covariates. We selected the top performing models based on their AIC value, and only included the detection variable identified in the top models were used in subsequent occupancy models (Erb et al., 2012). To estimate the occupancy probability of each species, all possible combinations of the six occupancy variables were examined and ranked according to the AIC values (Wang et al., 2014). A model-averaging approach was applied to calculate the weight-averaged weights for all variables included in the top models, as indicated by delta AIC values ≤ 2 (Burnham and Anderson, 2002). Occupancy variables with model-averaged weights larger than 0.4 were identified as most contributing variables, and were used in further species co-occurrence analysis.

During the process of model validation, we used the random 100 sample locations to construct receiver operating curves (ROC) for each species, and calculated the areas under ROC (AUC) to test the reliabilities of our species occupancy models. All

occupancy modelling was conducted using the “unmarked” package in R (Fiske and Chandler, 2011).

2.3.2. Modelling species co-occurrence

For construction of the species co-occurrence models, we followed an established approach (Waddle et al., 2010), and used the optimal detection and occupancy variables to construct the models within a Bayesian framework. By accounting for detection probabilities, species habitat preferences and interactions, the Bayesian approach used can obtain unbiased estimates of species interactions based on incomplete observation histories (Gotelli and Ulrich, 2010; Pollock et al., 2014). We assumed the giant panda occupancy and detection were dependent on the optimal occupancy and detection variables, as well as the presence or absence of the other more abundant species (i.e., takin, Asiatic black bear, wild boar, and cattle), but the occupancy and detection of the more abundant species was not dependent on the presence of giant panda.

Since giant pandas are constrained to forest with a bamboo understory (Liu et al., 2005; Zhang et al., 2011), we compared the conditional occupancy probabilities of giant panda within bamboo understories: if the occupancy probability of giant panda does not depend on the presence of more abundant species (species A), then $\Psi^{\text{Panda}|A}$ (conditional probability of occupancy of giant panda given that Species A is present) and $\Psi^{\text{Panda}|\bar{A}}$ (conditional probability of occupancy of giant panda given that Species A is absent) will be statistically equal.

We implemented the model in the software WinBUGS accessed through the program RStudio, version 0.98.977 using the package R2WinBUGS (BRugs et al., 2013). Three chains are launched for 100,000 iterations with a burn-in period of 50,000 iterations and MCMC convergence checked by visual inspection and the value of r -hat (Lecomte et al., 2013). A thinning of 10 iterations is performed in order to get rid of within-chain autocorrelation. The model code and run specifications can be found in the Supplementary material.

3. Results

From 2008 to 2013, we surveyed 953 locations in the three mountain ranges, including 592 locations in the Qinling Mountains, 318 locations in the Minshan Mountains, and 43 locations in the Qionglai Mountains. The total survey effort was 30,836 camera nights. Giant pandas were detected at 128 survey locations, takin were detected at 279 survey locations (45 locations overlapped with giant panda), wild boar were detected at 210 locations (36 locations overlapped with giant panda), Asiatic black bear were detected at 70 locations (9 locations overlapped with giant panda), and domestic cattle were detected at 29 locations (no overlap with giant panda). The survey locations where focal species were detected overlapped in their environmental attributes (Table S2).

3.1. Species habitat preferences

All six environmental variables were retained for model construction because no significant collinearity was detected (Spearman's $\rho < 0.5$). Each species had a unique set of important detection variables (Table 1 and 2 and S3). In the model selection for each species, we compared 64 plausible models using the AIC values, and selected the top models for each species (Table S3). The occupancy probabilities of giant pandas were highest in primary forest with a bamboo understory in areas where the slope was less steep. Takin's occupancy probabilities were highest in

conifer or mixed primary forest with bamboo understory at higher elevation. The Asiatic black bear had highest occupancy probabilities in primary broad-leaved forest at higher elevation. The occupancy probabilities of wild boar increased at sites with lower elevation, less slope, and closer to residences. The occupancy probabilities of domestic cattle decreased on steep slopes within primary forest with bamboo understory, and increased with elevation.

When comparing our predictive occupancy model to the validation dataset, the AUC values indicated strong predictive abilities of our species models (Fig. S1, AUC values: giant panda 0.734; takin 0.747; Asiatic black bear 0.706; wild boar 0.700; domestic cattle 0.825).

3.2. Species co-occurrence

Species showed similarity in habitat preference to giant panda through their association with bamboo understory (takin and wild boar), flat terrain (wild boar, Asiatic black bear, and domestic cattle), and primary forest (takin and Asiatic black bear) (Table 2). As giant pandas showed a significant affinity for forests with bamboo understory, we examined the pattern of their overlap with other focal species at locations within forests with a bamboo understory ($n = 747$). Four species co-occurrence models were constructed. The r -hat values of our parameter estimations were smaller than 1.01, which indicated good convergences of our models. The species-environment relationship predicted by co-occurrence models matched those identified by the occupancy models (Table S4), which indicated the consistency of our model performances.

For sample sites within forests with bamboo understory ($n = 747$), the occupancy probability (ψ) of giant panda was significantly lower (45% decrease) at locations occupied by domestic cattle ($\psi = 0.29 \pm 0.14$) than locations without domestic cattle ($\psi = 0.42 \pm 0.11$) (Table 3, Fig. 2). The occupancy probabilities of giant panda were not affected by the presence of the other herbivore species (i.e., takin or wild boar). Giant panda showed a strong co-occurrence with Asiatic black bear, as locations with Asiatic black bears ($\psi = 0.68 \pm 0.12$) were more likely to be occupied by giant pandas than locations without Asiatic black bears ($\psi = 0.19 \pm 0.05$) (Table 3).

Table 1

Top logistic models for giant panda. We selected the top performed occupancy models with smallest AIC values (as indicated by delta AIC values ≤ 2). The models are composed of both occupancy and detection (p) variables, and weighted by their delta AIC values.

p (Tem, Dly) ^a	K	LL ^b	AICc	delta. AICc	AIC weight	Est. p^c
Slo, Bam	4	-712.03	1432.10	0.00	0.23	0.103
Bam	3	-713.25	1432.52	0.42	0.19	0.103
Slo, Bam, Age	5	-711.46	1432.99	0.89	0.15	0.103
Bam, Age	4	-712.63	1433.31	1.20	0.13	0.103
Slo, Bam, For	5	-711.71	1433.49	1.38	0.12	0.103
Ele, Slo, Bam	5	-711.77	1433.61	1.51	0.11	0.103
Bam, For	4	-713.03	1434.11	2.00	0.08	0.103

^a p : detection probability; Tem: temperature; Dly: trigger delay; Lur: scent lure effectiveness; Ele: elevation; Slo: slope; Bam: bamboo understory; Res: distance to residences; For: forest composition; Age: forest age.

^b LL: LogLikelihood.

^c Est. p : estimated detection probability.

Table 2

Weights of environmental variables based on occupancy models. Significant environmental variables for each species' occupancy model were selected, and their weights were calculated based on the model-averaging method. Variables with weights less than 0.15 were not included in the table.

Species	Elevation	Slope	Bamboo	Distance to residences	Forest composition	Forest age
Giant panda		-(0.61)	+(1.00)		+(0.20)	+(0.28)
Takin	+(1.00)	+(0.17)	+(1.00)		+(0.69)	+(0.67)
Wild boar	-(1.00)	-(0.51)	+(1.00)	-(0.51)		-(0.21)
Asiatic black bear	+(1.00)	-(0.32)		+(0.18)	-(0.82)	+(0.33)
Domestic cattle	+(1.00)	-(0.49)	-(1.00)			-(0.28)

Table 3

Conditional occupancy probabilities of giant panda in forest with bamboo understory. The occupancy probability of giant panda ($\psi_{\text{giant panda}}$) was significantly lower at locations within bamboo forest that were occupied by domestic cattle, and were not affected by the presence of the other herbivore species (i.e., takin or wild boar). In addition, giant panda showed a strong co-occurrence with Asiatic black bear.

Species	Condition	$\psi_{\text{giant panda}} \pm \text{SD}$
Takin	Presence	0.40 \pm 0.07
	Absence	0.42 \pm 0.07
Asiatic black bear	Presence	0.68 \pm 0.12
	Absence	0.19 \pm 0.05
Wild boar	Presence	0.39 \pm 0.08
	Absence	0.42 \pm 0.08
Domestic cattle	Presence	0.29 \pm 0.14
	Absence	0.42 \pm 0.11

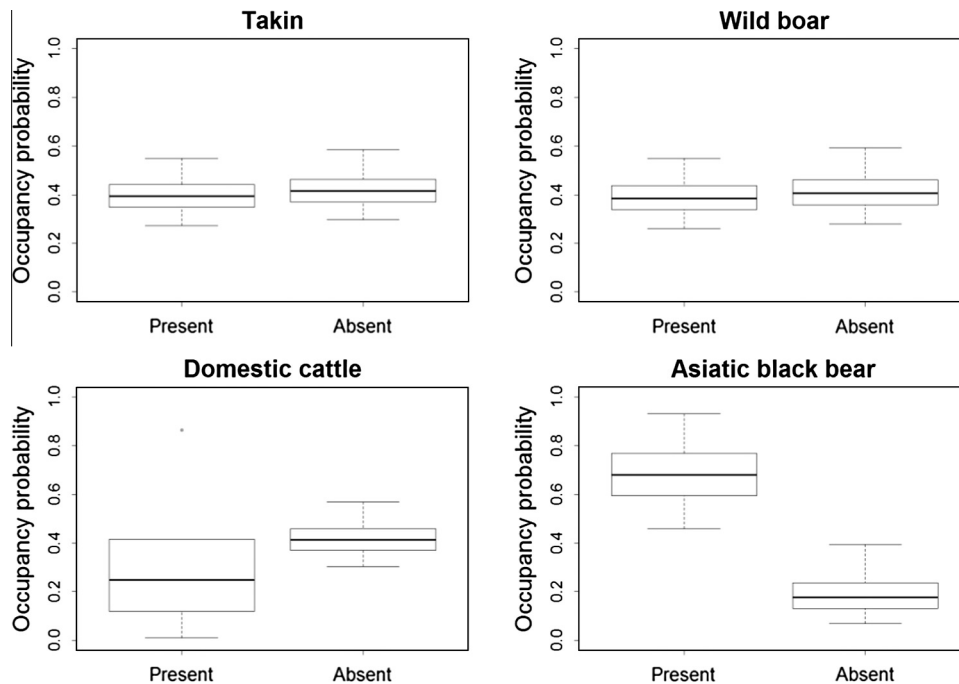


Fig. 2. The conditional occupancy probabilities of giant panda with target species within forests with bamboo understory. The occupancy probability of giant panda was significantly lower at locations where domestic cattle were present ($\psi_{\text{giant panda}} \pm \text{SD}$: 0.29 ± 0.14) than locations where domestic were absent (0.41 ± 0.11). The occupancy probability was higher at locations where Asiatic black bear were present (0.68 ± 0.12) than locations where Asiatic black bear were absent (0.19 ± 0.05). The occupancy probability of giant panda was not affected by the occupancy statuses of takin and wild boar.

4. Discussion

When nature reserves are established for the conservation of a single charismatic species, there is an implicit understanding that this conservation effort will act like an “umbrella” to protect other more common species within the ecosystem (Nicholson and Possingham, 2006; Roberge and Angelstam, 2004). The reserve system established for giant pandas in China is a perfect example of this concept (Kontoleon and Swanson, 2003; Lu et al., 2000). At a practical level, conservation of a focal species does not always result in co-occurring species increasing (Andelman and Fagan, 2000), as some species are limited by ecological factors that are not relevant to the umbrella species (Roberge and Angelstam, 2004), or the management requirements of two flagship species can conflict (Simberloff, 1998). For example, predator control in areas established to conserve endangered birds (Bolton et al., 2007) or mammals (Van Ballenberghe, 2006) are examples of how conservation priorities prevent the unregulated increase of all native species. Managers with focused conservation efforts often are concerned about other species interfering with their ability to meet objectives for their priority species.

For managers within reserves established for giant pandas, their initial concerns about establishing marked boundaries, patrolling stations and training staff have evolved to goals for population increases in giant pandas. The advantage of the giant panda census conducted at regular intervals is that relative (if not absolute) numbers of giant pandas can be tracked at the reserve level (State Forestry Administration, 2006; Zhang et al., 2011). When giant panda numbers decrease between census efforts, one possible explanation is that available habitat or food is limited within the reserve due to competition with sympatric wildlife (Gong et al., 2006; Ran et al., 2003). The last five years have seen repeated requests by reserve managers for permission to limit large mammal (usually ungulate) populations within giant panda reserves in order to reduce competition for bamboo (GU Xiaodong, personal communication).

Our occupancy models suggested that giant panda preferred primary forest over secondary forest, which is one of the most significant predictors determining its occupancy after bamboo understory and slope (Table 2), a result consistent that reported by Zhang et al. (2011). However, a broader review on the habitat selection of giant panda has indicated that, although improper logging or restoration practices (i.e., early successional forest after clearcutting) may have negative impact on habitat use of giant panda, they can select both primary and secondary forests, as long as sufficient bamboo understory is available (Hull et al., 2014a).

Our analysis found no evidence of native species limiting giant panda distributions within reserves set up for their conservation. With regards to interactions with giant pandas, we observed both habitat segregation and co-occurrence with sympatric large mammals. The only evidence for a negative interaction was between the distributions of giant panda and domestic cattle in forests with a bamboo understory. For the other species that consume bamboo leaves (takin) or shoots (Asiatic black bears or wild boar) or share winter den characteristics (Asiatic black bears), the high spatial overlap did not decrease the presence of giant pandas. We acknowledge that not all competition between pandas and the other species would be reflected in spatial avoidance, but spatial avoidance is one strong indicator that interactions exist (Pollock et al., 2014; Waddle et al., 2010).

Our primary concern was the relationship between giant pandas and two other threatened species in the region, takin and Asiatic black bears. All three species are conservation-dependent species that rely on the protection afforded by the newly created reserves to persist in a human dominated landscape (Li et al., 2007; Liu et al., 2009). Takin are major consumers of bamboo during winter months (Guan et al., 2015; Wu and Hu, 2000), and exhibit the same positive association with primary forest as observed in giant pandas (Zhang et al., 2011), but we found no evidence for avoidance of takin by giant pandas. Our results were in contrast with other studies that postulated giant pandas were negatively affected by takin (Gao et al., 2006; Gong et al., 2006; Wan et al.,

2005). The segregation between the two conservation-dependent species would create a planning conflict for nature reserves with both species. These studies based their conclusion on extensive habitat overlap, which we also found, but our Bayesian approach to co-occurrence modelling allowed us to better isolate correlated factors and we found no reason for conservation concern. The Bayesian approach has been used to examine other dyads. For example, the start of hunting seasons (Ordiz et al., 2012) and direct encounters (Ordiz et al., 2013) with people were found to alter brown bear (*Ursus arctos*) movements in Scandinavia.

The frequent human-wildlife conflicts involving Asiatic black bears along the boundaries of reserves (Liu et al., 2011) make reserve managers reluctant to support increased bear numbers, especially if such an increase threatened their primary mission of increasing giant panda populations. The positive co-occurrence pattern between giant panda and Asiatic black bear was unexpected. It may not represent the actual species interactions, but rather was the consequence of their shared avoidance of humans. As a habitat generalist distributed over a large expanse in China (Reid et al., 1991), black bears are not under the same habitat limitations experienced by giant pandas (e.g. we found a neutral association with bamboo understory), so the observation is not due to a shared microhabitat preference (Arnan et al., 2011). The continued positive association outside of bamboo forests, even when giant panda detections were very low, supports the hypothesis that the association is not habitat related. However, the Asiatic black bears are under severe poaching threats, as the bears are killed mainly for their gall bladder and paws (Liu et al., 2011). In our study, the shared occupancy of Asiatic black bear and giant panda might represent the occurrence of less poaching pressures within better managed reserves (Wang et al., 2006).

The significant negative relationship between domestic cattle and giant panda in forests with a bamboo understory builds on the results of previous studies (Hull et al., 2014b; Kang et al., 2011; Ran et al., 2002b). Ran et al. (2002a,b) observed that grazing cattle overlapped in elevation with giant panda in the Xiaoxiangling Mountains, and they hypothesized such overlap would cause major disturbance on giant panda population. Further north in the Minshan Mountains, Kang et al. (2011) speculated the similarity in habitat selection of giant panda and livestock may lead to resource competition, and our co-occurrence analysis lends support to their hypotheses. Both studies advocated strict grazing controls based on habitat overlap and our results support this recommendation. Studies of other large mammal systems have described a broad spectrum of negative effects of livestock on wildlife. In xeric ecosystems of North America, 11 of 16 analyses revealed significant detrimental effects of cattle grazing on wildlife communities (Jones, 2000). Resource competition was observed between cattle and zebras in a semi-arid savanna in Laikipia, Kenya (Young et al., 2005). Common mammal species were negatively influenced by livestock, and relative conservation decisions were advocated in Mediterranean forests that were human-altered (Mangas and Rodríguez-Estival, 2010). Our study, conducted in a moist temperate forest, found similar impacts by livestock on native species.

Our study was not designed to determine the nature of the negative relationship between domestic cattle and giant panda. We speculated two possible reasons that could explain the negative associations between giant panda and domestic cattle: (1) giant pandas are avoiding human activities related to cattle; or (2) the domestic cattle altered the habitat attributes and lowered habitat suitability to giant panda. Among 157 locations that had giant panda or domestic cattle detections, only 5 locations detected human activities. Although local villagers travel deep into the nature reserves to check their cattle, the low villager detection rate suggested the observed giant panda avoidance was due to livestock

activities. Domestic cattle are free-ranging and annually spend up to ten months inside the reserves. Livestock can alter forest dynamics by reducing the biomass of understory grasses in upland forests in western United States (Belsky and Blumenthal, 1997), so it is possible livestock remove sufficient bamboo to reduce habitat suitability for giant pandas. In addition to possible competition over forage between domestic cattle and giant panda, cattle grazing may further affect other ungulate species by introducing disease into wild populations (Cleaveland et al., 2001). As grazing activities in nature reserves in southwestern China have significantly increased in the past decade (Hull et al., 2014b; Kang et al., 2011), we believe strict grazing control of domestic cattle in protected areas should be reinforced until the extent of their interaction with native large mammals can be determined.

The persistence of biodiversity is the primary goal of conservation planning (Nicholson and Possingham, 2006), and requires managers to shift from single species conservation initiatives to multiple-species conservation plans (Barrows et al., 2005). Although each species had different habitat preferences, all the three conservation-dependent species in our study (giant panda, takin, and Asiatic black bear) had a positive relationship with mature forest and bamboo understory. Current restoration activities within these reserves is focused on protecting forests and restoring the bamboo understory (Shen et al., 2008; Zhang et al., 2011), activities which will increase available habitat for all three species and reserve managers should have minimal concern for negative interactions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.03.032>.

References

- Acebes, P., Traba, J., Malo, J.E., 2012. Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *J. Arid Environ.* 77, 39–44.
- Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proc. Natl. Acad. Sci.* 97, 5954–5959.
- Angelini, C., Altieri, A.H., Silliman, B.R., Bertness, M.D., 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience* 61, 782–789.
- Arnan, X., Gaucherel, C., Andersen, A., 2011. Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. *Oecologia* 166, 783–794.
- ASTER, G., 2009. Validation Team, In ASTER Global DEM Validation Summary Report.
- Barea-Azcón, J.M., Virgós, E., Ballesteros-Duperón, E., Moleón, M., Chiroso, M., 2007. Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. *Biodivers. Conserv.* 16, 1213–1230.
- Barrows, C.W., Swartz, M.B., Hodges, W.L., Allen, M.F., Rotenberry, J.T., Li, B.-L., Scott, T.A., Chen, X., Morrison, 2005. A framework for monitoring multiple-species conservation plans. *J. Wildlife Manage.* 69, 1333–1345.

- Belsky, A.J., Blumenthal, D.M., 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conserv. Biol.* 11, 315–327.
- Bolton, M., Tyler, G., Smith, K.E.N., Bamford, R.O.Y., 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. *J. Appl. Ecol.* 44, 534–544.
- BRUGS, S., WinBUGS, S., Ligges, M.U., 2013. Package 'R2WinBUGS'.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer.
- Cleaveland, S., Laurenson, M., Taylor, L., 2001. Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 356, 991–999.
- Crooks, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv. Biol.* 16, 488–502.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Erb, P.L., McShea, W.J., Guralnick, R.P., 2012. Anthropogenic influences on macro-level mammal occupancy in the Appalachian trail corridor. *PLoS ONE* 7, e42574.
- ESRI, 2013. 10.2 Desktop help. ESRI, Redlands, CA. ArcGIS 10.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* 43, 1–23.
- Gao, X.-Y., Liu, Y., Liu, D.-Z., 2006. Analysis on the growth of bamboo species *Bashania fargesii* selection of giant pandas in Qinling mountains. *Zool. Res.* 2, 157–162.
- Gong, H., Zeng, Z., Gao, X., 2006. Species of birds and mammals feeding on bamboo in Foping national nature reserve. *Chin. J. Zool.* 41, 31.
- Gotelli, N., Ulrich, W., 2010. The empirical Bayes approach as a tool to identify non-random species associations. *Oecologia* 162, 463–477.
- Guan, T., Wang, F., Li, S., McShea, W.J., 2015. Nature reserve requirements for landscape-dependent ungulates: The case of endangered takin (*Budorcas taxicolor*) in Southwestern China. *Biol. Conserv.* 182, 63–71.
- Hijmans, R., Cameron, S., Parra, J., Jones, P., Jarvis, A., 2004. The WorldClim interpolated global terrestrial climate surfaces. Version 1.3.
- Hull, V., Roloff, G., Zhang, J., Liu, W., Zhou, S., Huang, J., Xu, W., Ouyang, Z., Zhang, H., Liu, J., 2014a. A synthesis of giant panda habitat selection. *Ursus* 25 (2), 148–162.
- Hull, V., Zhang, J., Zhou, S., Huang, J., Viña, A., Liu, W., Tuanmu, M.-N., Li, R., Liu, D., Xu, W., Huang, Y., Ouyang, Z., Zhang, H., Liu, J., 2014b. Impact of livestock on giant pandas and their habitat. *J. Nat. Conserv.* 22, 256–264.
- IUCN, S.S.C., 2000. IUCN Red List of threatened species. IUCN, the World Conservation Union.
- Jones, A., 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. *Western North Am. Nat.* 60, 155–164.
- Kamilar, J.M., Ledogar, J.A., 2011. Species co-occurrence patterns and dietary resource competition in primates. *Am. J. Phys. Anthropol.* 144, 131–139.
- Kang, D., Zhao, L., Song, G., 2011. Competition relationship between giant panda and livestock in wanglang national nature reserve, Sichuan. *J. Northeast For. Univ.* 7, 022.
- 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 Econom.* 79, 483–499.
- Lecomte, J.B., Benoit, H.P., Etienne, M.P., Bel, L., Parent, E., 2013. Modeling the habitat associations and spatial distribution of benthic macroinvertebrates: A hierarchical Bayesian model for zero-inflated biomass data. *Ecol. Model.* 265, 74–84.
- Li, S.-H., Wang, J.-L., Chen, Y., 2007. A primary study on habitat selection of Gaoligong mountain takin. *Sichuan J. Zool.* 1, 013.
- Li, S., McShea, W.J., Wang, D., Shao, L., Shi, X., 2010a. The use of infrared-triggered cameras for surveying phasianids in Sichuan Province, China. *Ibis* 152, 299–309.
- Li, S., Wang, D., Gu, X., McShea, W.J., 2010b. Beyond pandas, the need for a standardized monitoring protocol for large mammals in Chinese nature reserves. *Biodivers. Conserv.* 19, 3195–3206.
- Li, S., McShea, W.J., Wang, D., Lu, Z., Gu, X., 2012. Gauging the impact of management expertise on the distribution of large mammals across protected areas. *Divers. Distrib.* 18, 1166–1176.
- Liu, X., Tsopeus, A.G., Skidmore, A.K., Shao, X., Dang, G., Wang, T., Prins, H.H., 2005. Giant panda habitat selection in Foping nature reserve, China. *J. Wildlife Manage.* 69, 1623–1632.
- Liu, F., McShea, W., Garshelis, D., Zhu, X., Wang, D., Gong, J.e., Chen, Y., 2009. Spatial distribution as a measure of conservation needs: an example with Asiatic black bears in south-western China. *Divers. Distrib.* 15, 649–659.
- Liu, F., McShea, W.J., Garshelis, D.L., Zhu, X., Wang, D., Shao, L., 2011. Human-wildlife conflicts influence attitudes but not necessarily behaviors: factors driving the poaching of bears in China. *Biol. Conserv.* 144, 538–547.
- Loucks, C.J., Lü, Z., Dinerstein, E., Wang, H., Olson, D.M., Zhu, C., Wang, D., 2001. Giant pandas in a changing landscape. *Science* 294, 1465.
- Lu, Z., Pan, W., Zhu, X., Wang, D., Wang, H., 2000. What has the panda taught us? *Conserv. Biol. Ser. – Cambridge*, 325–334.
- MacKenzie, D.I., Bailey, L.L., Nichols, J.D., 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *J. Anim. Ecol.* 73, 546–555.
- Mangas, J.G., Rodríguez-Estival, J., 2010. Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. *For. Ecol. Manage.* 260, 1274–1281.
- Miller, D.A.W., Brehme, C.S., Hines, J.E., Nichols, J.D., Fisher, R.N., 2012. Joint estimation of habitat dynamics and species interactions: disturbance reduces co-occurrence of non-native predators with an endangered toad. *J. Anim. Ecol.* 81, 1288–1297.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nicholson, E., Possingham, H.P., 2006. Objectives for multiple-species conservation planning. *Conserv. Biol.* 20, 871–881.
- Ordiz, A., Stoen, O., Sabo, S., Kindberg, J., Delibes, M., Swenson, J.E., 2012. Do bears know they are being hunted? *Biol. Conserv.* 152, 21–28.
- Ordiz, A., Stoen, O., Sabo, S., Sahlen, V., Pedersen, B.E., Kindberg, J., Swenson, J.E., 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. *J. Appl. Ecol.* 50, 306–314.
- Ovaskainen, O., Hottola, J., Siitonen, J., 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology* 91, 2514–2521.
- Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesik, P.A., McCarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods Ecol. Evol.* 5, 397–406.
- Ran, J., Liu, S., Wang, H., Sun, Z., Zeng, Z., Liu, S., 2002a. Effect of grazing on giant pandas' habitat in Yele nature reserve. *Acta Theriologica Sinica* 23, 288–294.
- Ran, J., Liu, S., Wang, H., Sun, Z., Zeng, Z., Liu, S., 2002b. Habitat selection by giant pandas and grazing livestock in the Xiaoxiangling Mountains of Sichuan Province. *Acta Ecol. Sin.* 23, 2253–2259.
- Ran, J., Liu, S., Wang, H., Zeng, Z., Sun, Z., Liu, S., 2003. A survey of disturbance of giant panda habitat in the Xiaoxiangling Mountains of Sichuan province. *Acta Theriologica Sinica* 24, 277–281.
- Reid, D., Jiang, M., Teng, Q., Qin, Z., Hu, J., 1991. Ecology of the Asiatic black bear (*Ursus thibetanus*) in Sichuan, China. *Mammalia* 55, 221–238.
- Roberge, J.-M., Angelstam, P.E.R., 2004. Usefulness of the umbrella species concept as a conservation tool. *Conserv. Biol.* 18, 76–85.
- Schaller, G.B., Qitao, T., Johnson, K.G., Xiaoming, W., Heming, S., Jinchu, H., 1989. The feeding ecology of giant pandas and Asiatic black bears in the Tangjiahe Reserve, China. In: *Carnivore Behavior, Ecology, and Evolution*. Springer, pp. 212–241.
- Shen, G., Feng, C., Xie, Z., Li, J., Pascal, M., 2008. Proposed conservation landscape for giant pandas in the Minshan Mountains, China. *Conserv. Biol.* 22, 1144–1153.
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biol. Conserv.* 83, 247–257.
- State Forestry Administration, 2006. The 3rd National Survey Report on Giant Panda in China. Science Press, Beijing.
- Tang, C., Ohsawa, M., 2002. Coexistence mechanisms of evergreen, deciduous and coniferous trees in a mid-montane mixed forest on Mt. Emei, Sichuan, China. *Plant Ecol.* 161, 215–230.
- Tobler, M., Carrillo-Percegué, S., Leite Pitman, R., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Anim. Conserv.* 11, 169–178.
- Van Ballenberghe, V., 2006. Predator control, politics, and wildlife conservation in Alaska. *Alces* 42, 1–11.
- Waddle, J.H., Dorazio, R.M., Walls, S.C., Rice, K.G., Beauchamp, J., Schuman, M.J., Mazzotti, F.J., 2010. A new parameterization for estimating co-occurrence of interacting species. *Ecol. Appl.* 20, 1467–1475.
- Wan, Q., Fang, S., Li, J., Zhang, L., Ou, W., Xian, F., Chen, W., 2005. A family net of giant pandas in the Tangjiahe natural reserve: assessment of current individual migration. *Chin. Sci. Bull.* 50, 1879–1886.
- Wang, D., Li, S., McShea, W.J., Li, M., 2006. Use of remote-trip cameras for wildlife surveys and evaluating the effectiveness of conservation activities at a nature reserve in Sichuan Province, China. *Environ. Manage.* 38, 942–951.
- Wang, F., McShea, W.J., Wang, D., Li, S., Zhao, Q., Wang, H., Lu, Z., 2014. Evaluating landscape options for corridor restoration between giant panda reserves. *PLoS ONE* 9, e105086.
- Wei, F., Zhou, A., Hu, J., Wang, W., Yang, G., 1995. Habitat selection by giant pandas in Mabian Dafengding Reserve. *Acta Theriologica Sinica* 16, 241–245.
- Winchell, C.S., Doherty, P.F., 2008. Using California Gnatcatcher to test underlying models in habitat conservation plans. *J. Wildl. Manage.* 72, 1322–1327.
- Wu, H., Hu, J., 2000. A comparison in spring and winter habitat selection of Takin, Sswift and Goral and Tangjiahe, Sichuan. *Acta Ecologica Sinica* 21, 1627–1633.
- Young, T.P., Palmer, T.M., Gadd, M.E., 2005. Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biol. Conserv.* 122, 351–359.
- Zhang, Q.-W., 2001. Studies on the composition, characteristics and geographic element of the family of seed plant flora in Qinling Mt. *Bull. Bot. Res.* 4, 010.
- 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. *Biol. Lett.* 7, 403–406.