



## Divergent responses of sympatric species to livestock encroachment at fine spatiotemporal scales



Jindong Zhang<sup>a,b,\*</sup>, Vanessa Hull<sup>a,c</sup>, Zhiyun Ouyang<sup>d</sup>, Rengui Li<sup>e</sup>, Thomas Connor<sup>a</sup>, Hongbo Yang<sup>a</sup>, Zejun Zhang<sup>b</sup>, Brad Silet<sup>a</sup>, Hemin Zhang<sup>e</sup>, Jianguo Liu<sup>a,\*\*</sup>

<sup>a</sup> Center for Systems Integration and Sustainability, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA

<sup>b</sup> Key Laboratory of Southwest China Wildlife Resources Conservation, China West Normal University, Ministry of Education, Nanchong, China

<sup>c</sup> Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

<sup>d</sup> State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-environmental Sciences, Chinese Academy of Sciences, Beijing, China

<sup>e</sup> China Conservation and Research Center for the Giant Panda (CCRCGP), Wolong Nature Reserve, Sichuan, China

### ARTICLE INFO

#### Article history:

Received 16 November 2016

Received in revised form 1 January 2017

Accepted 6 February 2017

Available online xxxx

#### Keywords:

Coupled human and natural systems

Livestock

Protected areas

Sustainability

### ABSTRACT

Livestock are a major human-induced threat to wildlife worldwide, especially in forest landscapes where livestock degrade the food and habitat of forest-dwelling wildlife. However, few empirical studies on this topic have been conducted at fine spatiotemporal scales that are crucial for wildlife-livestock interactions, in particular those involving multiple sympatric wildlife species under policy changes. Here, we demonstrate wildlife-livestock interactions through examining the interactions of several sympatric, threatened wildlife species with livestock in Wolong Nature Reserve, China, using data collected from infrared camera traps, DNA analysis of panda fecal samples and panda distribution predictive modeling along with habitat predictors. Camera trapping revealed an increase in livestock after the government implemented an incentive policy to encourage livestock production midway through the study. Three species (giant panda, red panda, and golden snub-nosed monkey) were displaced as more livestock encroached on forest habitat. In contrast, the detection rate of sambar deer was not affected by livestock encroachment, but sambar shifted the timing of visiting water sources (streams) to dusk (when livestock disturbance and other human activities were lower). The number of giant pandas detected via DNA testing of feces was relatively stable, but panda distribution modeling showed that pandas occurred across a wider area after disturbance. Our research shows that with increased livestock, different wildlife species may respond in different ways, which is likely associated with their biological traits (e.g., life history strategy and diet). Our study underscores the need for careful livestock policy making and planning.

© 2017 Elsevier Ltd. All rights reserved.

### 1. Introduction

With the increase in the global human population and industrialization of human societies, competition between people and wildlife for limited resources such as space has become increasingly intense (Cohen, 2003; Imhoff et al., 2004; Liu et al., 2016a). To help reduce habitat and species losses, protected areas have been established worldwide. In fact, the number of protected areas has increased over 200% from 1990 to 2014 (Juffe-Bignoli et al., 2014). However, in many instances, habitats have declined even after protected areas are established due to the inability to curb increasing human pressures (Liu et al., 2001; Wittemyer et al., 2008). A clear understanding of the

responses of wildlife to such human encroachment has become one of the most important research needs to inform the design and management of protected areas (Carter et al., 2012; Carter et al., 2014; Wittemyer et al., 2007).

The threat of livestock to wildlife has increased in recent years in many protected areas worldwide (Namgail et al., 2007; Steinfeld et al., 2006; Hull et al., 2014). This is especially the case in forest landscapes, where livestock may trample seedlings, remove understory vegetation, alter forest structure, introduce invasive species, compete for food with wildlife, and degrade soils (Endress et al., 2004; Hobbs, 2001; Hull et al., 2014; Wassie et al., 2009). These impacts in turn have cascading effects on forest-dwelling wildlife that rely on forest resources for survival (Madhusudan, 2004; Mishra et al., 2004; Namgail et al., 2007). Yet compared to other human activities such as hunting and logging, livestock grazing is often regarded as a low-level human disturbance and is usually not restricted, even in protected areas (Bragina et al., 2015; Liu et al., 2001). As a result, studies about the impacts of livestock on wildlife are relatively scarce and have mainly focused on a single species, including

\* Correspondence to: J. Zhang, Center for Systems Integration and Sustainability (CSIS), Michigan State University, 1405 S. Harrison Road, Suite 115 Manly Miles Bldg., East Lansing, MI 48823-5243, USA.

\*\* Corresponding author.

E-mail addresses: [zhangjd224@163.com](mailto:zhangjd224@163.com) (J. Zhang), [liuji@msu.edu](mailto:liuji@msu.edu) (J. Liu).

umbrella species such as tigers (*Panthera tigris*) (Carter et al., 2012), giant pandas (*Ailuropoda melanoleuca*) (Hull et al., 2014), leopards (*Panthera pardus*) (Carter et al., 2015), or brown bears (*Ursus arctos Linnaeus, 1758*) (van Gils et al., 2014). Information gathered from such studies, when taken alone, might mislead the managers to implement policies that protect one species at the expense of other species. Studies at fine spatial-temporal scales and in response to on-the-ground policies are particularly lacking. Such studies could inform the design of policies and management plans aimed at co-managing humans and nature, particularly in dynamic systems where perturbations such as sudden policy shifts can have surprising or unintended consequences (Liu et al., 2015a; Mawdsley et al., 2009).

To fill the important knowledge gaps, here we present a fine-scale analysis of the spatiotemporal patterns of behavior of several sympatric and threatened wildlife species monitored using infrared camera trapping over a four-year period (2011–2014) in Wolong Nature Reserve, Sichuan, China. We estimated the relative abundance of wildlife and the relative intensities of livestock grazing and other human activities (e.g. medicinal herb collection and poaching) over time and space. In particular, we explored the response of the different wildlife species to a sudden change in policy in the reserve that promoted livestock grazing mid-way through our study period. To provide further context for the camera trapping results, we also compared changes in detections of giant pandas (a key species of interest in our study area) before and after the livestock policy using (a) individual identification of pandas via DNA analysis of feces and (b) predictions of the giant panda habitat distribution derived from maximum entropy models on panda feces presence points sampled over time. Our study has implications

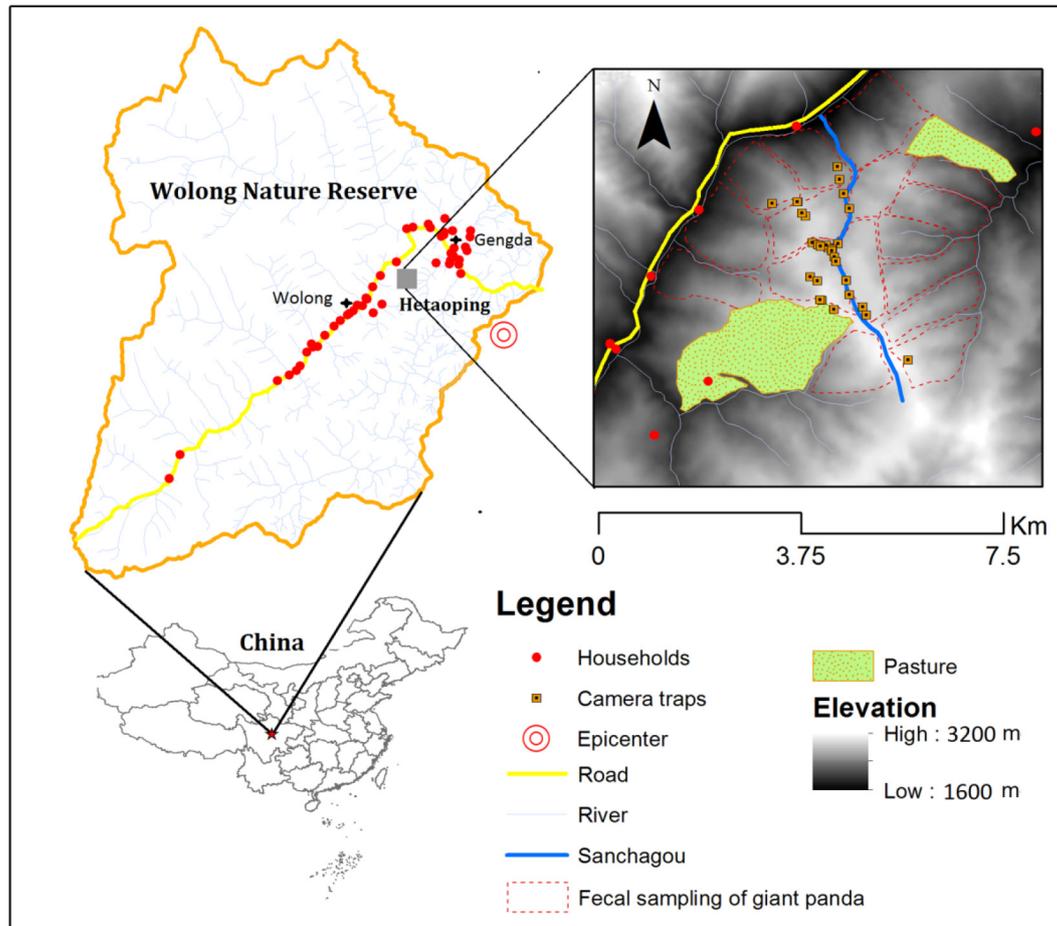
for the design and management of protected areas worldwide which aim to conserve sympatric wildlife species undergoing close interactions with livestock.

## 2. Materials and methods

### 2.1. Study area

The study was carried out in Wolong Nature Reserve (102°52'–103°24'E, 30°45'–31°25'N), which lies in Sichuan Province, southwest China (Fig. 1). This flagship reserve was established in 1963 and is one of the earliest protected areas for conserving giant pandas (*Ailuropoda melanoleuca*) and forest ecosystems in China, covering an area of about 2000 km<sup>2</sup>. The reserve is located within one of the top 25 global biodiversity hotspots, and houses over 100 wild giant pandas (Myers et al., 2000; Sichuan Provincial Forestry Department, 2015). There are also thousands of other plant and animal species living in the reserve, including several endangered and threatened species such as the sambar (*Cervus unicolor*), golden snub-nosed monkey (*Rhinopithecus roxellanae*), red panda (*Ailurus fulgens*), and takin (*Budorcas taxicolor*).

There are two towns located in the reserve (Wolong and Gengda) (Fig. 1), each of which has 3 villages. As of 2012, there were 4933 local residents in around 1436 households located within the reserve (Liu et al., 2016a). Local people mainly farm for their livelihood and affect the local biodiversity in a number of ways, including cultivation, medicinal herb collection, livestock rearing, fuelwood collection, poaching, and road construction (An et al., 2001; Liu et al., 2016a; Liu et al., 2001; Liu et al., 1999a). These activities have in



**Fig. 1.** Study area for infrared camera trap monitoring of wildlife and human activities in Wolong Nature Reserve, China. Elevation was extracted from a Digital Elevation Model obtained by the National Aeronautics and Space Administration's (NASA) Advanced Space borne Thermal Emission and Reflection Radiometer (ASTER).

wildlife habitat degradation and wildlife population decline in the reserve (Liu et al., 2001; Loucks et al., 2001; Sichuan Provincial Forestry Department, 2015). Regarding livestock, local people mainly raise yaks, cattle, pigs, goats and horses for meat and money (Hull et al., 2014; Wolong Nature Reserve, 2008). The main Chinese medical herbs collected include tall gastrodia tuber (*Gastrodia elata*), Evergreen clematis (*Caulis Clematidis Armandii*), wild ginger groundcover (*Radix et Rhizoma Asari*), and honeysuckle flower (*Lonicera japonica*). Ungulates (e.g., sambar, takin) are the main hunting targets (Wolong Nature Reserve, 2008).

In 2008, the epicenter of the Wenchuan earthquake (magnitude 8.0) was just outside of Wolong and had devastating effects (Fig. 1), including destroying the majority of the infrastructure and crippling the economy in Wolong (Viña et al., 2011; Wang et al., 2008; Yang et al., 2013). The local government implemented a series of policies to facilitate economic development during reconstruction. In early 2013, the local government initiated an incentive for local households to raise livestock (cows, sheep, and yaks). The incentive included a loan without interest to 10 households in each village to support them to raise livestock. Each household received a 30,000 RMB (1 USD = 6.1 RMB in January 2013) loan. This policy took effect in June 2013, and was in part an attempt to quell the frustrations of local people in response to a ban on all horse grazing instituted in the previous year due to conflicts between horse grazing and panda conservation (Hull et al., 2014).

We conducted this research in Hetaoping, a roughly 40-km<sup>2</sup> area in the northeastern portion of the reserve. The study area has an elevation range of approximately 1600 to 3200 m. The northwest, northeast, southwest borders of the study area consist of a road and two pastures, from which the local people may take their livestock into wildlife habitat. A stream named Sanchagou runs from the southwest corner to the northeast corner (Fig. 1). This stream serves as the main water resource for giant pandas and other wildlife in the area during winter, when other water sources freeze over. The area is suitable habitat for giant pandas and several other wildlife species, containing three forest types - deciduous broad-leaved, mixed coniferous and deciduous broad-leaved and subalpine coniferous (Liu et al., 1999b). The main food sources for giant pandas - arrow (*Bashania fangiana*), umbrella (*Fargesia robusta*) and Yushan (*Yushania bravipaniculata*) bamboo are found in the understory (Schaller et al., 1985).

## 2.2. Camera trapping

We installed infrared cameras (Ltl Acorn ltl5210 ATM, Shenzhen, China) along streams and animal paths throughout the Hetaoping area (Fig. 1) because they were frequently used locations. Traps spanned an elevation gradient from 2600 to 3000 m, and the distance between two traps was 0.1–0.2 km.

We sampled 20 camera traps from November 2011 to August 2012 and added 10 additional traps (yielding a total of 30) for the period of December 2012 to March 2014 (Fig. 1). There were no data from September to November 2012 because eleven of the cameras were stolen. All trap locations were recorded using a global positioning system (GPS) receiver. Cameras were set to operate 24 h per day. After detecting motion, cameras were programmed to take up to 2 photographs (spaced 2 s apart) followed by 10 s of video (if motion was still detected).

For each photograph obtained from the camera traps, we recorded the location (trap identification), date, and time. We identified and recorded each entity by type- wildlife species, human, or livestock species. If humans were detected in the photograph, we identified the type of human activity observed (i.e. livestock grazing, medicinal herb collection and poaching). Poaching activity was identified by the presence of a person with a gun or domestic hunting dogs in the photograph or video. Livestock grazing was easily distinguishable due to the presence of livestock animals accompanying (or detected within minutes of) the person. Medicinal

herb collection was distinguishable due to the presence of extraction tools and collection baskets. To reduce the probability of repeated measurement of the same individuals in a short time interval, we only included photographs in our analysis that met the following criteria: (i) consecutive photographs of different animals or humans and (ii) photographs of animals or humans occurring >0.5 h apart (Johnson et al., 2006).

We summed up the number of photographs of each type for each trap and for the entire study area. To control for varying numbers of traps in different periods, we calculated the monthly relative abundance index (RA) for each of the subject types (total number of captures of each subject divided by total number of cameras operating in the month) (Liu et al., 2013b). We calculated the monthly relative proportion of the camera traps (PT) pertaining to each type (total number of cameras capturing a subject type divided by the total number of cameras operating in the month). We also calculated the mean percentage of all photo captures of each type occurring in each hour over a 24-hour period. To address the effect of the livestock incentive policy on wildlife, we conducted (a) a Wilcoxon test to compare the number of photo captures before and after livestock introduction and (b) a Spearman correlation analysis to compare the change in total numbers of wildlife and livestock photos at each trap before and after livestock introduction. To control for different data availabilities in different seasons across the two time periods, we limited these tests to the periods of December 2012–March 2013 (before policy) and December 2013–March 2014 (after policy).

## 2.3. Comparison to panda feces data

We collected fecal samples in the study area from May 2012 to March 2014. Sampling was done in a systematic manner that involved visiting separate cells of the study area on separate sampling days and searching for fecal deposits (Fig. 1). The search effort was consistent before and after the livestock policy but covered a larger proportion of the study area than the camera traps, which were mainly located along streams. For both before and after the policy, we collected samples twice, once in autumn and once in winter of the given year. Genetics information was extracted from fresh samples using the methods described in Huang et al. (2015).

We used a Maximum Entropy (MaxEnt) model (Phillips et al., 2006) to investigate the impact of the livestock policy on giant panda habitat distribution. MaxEnt is a machine learning method that uses presence-only data and environmental variables included in the model to predict the habitat suitability for that species across an area. Panda fecal locations were used as the occurrence input into the model. We used three predictors important to panda habitat areas environmental variables: elevation, slope, and forest cover (Liu et al., 2001). Slope was derived from a 90-m SRTM digital elevation model (DEM), and forest/non-forest layer was obtained from Landsat TM imagery of 2007 at a resolution of 30 m estimated by supervised classification (Viña et al., 2011). Because the changes we observed to the forest layer in our study area during the course of the study were concentrated in the forest understory (i.e., livestock consumption of bamboo and shrubs), they were not discernible using available remote sensing imagery and did not appear to impact Landsat classification. Therefore, this single time point of imagery used to represent forest and non-forest satisfied our purpose for ascertaining changes in forest use by pandas over time.

We ran a MaxEnt model on giant panda presence points collected before the livestock introduction ( $n = 36$ ), and a second model on presence points collected after the livestock introduction ( $n = 31$ ). We also compared habitat characteristics of predicted habitat (above 0.5 probability of occurrence) across the two models. To ensure the effectiveness of the model, we first calibrated model with 80% of our presence points and then used the remaining 20% of the data to validate the model. Model performances were evaluated

using area under the receiving characteristic operating curve (AUC) metrics. Both training models achieved an AUC of approximately 0.80, indicating moderate discriminatory ability (Swets, 1988). After this satisfactory performance, the models were run on the whole datasets. The analysis was performed using the “dismo” package (Hijmans and Elith, 2016) in R (R Development Core Team, 2016).

### 3. Results

#### 3.1. Summary of wildlife, livestock and human activities

We obtained 1588 wildlife photos, which depicted the presence of 17 species of mammals and 6 species of birds (Fig. 2). Of those, 4 large and middle body size mammals represented about 82% of the captures. The sambar deer ( $n = 665$ ) had the highest number of photos, followed by the giant panda ( $n = 320$ ), red panda ( $n = 175$ ), and golden snub-

nosed monkey ( $n = 135$ ). These four species were also the most widely spatially distributed, photographed at 100%, 70%, 47% and 73% of camera traps, respectively (Fig. 2). There were 320 giant panda photos taken and 198 videos recorded.

The most common human activity recorded was livestock grazing ( $n = 121$  photos of humans). Livestock included sheep ( $n = 223$ ), yaks ( $n = 130$ ), and horses ( $n = 8$ ). This activity was followed by medicinal herb collection ( $n = 33$ ) and poaching ( $n = 4$  photos of hunting dogs,  $n = 1$  of which also included humans) (Fig. 3). Similarly, livestock grazing also had the widest distribution across the study area ( $n = 83\%$  of camera traps), followed by medicinal herb collection ( $n = 33\%$ ) and poaching ( $n = 10\%$  of traps) (Fig. 3).

#### 3.2. Seasonal patterns of human activities, livestock and wildlife

Human disturbance varied with seasons (Fig. 4). For example, medicinal herb collection mainly was detected during the spring and

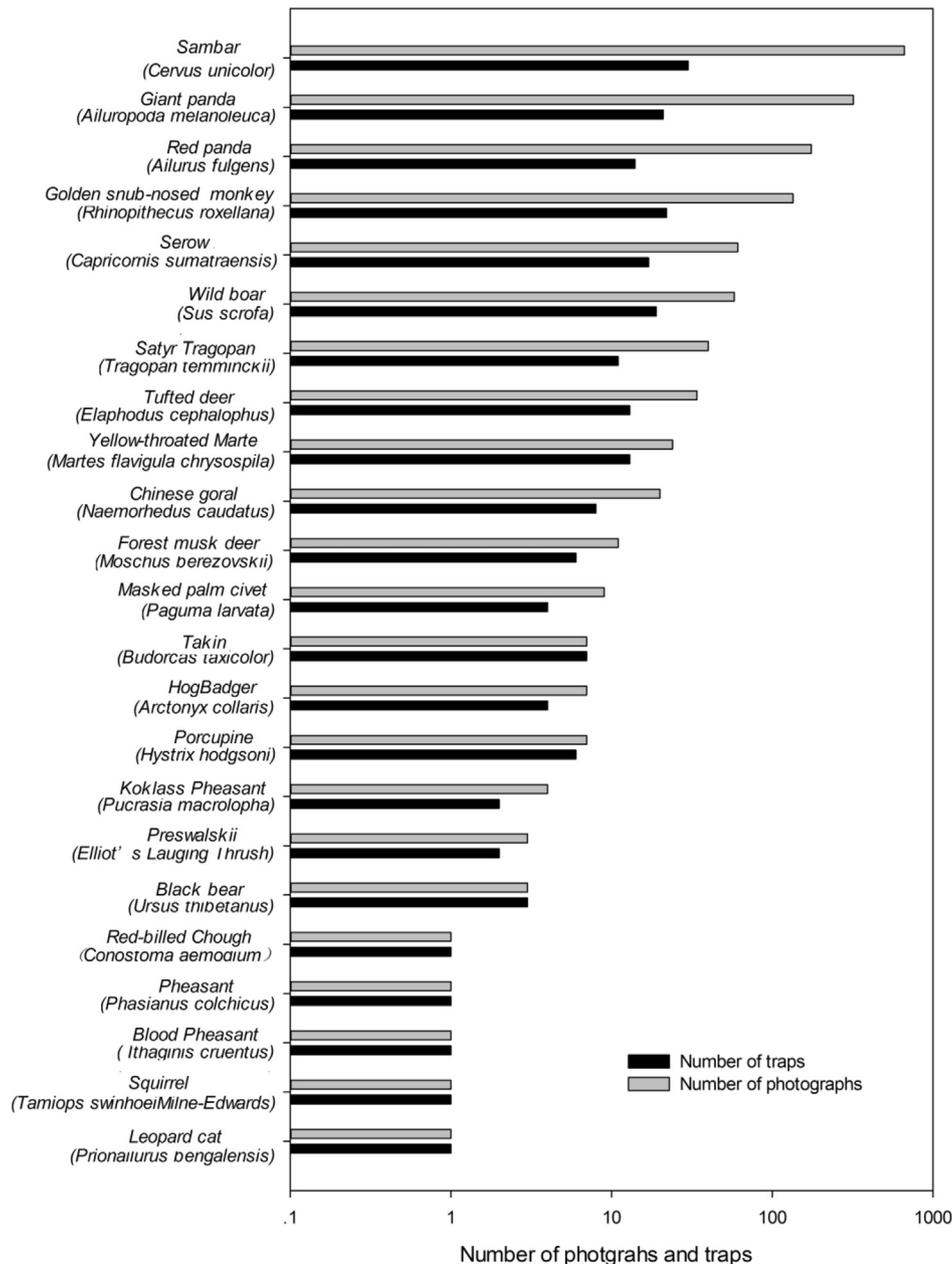
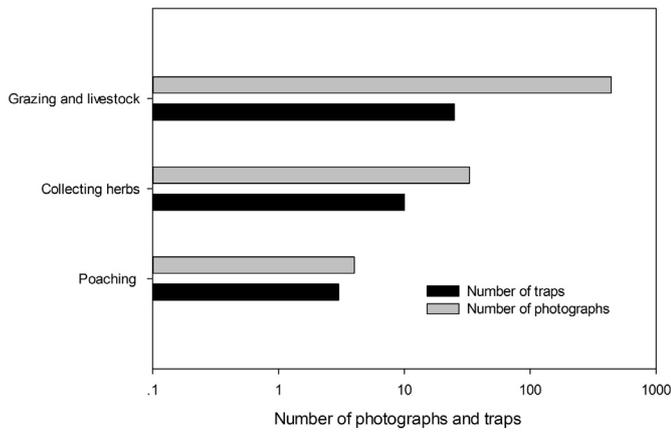


Fig. 2. The total number of camera traps and total number of photos captured of all wildlife species detected using infrared cameras in Wolong Nature Reserve, China, from November 2011 to March 2014.



**Fig. 3.** The total number of camera traps and total number of photos captured of humans participating in activities including livestock grazing, poaching and medicinal herb collection detected using infrared cameras in Wolong Nature Reserve, China from November 2011 to March 2014.

summer of 2013 [mean relative abundant index (RA) = 19%, mean proportion of the camera traps capturing a subject type (PT) = 12%], with almost no detection during other seasons (Fig. 4). Poaching was rarely detected and did not show a strong seasonal or temporal pattern. Humans participating in livestock grazing increased over time, with no detections until December 2012, followed by a sharp increase from January 2013 to August 2013 (peaks of RA = 93.3% and PT = 30%) and then a gradual decline to a moderate level (Fig. 4). Presence of livestock followed a similar pattern, with few photographs obtained prior to summer 2013, an increasing trend throughout the summer of 2013, followed by fluctuations and a peak in March 2014 (RA = 253% and PT = 43%, Fig. 5).

Wildlife presence also changed among seasons (Fig. 5). Giant pandas and red pandas had higher detection rates during winter compared to other seasons (75% and 49% higher mean RA in winter for pandas and red pandas, respectively and 14–15% higher mean PT in winter for both species). On the contrary, sambar and golden snub-nosed monkey had lower detection rates in winter compared to other seasons (mean RA was 29% and 16% lower for sambar and snub-nosed monkey in winter; although PT differed little across seasons).

Giant pandas, red pandas, and snub-nosed monkeys all showed declines in detection after the livestock policy (declines of mean RA by 70%, 25%, and 37% for giant pandas, red pandas, and snub-nosed monkeys from the winter before the policy to the winter after, declines of 8–11% in mean PT across species). The magnitude of change was greater for RA than PT, especially for giant pandas, suggesting that the animals used many of the same trap areas, but visited them less frequently after the disturbance. Declines in number of captures during winter were statistically significant for golden snub-nosed monkey ( $Z = -3.329$ ,  $P < 0.01$ ) and red panda ( $Z = -2.613$ ,  $P < 0.01$ ), but not giant panda. In contrast, sambar maintained high detection rates after the livestock policy, and peaked in June of 2013 (with 400% and 63% for RA and PT, respectively). Number of captures in the winter after the implementation of the livestock policy was significantly higher than before ( $Z = 1.946$ ,  $P = 0.05$ ). At individual traps, declines in wildlife captures after the livestock policy were only significantly correlated to increases in livestock captures for red panda ( $r = -0.524$ ,  $P < 0.05$ ) and golden snub-nosed monkey ( $r = -0.411$ ,  $P < 0.05$ ).

### 3.3. Daily detection patterns before and after livestock encroachment

Human activities including grazing livestock, collecting medicinal herbs, and poaching wildlife were unimodal, peaking during the daytime (10:00–16:00) (Fig. 6). Livestock were also more often photographed during the daytime (6:00–18:00) (Fig. 6). In contrast,

giant pandas exhibited a detection pattern with multiple alternating peaks and valleys. The red panda and golden snub-nosed monkey had three detection peaks in the daytime – in the morning, noon and mid-afternoon. The only species that had different detection patterns after the livestock policy compared to before was the sambar, which changed from multiple peaks before the policy to one peak around dusk after the policy (Fig. 6).

### 3.4. Spatial patterns before and after livestock encroachment

Giant pandas, red pandas, and golden snub-nosed monkeys showed marked decreases in the spatial extent of photo captures from the pre-livestock policy to post-livestock policy periods (Fig. 7). All were originally well distributed throughout the main forested portion of the study area, particularly surrounding the stream. In some instances, all three species were even photographed in camera traps located in close proximity to the pasture, but these instances declined after the livestock policy. Sambar was also the most widely distributed animals throughout the study area with the most even distribution across camera traps in both before and after periods (Fig. 7). Livestock were originally distributed close to the pasture in the study area, but after the livestock policy they extended their distribution along the stream and into new areas of the forest where they were not previously photographed (Fig. 7).

### 3.5. Panda individual detections and distribution before and after livestock introduction

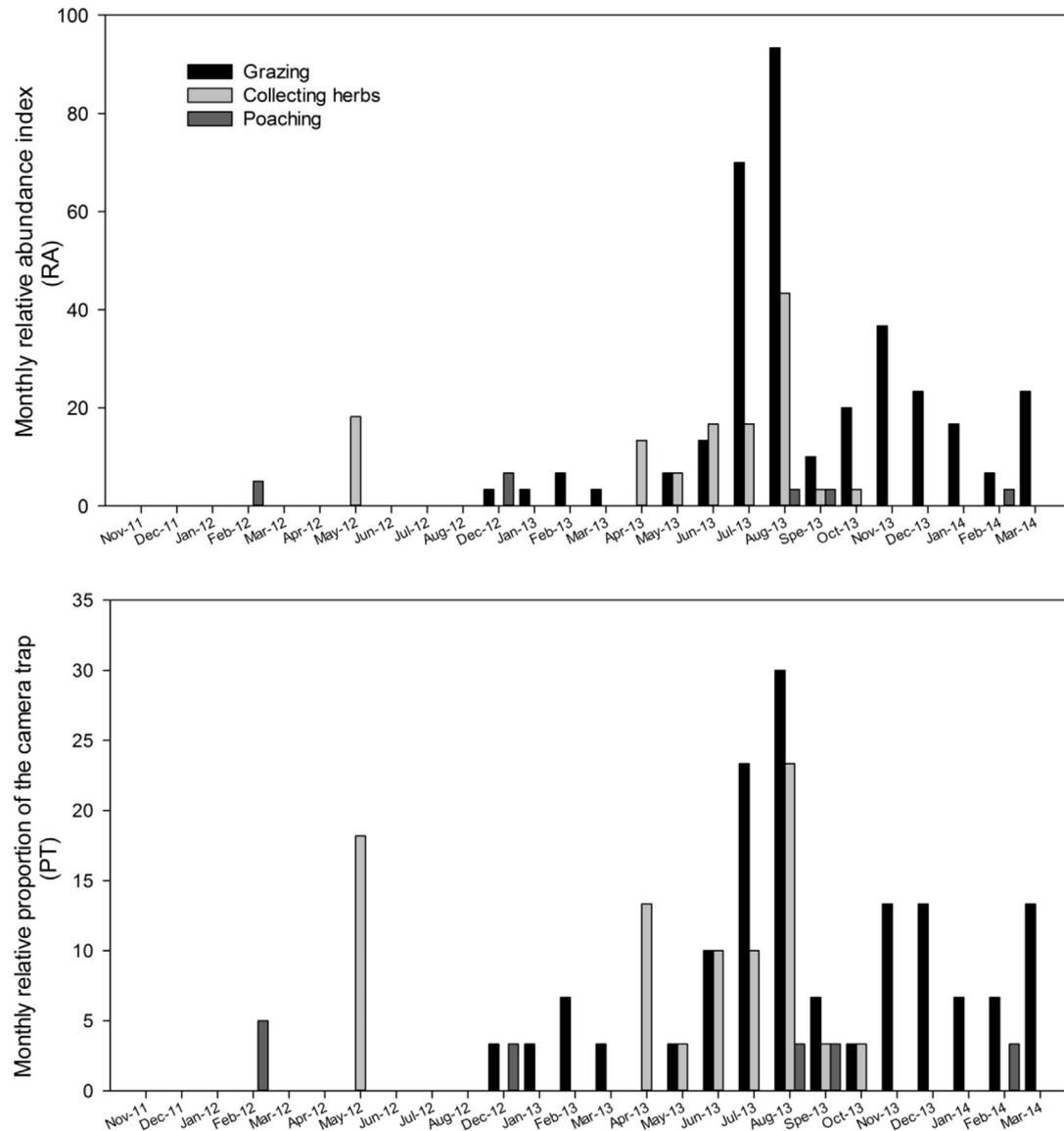
DNA analysis of fecal samples detected 27 unique pandas. There were 22 individuals found before and 21 individuals identified after livestock was introduced, while 16 of the same individuals were found both before and after.

The MaxEnt models of panda occurrence had satisfactory model performance (before policy AUC = 0.85, after policy AUC = 0.80). The habitat variable that contributed most to the models was elevation (before = 50%, after = 60%), followed by forest (before = 32%, after = 34%), and slope (before = 18%, after = 8%). The probability distributions for panda occurrence predictions were more strongly left-skewed before the policy and more uniformly distributed after (Fig. 8). In other words, a greater proportion of the study area had a higher probability of supporting pandas after the livestock policy compared to before (Fig. 9). Areas most likely to support pandas (with predicted probability of above 0.5) had steeper slope, lower elevation and lower forest cover after the policy compared to before (Table 1).

## 4. Discussion

Findings from this study indicate that livestock have significant impacts on the giant pandas and other wildlife species, in contrast to the conventional wisdom that livestock are not a significant threat to pandas and some other protected wildlife species worldwide (Bragina et al., 2015; Ran et al., 2003). As livestock were detected more often than any other human disturbance in the most recent national panda survey across the geographic range of the giant panda in three provinces of China (Sichuan Provincial Forestry Department, 2015), our study provided a good foundation for quantifying livestock impacts on giant pandas and other wildlife species beyond Wolong Nature Reserve.

It was also meaningful to document differences in response to livestock across multiple different sympatric wildlife species. These findings highlight the potential dangers of using single “umbrella species” to represent broad trends in wildlife response to human impacts, a practice that may be misleading when different wildlife species respond differently. Photo captures of giant pandas, red pandas, and snub-nosed monkeys declined after the local livestock incentive policy. In contrast, detection frequencies of sambar

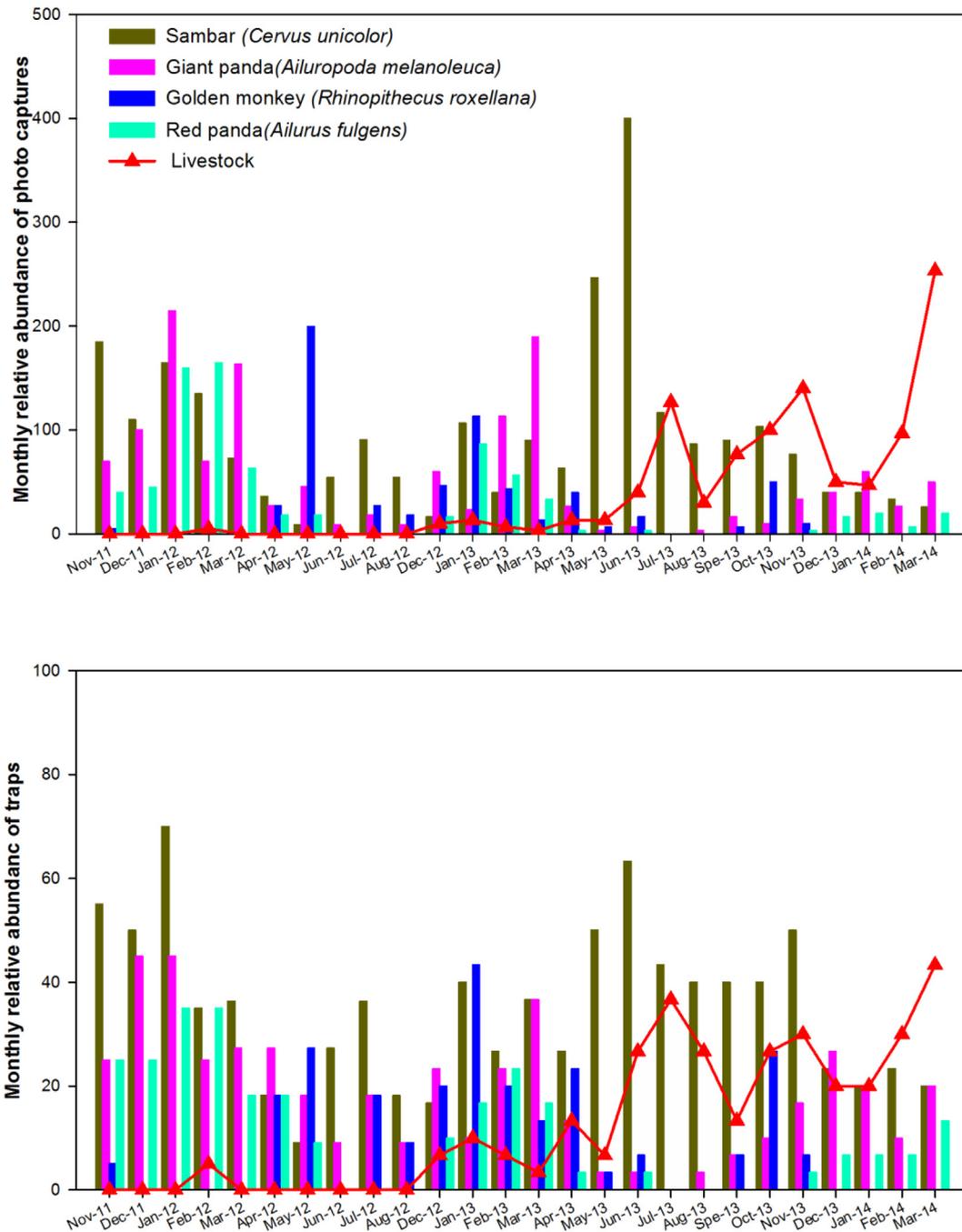


**Fig. 4.** The monthly relative abundance index (RA) of photo captures and monthly relative proportion of the camera traps (PT) for human activities in Wolong Nature Reserve, China from November 2011 to March 2014. RA was calculated by dividing total number of captures or traps of each subject type divided by total number of cameras operating in the month. PT was calculated by dividing the number of cameras capturing a subject type by the total number of cameras operating in the month. Livestock grazing, herb collection, and poaching correspond to photographs of people participating in the activities.

remained high and even increased throughout the study period despite increases in livestock.

Reasons for these differences can possibly be surmised from the species' biological traits and resource requirements. All species included in this study rely on water sources, especially during winter (Zhang et al., 2014). When faced with livestock disturbances around water sources, the wildlife species in question must either move to other areas or adjust temporal patterns of behavior in order to coexist with the livestock (Carter et al., 2012). The sambar appears to have done the latter by adjusting their daily timing of visiting the streams and travel routes to dusk, a time of day when human disturbances in these central locations were less frequent. Previous studies showed that sambar grazed most actively during the night, late afternoon and evening, almost consistent with our pre-livestock policy findings (Semiadi et al., 1993). Sambar may have been able to adjust daily patterns because they are ruminants. They may be able to forage more intensively during a shorter time period and spend the remaining time resting and ruminating. In contrast, giant pandas and red pandas are bamboo specialists that need to spend a large

proportion of their time foraging to compensate for the low nutrition of bamboo (Schaller et al., 1985). It may therefore be more difficult for red and giant pandas to simply shift the timing of visiting streams and travel routes to the evenings while maintaining the same number of visitations. Thus the number of captures declined. From the DNA analysis and panda distribution modeling, it appears that although giant pandas were displaced by livestock at camera trapping sites, they did not move out of our study area. Giant pandas appear instead to have shifted their habitat use patterns to other locations, in part by spreading to areas of lower elevation and forest cover, and steeper slope. The elevations occupied by pandas after livestock encroachment are less suitable for pandas, since they prefer relatively high elevations during summer, autumn and winter in this part of Wolong (Hull et al., 2016). Pandas also prefer gentle or moderate slopes for ease of travel and forest cover which is related to food and shelter provisions (Liu et al., 1999b). Thus the shift in predicted broader distribution of pandas after the livestock disturbance appears to be tied to pandas being displaced to areas that may have lower habitat suitability.

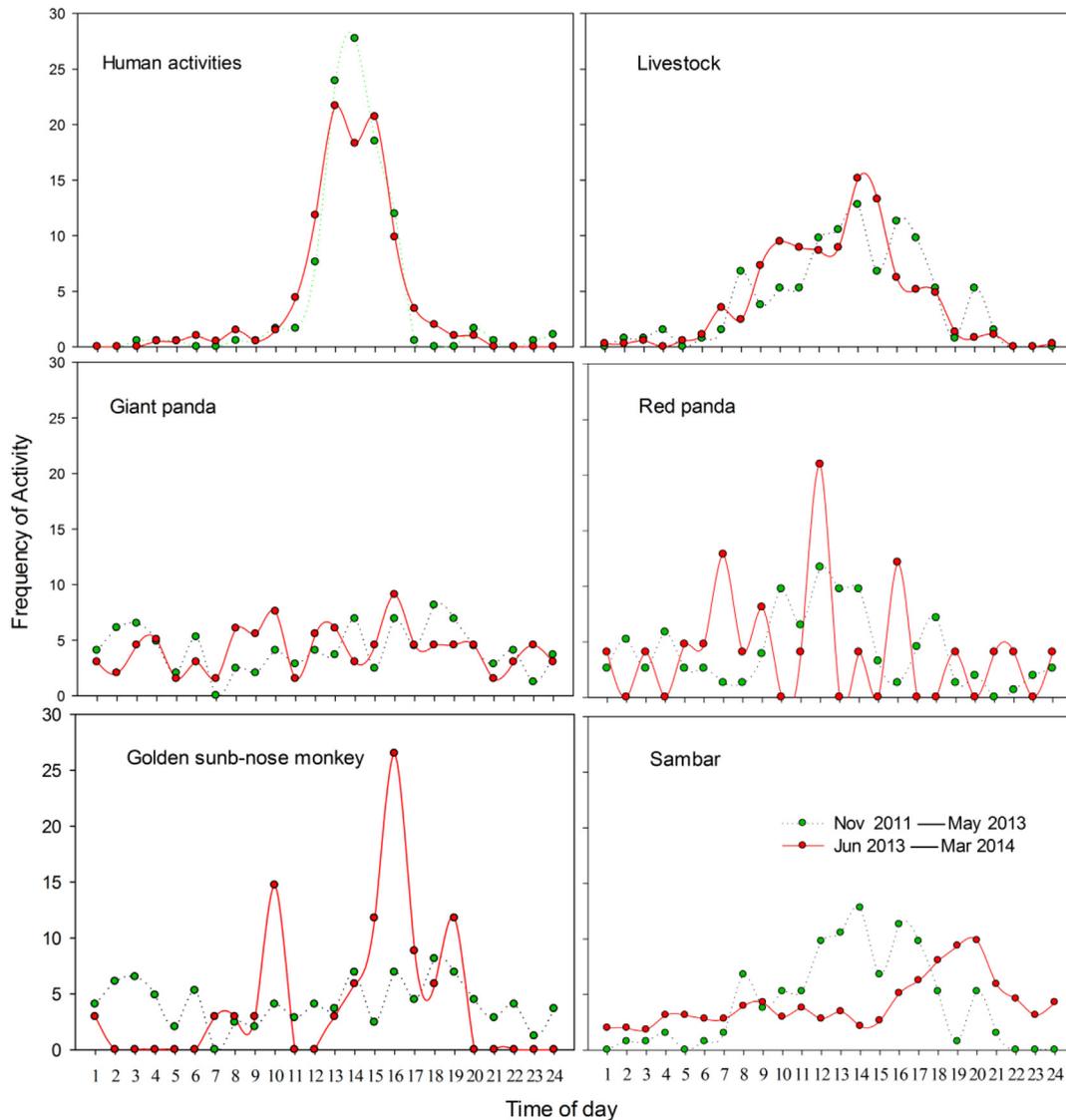


**Fig. 5.** The monthly relative abundance index (RA) of photo captures and monthly relative proportion of the camera traps (PT) for the four most commonly photographed wildlife species in Wolong Nature Reserve, China from November 2011 to March 2014. RA and PT were calculated as in Fig. 4. Solid line represents calculations on all photographs involving livestock (yaks, cows and sheep).

Golden snub-nosed monkeys also appeared to have been displaced from the immediate camera trap areas. These animals have a diverse diet that would presumably allow them some flexibility in the timing of their activity patterns, but they tend to avoid human disturbances in the forest (Quan and Xie, 2002). There is a low density of snub-nosed monkeys and plentiful food in Wolong, which suggests that this species may be readily able to move to nearby available habitat if one area is disturbed, negating the need for temporal adjustments.

Our study emphasizes that biological information such as behavioral patterns at fine spatial scales and diet composition are important considerations for conservation and management of wildlife.

This is especially true when some species with strict or limiting diet requirements that may make them less flexible to fine-scale coexistence with humans. These results highlight the importance of conservation measures that seek to segregate human activities and conservation in protected landscapes to achieve coexistence at broader scales (Berkes, 2007; Western et al., 2009), such as establishment of a buffer zone between core and experimental zone in giant panda nature reserves (Hull et al., 2011) or moving human communities away from threatened wildlife habitat (Agrawal and Redford, 2009). Our study also highlights the importance of carefully considering diverse potential impacts of policies geared toward co-managing conservation and human wellbeing, especially in



**Fig. 6.** Mean hourly photo captures of human activities, livestock, and the four most commonly photographed wildlife (sambar, giant panda, red panda and golden snub-nosed monkey) before and after a 2013 livestock incentive policy instituted by the local government.

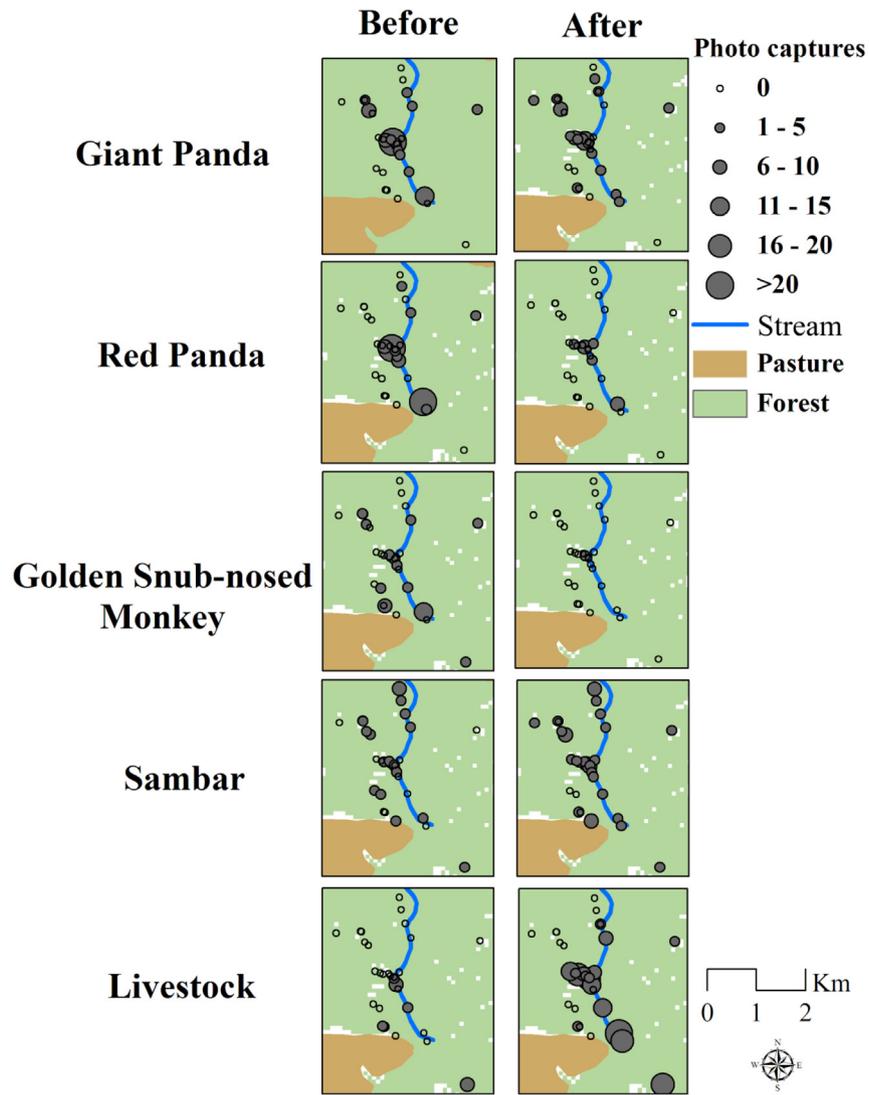
protected areas where undergoing immediate natural disasters (e.g., earthquake and volcano). Otherwise, unexpected impacts can occur.

Based on our novel findings in this study, we suggest that livestock should be removed from protected wildlife habitat, especially from key water resource areas during winter. Monitoring of core panda habitat areas should also be improved to prevent livestock illegally grazing in forests. On the other hand, facilitating economic development and securing a better livelihood for local people are also important endeavors, since local communities are closely associated with long-term conservation objectives (Berkes, 2004; Brown, 2002). Although the 2008 Wenchuan earthquake only mildly affected the panda habitat overall (Ouyang et al., 2008; Zhang et al., 2011), it damaged the main infrastructure needed for agricultural trade and tourism (Liu et al., 2016b). Thus, local people came to increasingly rely on livestock to generate income and set the stage for the 2013 livestock incentive policy. Livestock were being sold to outside markets in the winter when road conditions are more stable than other seasons suitable for tourism and trade of crop products. As of October 2016, the traffic between Wolong and the nearest city-Chengdu has completely recovered and tourism facilities have begun to recover and develop (Hong Kong Special Administrative Region, 2016). We suggest that instead of building

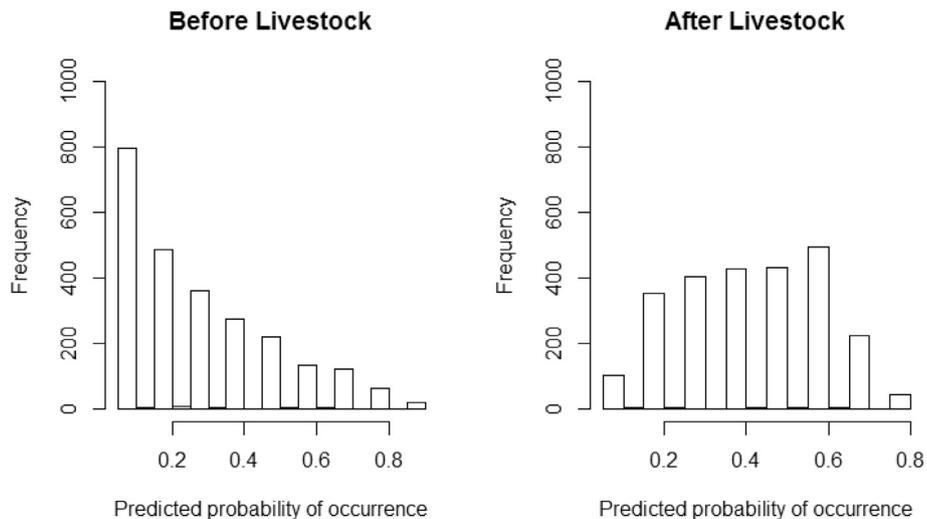
up the livestock sector, the local government and people should turn to develop the livelihoods related to the trading of goods and services with the outside world, such as nature-based tourism and crop production. Furthermore, enhancing the connection between the reserve and the outside world may be important, since those lower-impact livelihoods (e.g., cash crops and tourism) in rural areas increasingly rely on outside markets in the telecoupled world (Liu et al., 2013a; Liu et al., 2015b; Liu et al., 2012).

#### Acknowledgements

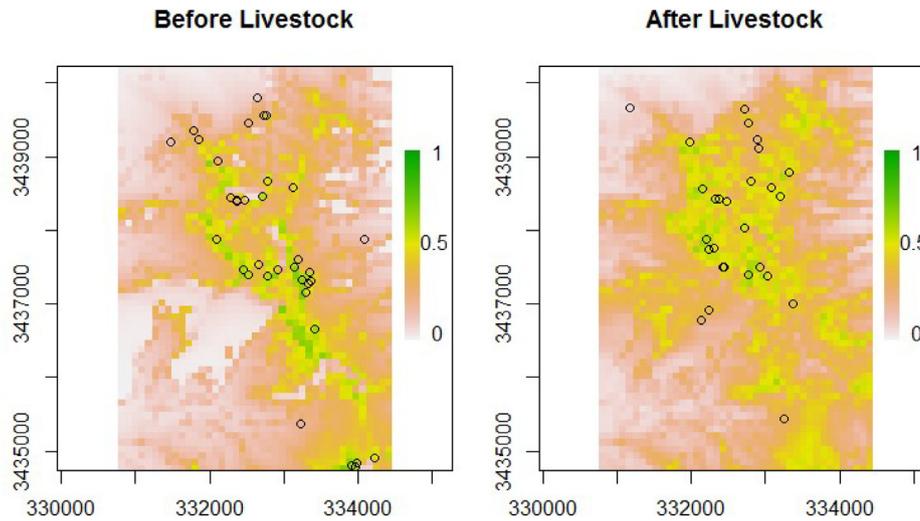
We thank the Wolong Nature Reserve Administration and the staff at the China Conservation and Research Center for the Giant Panda (CCRCGP) for their support. We thank S. Zhou, J. Huang, D. Liu, W. Yang, and H. Yang for carrying out fieldwork. We thank J. Huang and M. Qiao for conducting lab work. We acknowledge the following sources of funding: the National Natural Science Foundation of China (41571517; 31572293; 31370412), National Science Foundation (NSF) (EF-1340812), the National Aeronautics and Space Administration (NASA) (11-Earth11F-196), Michigan AgBioResearch, the Michigan State University Distinguished Fellowship Program, the William W. and Evelyn M. Taylor International Engagement Program, Research innovation



**Fig. 7.** Change in photo captures of livestock and the four most commonly photographed wildlife (giant panda, red panda, golden snub-nosed monkey, and sambar) in our study are in Wolong Nature Reserve before and after a livestock incentive policy was implemented. Before and after data were collected over two 4-month periods (from December 2012–March 2013 and December 2013–March 2014). Forest cover was obtained from a supervised classification of Landsat TM (2007) imagery (49).



**Fig. 8.** Probability distributions for panda occurrence predictions before and after the livestock policy. Frequencies are numbers of cells in the study area belonging to each predicted probability of occurrence class. MaxEnt model estimation was used with fecal samples as presence data and elevation, slope and forest as environmental factors.



**Fig. 9.** Predictions of giant panda distribution in Hetaoping, Wolong Nature Reserve, China before and after livestock introduction. MaxEnt model estimation was used with fecal samples as presence data and elevation, slope and forest as environmental factors.

**Table 1**

Habitat characteristics in the entire Hetaoping study area and in areas of higher predicted probability of use by giant pandas (above 50%) derived from MaxEnt modeling on feces collected before and after a livestock policy was introduced into the study area in 2013.

	Whole study area		Areas in higher predicted probability (above 50%)			
	Mean	Range	Before livestock		After livestock	
			Mean	Range	Mean	Range
Slope (°)	27.26	1.35–68.82	20.48	1.35–40.23	22.26	1.35–42.23
Elevation (m)	2659	2020–3119	2904	2523–3109	2843	2592–3058
Forest cover (%)	78	0–100	82	28–100	77	0–100

team funding project of China West Normal University (CXTD2014-3), the Key Laboratory of Southwest China Wildlife Resources Conservation (China West Normal University), Ministry of Education, China (XNYB17-2), the State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences (SKLURE2008-1), and the fund of China West Normal University (14B01).

## References

- Agrawal, A., Redford, K., 2009. Conservation and displacement: an overview. *Conserv. Soc.* 7, 1–10.
- An, L., Liu, J., Ouyang, Z., Linderman, M., Zhou, S., Zhang, H., 2001. Simulating demographic and socioeconomic processes on household level and implications for giant panda habitats. *Ecol. Model.* 140, 31–49.
- Berkes, F., 2004. Rethinking community-based conservation. *Conserv. Biol.* 18, 621–630.
- Berkes, F., 2007. Community-based conservation in a globalized world. *Proc. Natl. Acad. Sci.* 104, 15188–15193.
- Bragina, E., Radeloff, V., Baumann, M., Wendland, K., Kuemmerle, T., Pidgeon, A., 2015. Effectiveness of protected areas in the Western Caucasus before and after the transition to post-socialism. *Biol. Conserv.* 184, 456–464.
- Brown, K., 2002. Innovations for conservation and development. *Geogr. J.* 168, 6–17.
- Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B., Liu, J., 2012. Coexistence between wildlife and humans at fine spatial scales. *Proc. Natl. Acad. Sci.* 109, 15360–15365.
- Carter, N.H., Viña, A., Hull, V., McConnell, W.J., Axinn, W., Ghimire, D., Liu, J., 2014. Coupled human and natural systems approach to wildlife research and conservation. *Ecol. Soc.* 19, 43.
- Carter, N., Jasny, M., Gurung, B., Liu, J., 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. *Global Ecology and Conservation* 3, 149–162.
- Cohen, J.E., 2003. Human population: the next half century. *Science* 302, 1172–1175.
- Endress, B.A., Gorshov, D.L., Noble, R.B., 2004. Non-timber forest product extraction: effects of harvest and browsing on an understory palm. *Ecol. Appl.* 14, 1139–1153.
- Hijmans, R.J., Elith, J., 2016. Species distribution modeling with R. <http://www.idg.pl/mirrors/CRAN/web/packages/dismo/vignettes/sdm.pdf>.
- Hobbs, R.J., 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conserv. Biol.* 15, 1522–1528.
- Hong Kong Special Administrative Region, 2016. Hksar's post-quake reconstruction support work in Sichuan concludes successfully. [http://www512rjchk/en/prog/news\\_20161028.htm](http://www512rjchk/en/prog/news_20161028.htm).
- Huang, J., Li, Y.-Z., Du, L.-M., Yang, B., Shen, F.-J., Zhang, H.-M., Zhang, Z.-H., Zhang, X.-Y., Yue, B.-S., 2015. Genome-wide survey and analysis of microsatellites in giant panda (*Ailuropoda melanoleuca*), with a focus on the applications of a novel microsatellite marker system. *BMC Genomics* 16, 61.
- Hull, V., Xu, W., Liu, W., Zhou, S., Viña, A., Zhang, J., Tuanmu, M.N., Huang, J., Linderman, M., Chen, X., 2011. Evaluating the efficacy of zoning designations for protected area management. *Biol. Conserv.* 144, 3028–3037.
- Hull, V., Zhang, J., Zhou, S., Huang, J., Vina, A., Liu, W., Tuanmu, M.-N., Li, R., Liu, D., Xu, W., 2014. Impact of livestock on giant pandas and their habitat. *J. Nat. Conserv.* 22, 256–264.
- Hull, V., Zhang, J., Huang, J., Zhou, S., Viña, A., Shortridge, A., Li, R., Liu, D., Xu, W., Ouyang, Z., 2016. Habitat use and selection by giant pandas. *PLoS One* 11, e0162266.
- Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R., Lawrence, W.T., 2004. Global patterns in human consumption of net primary production. *Nature* 429, 870–873.
- Johnson, A., Vongkhamheng, C., Hedemark, M., Saithongdam, T., 2006. Effects of human-carnivore conflict on tiger (*Panthera tigris*) and prey populations in Lao PDR. *Anim. Conserv.* 9, 421–430.
- Juffe-Bignoli, D., Burgess, N.D., Bingham, H., Belle, E., de Lima, M., Deguignet, M., Bertzky, B., Milam, A., Martinez-Lopez, J., Lewis, E., 2014. *Protected Planet Report 2014*. UNEP-WCMC, Cambridge, UK.
- Liu, J., Ouyang, Z., Tan, Y., Yang, J., Zhang, H., 1999a. Changes in human population structure: implications for biodiversity conservation. *Popul. Environ.* 21, 45–58.
- Liu, J., Ouyang, Z., Taylor, W.W., Groop, R., Tan, Y., Zhang, H., 1999b. A framework for evaluating the effects of human factors on wildlife habitat: the case of giant pandas. *Conserv. Biol.* 13, 1360–1370.
- Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J., Zhang, H., 2001. Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science* 292, 98–101.
- Liu, W., Vogt, C.A., Luo, J., He, G., Frank, K.A., Liu, J., 2012. Drivers and socioeconomic impacts of tourism participation in protected areas. *PLoS One* 7, e35420.
- Liu, J., Hull, V., Batistella, M., DeFries, R., Dietz, T., Fu, F., Hertel, T.W., Izaurralde, R.C., Lambin, E.F., Li, S., 2013a. Framing sustainability in a telecoupled world. *Ecol. Soc.* 18, 26.
- Liu, X., Wu, P., Songer, M., Cai, Q., He, X., Zhu, Y., Shao, X., 2013b. Monitoring wildlife abundance and diversity with infra-red camera traps in Guanyinshan Nature Reserve of Shaanxi Province, China. *Ecol. Indic.* 33, 121–128.
- Liu, J., Mooney, H., Hull, V., Davis, S.J., Gaskell, J., Hertel, T., Lubchenco, J., Seto, K.C., Gleick, P., Kremen, C., 2015a. Systems integration for global sustainability. *Science* 347, 1258832.
- Liu, J., Hull, V., Luo, J., Yang, W., Liu, W., Viña, A., Vogt, C., Xu, Z., Yang, H., Zhang, J., 2015b. Multiple telecouplings and their complex interrelationships. *Ecol. Soc.* 20, 44.
- Liu, J., Hull, V., Yang, W., Viña, A., Chen, X., Ouyang, Z., Zhang, H., 2016a. *Pandas and People: Coupling Human and Natural Systems for Sustainability*. Oxford University Press.
- Liu, W., Vogt, C.A., Lupi, F., He, G., Ouyang, Z., Liu, J., 2016b. Evolution of tourism in a flagship protected area of China. *J. Sustain. Tour.* 24, 203–226.
- 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.
- Madhusudan, M., 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *J. Appl. Ecol.* 41, 858–869.
- Mawdsley, J.R., O'MALLEY, R., Ojima, D.S., 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conserv. Biol.* 23, 1080–1089.

- Mishra, C., Van Wieren, S.E., Ketner, P., Heitkönig, I., Prins, H.H., 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian Trans-Himalaya. *J. Appl. Ecol.* 41, 344–354.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Namgail, T., Fox, J.L., Bhatnagar, Y.V., 2007. Habitat shift and time budget of the Tibetan argali: the influence of livestock grazing. *Ecol. Res.* 22, 25–31.
- Ouyang, Z., Xu, W., Wang, X., Wang, W., Dong, R., Zheng, H., Li, D., Li, Z., Zhang, H., Zhuang, C., 2008. Impact assessment of Wenchuan earthquake on ecosystems. *Acta Ecol. Sin.* 28, 5801–5809 (in Chinese).
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Quan, G.Q., Xie, J.Y., 2002. Golden Monkey Research. Shanghai Public House of Science and Education, Shanghai, China (In Chinese).
- R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ran, J., Liu, S., Wang, H., Sun, Z., Zeng, Z., Liu, S., 2003. Habitat selection by giant pandas and grazing livestock in the Xiaoxiangling Mountains of Sichuan Province. *Acta Ecol. Sin.* 23, 2253–2259 (in Chinese).
- Schaller, G.B., Hu, J., Pan, W., Zhu, J., 1985. The Giant Pandas of Wolong. University of Chicago Press Chicago, Illinois, USA.
- Semiadi, G., Muir, P., Barry, T., Veltman, C., Hodgson, J., 1993. Grazing patterns of sambar deer (*Cervus unicolor*) and red deer (*Cervus elaphus*) in captivity. *N. Z. J. Agric. Res.* 36, 253–260.
- Sichuan Provincial Forestry Department, 2015. Sichuan's Giant Panda—The Report of the Fourth Giant Panda Survey of Sichuan Province. Sichuan Science and Technology Press (in Chinese).
- Steinfeld, H., Gerber, P., Wassenaar, T., Castel, V., de Haan, C., 2006. Livestock's Long Shadow: Environmental Issues and Options. Food & Agriculture Org.
- Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293.
- van Gils, H., Westinga, E., Carafa, M., Antonucci, A., Ciaschetti, G., 2014. Where the bears roam in Majella National Park, Italy. *J. Nat. Conserv.* 22, 23–34.
- Viña, A., Chen, X., McConnell, W.J., Liu, W., Xu, W., Ouyang, Z., Zhang, H., Liu, J., 2011. Effects of natural disasters on conservation policies: the case of the 2008 Wenchuan Earthquake, China. *Ambio* 40, 274–284.
- Wang, D., Li, S., Sun, S., Wang, H., Chen, A., Li, J., Lu, Z., 2008. Turning earthquake disaster into long term benefits for the panda. *Conserv. Biol.* 22, 1356–1360.
- Wassie, A., Sterck, F.J., Teketay, D., Bongers, F., 2009. Effects of livestock exclusion on tree regeneration in church forests of Ethiopia. *For. Ecol. Manag.* 257, 765–772.
- Western, D., Russell, S., Cuthill, I., 2009. The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS One* 4, e6140.
- Wittemyer, G., Getz, W., Vollrath, F., Douglas-Hamilton, I., 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behav. Ecol. Sociobiol.* 61, 1919–1931.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., Brashares, J.S., 2008. Accelerated human population growth at protected area edges. *Science* 321, 123–126.
- Wolong Nature Reserve, 2008. The History of Wolong Development. Sichuan Science and Technology Press (in Chinese).
- Yang, W., Dietz, T., Kramer, D.B., Chen, X., Liu, J., 2013. Going beyond the Millennium Ecosystem Assessment: an index system of human well-being. *PLoS One* 8, e64582.
- Zhang, J., Hull, V., Xu, W., Liu, J., Ouyang, Z., Huang, J., Wang, X., Li, R., 2011. Impact of the 2008 Wenchuan earthquake on biodiversity and giant panda habitat in Wolong Nature Reserve, China. *Ecol. Res.* 26, 523–531.
- Zhang, Z., Sheppard, J.K., Swaisgood, R.R., Wang, G., Nie, Y., Wei, W., Zhao, N., Wei, F., 2014. Ecological scale and seasonal heterogeneity in the spatial behaviors of giant pandas. *Integrative Zoology* 9, 46–60.