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Impact of livestock on giant pandas and their habitat

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ARTICLE INFO

ABSTRACT

Livestock production is one of the greatest threats to biodiversity worldwide. However, impacts of livestock on endangered species have been understudied, particularly across the livestock–wildlife interface in forested protected areas. We investigated the impact of an emerging livestock sector in China's renowned Wolong Nature Reserve for giant pandas. We integrated empirical data from field surveys, remotely sensed imagery, and GPS collar tracking to analyze (1) the spatial distribution of horses in giant panda habitat, (2) space use and habitat selection patterns of horses and pandas, and (3) the impact of horses on pandas and bamboo (panda's main food source). We discovered that the horse distribution overlapped with suitable giant panda habitat. Horses had smaller home ranges than pandas but both species showed similarities in habitat selection. Horses consumed considerable amounts of bamboo, and may have resulted in a decline in panda habitat use. Our study highlights the need to formulate policies to address this emerging threat to the endangered giant panda. It also has implications for understanding livestock impacts in other protected areas across the globe.

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Introduction

One of the most significant drivers of global land use change is livestock production, a fast growing economic sector currently affecting 23 of the 35 global biodiversity hotspots (Rindfuss et al. 2008; Steinfeld et al. 2006). Livestock can have a profound impact on biodiversity by promoting habitat loss and degradation, global climate change, pollution, spread of invasive species, and disease transmission (Steinfeld et al. 2006). Livestock also may directly compete with wildlife species for limited food and space, in turn threatening their survival (Madhusudan 2004; Mishra et al. 2004). Vulnerable to such competition are herbivorous species (particularly threatened/endangered species) that share similar dietary restrictions and foraging strategies as livestock (Beck & Peek 2005; Namgail et al. 2007; Young et al. 2005).

One endangered animal species that may be affected by livestock production is the giant panda, a large herbivorous mammal and international symbol for biodiversity conservation (Hull et al. 2011). The ca. 1600 remaining wild pandas are native to the mixed deciduous and coniferous forests in southwestern China (State Forestry Administration 2006), where they inhabit isolated mountain ranges fragmented by the activities of a growing human population, including farming, road construction and timber harvesting (Chen et al. 2010). Over 60 nature reserves have been established to protect giant pandas (Viña et al. 2010), but reserves may not always provide a sufficient regulatory framework to prevent further panda habitat degradation (Liu et al. 2001).

In the most comprehensive survey of giant pandas and their habitat to date, the 3rd National Giant Panda Survey, surveyors spanned the entire geographic range of the species to document evidence of both giant panda habitat use and human disturbance (State Forestry Administration 2006). In this survey, out of ten different types of human disturbance identified, livestock grazing was the second most commonly encountered type (11% of 34,187 plots, 17% of all disturbances), behind only timber harvesting (28% of the plots, 41% of all disturbances). However, timber harvesting was determined to be a legacy effect (i.e., not occurring at the time of

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survey) in more than 90% of the observed cases due to a successful national timber harvesting ban (State Forestry Administration 2006). On the other hand, 93% of livestock grazing incidences were deemed to be ongoing at the time of the survey. Livestock grazing was also the most prevalent disturbance in one recent study spanning the entire Minshan mountain range (livestock disturbance found in 19% of over 1600 sample plots, Wang 2008). However, as far as we know, there is little monitoring and management of livestock production in the panda's geographic range, even inside nature reserves.

Despite the recorded prevalence of livestock across giant panda habitat, research on the nature of the impacts on pandas and their habitat is limited to a small number of case studies in the Chinese literature (Kang et al. 2011; Ran, 2003; Ran et al., 2003; Ran et al., 2004). These studies reiterated the findings of the 3rd Giant Panda Survey about the prevalence of livestock disturbance in panda habitat, in addition to showing that there is some overlap in the habitat selection of pandas and livestock. However, many questions remain regarding the space use and habitat selection of individual livestock animals, spatial distribution of livestock impacts on panda habitat and the nature of the impacts. Of particular concern is whether livestock could threaten the sustainability of the giant panda's main food, understory bamboo, a food source that is not believed to be threatened by any other animal competitor (Schaller et al. 1985).

We set out to fill these information gaps in Wolong Nature Reserve, a flagship reserve for giant panda research and a driver of policy making for the conservation of this endangered species (Tuanmu et al. 2010; Viña et al. 2008). We analyzed data obtained from forest surveys, remote sensing and Global Positioning System (GPS) collar telemetry to investigate the effects of an emerging livestock sector in this Reserve—the rearing of domestic horses. Our primary interest was in determining whether forest encroachment by horses could threaten the giant panda by occupying suitable habitat and consuming bamboo. Our objectives were to: (1) assess horse distribution with respect to panda habitat suitability and panda distribution, (2) compare space use and habitat selection patterns of horses and wild pandas, and (3) analyze the impact of the horse herds on bamboo biomass and on panda habitat use.

Methods

Study area

Wolong Nature Reserve is located in Wenchuan County, Sichuan province, China (102°52′–103°24′E, 30°45′–31°25′N, Schaller et al. 1985, Fig. 1). It is one of the largest reserves for the conservation of giant pandas (2000 km^2) and harbors 10% of the total wild giant panda population (Liu et al. 2001; State Forestry Administration 2006). There are also over 10,000 plant and animal species found in the Reserve (Tan et al. 1995) owing to its wide elevational range (1200–6250 m, Schaller et al. 1985). The giant pandas mainly inhabit mixed deciduous broadleaved coniferous forests at intermediate elevations of 2250–2750 where they forage on bamboo, which can cover up to 95% of the forest understory area (Schaller et al. 1985). Giant pandas are solitary mammals and are obligate bamboo foragers, with bamboo making up over 99% of their diet throughout all seasons of the year (Schaller et al. 1985).

The Reserve is also home to nearly 5000 human residents who are mainly farmers. With respect to livestock, residents raise cattle, pigs, goats, and yaks for meat (Ghimire 1997). Yaks make up the largest group of livestock, with over 3000 animals in the Reserve, followed by goats and cows (~1500 animals each, Wolong Nature Reserve 2008). Historically, horse rearing was rare in the Reserve (less than 25 horses occurred in the entire Reserve as recently as 1998). Although horses now make up the smallest proportion of all

Table 1
Summary of four domestic, free-ranging horse herds monitored in giant panda habitat in Wolong Nature Reserve, China.

Horse herd	n	Year introduced	Type of analysis
Fangzipeng	16	2007	Field survey
Papagou	12	2004	GPS collar
Qicenglou	5	2011[a]	GPS collar
Yusidong	23	2004	GPS collar, field survey

[a] But previously held as part of a larger herd ($n = 20$) at Huangcaoping and Laowashan; was moved back to Huangcaoping on 2/7/2012 (see Fig. 1).

livestock animals at just under 350 heads (in approximately 20–30 herds), the number of horses has increased tenfold from 1996 to 2008 (Wolong Nature Reserve 1996, 2008). The growth in this sector can be attributed to telecoupling processes (Liu et al. 2013) such as selling horses to regions far away from Wolong and to strengthening agricultural business exchanges between Wolong residents and those in Xiaojin township (located outside of giant panda habitat and adjacent to the Reserve on its western side), where horse rearing is prominent.

Horses are supposed to be contained year round in existing grazing areas. However, in recent years, some horse herds have been excluded from grazing areas because they over-consumed grasses. As a result, horse herders have sent their horses to nearby forests (and panda habitat) to graze separately from the cattle. In these forests we have observed horses to forage largely on bamboo, since it is the most available plant matter present in the understory. To our knowledge, this practice has occurred with at least four horse herds in Wolong. Horse herders only visit their herds approximately once per month and do not spatially contain their activities.

Study subjects

We monitored four focal herds of horses (hereafter Yusidong, Qicenglou, Papagou and Fangzipeng, after the name of the local regions where they graze) inhabiting giant panda habitat in Wolong. These herds were not chosen as representative of all livestock production systems occurring across the entire reserve but for analyzing the emerging trend of forest encroachment by horses (i.e., the herds chosen inhabit forests in the Reserve). All herds have only recently been introduced to their respective forest areas (Table 1). The Yusidong, Qicenglou, and Papagou herds were monitored by placing a GPS collar on one member of each herd. Of those, the Yusidong herd is the largest (23 horses). The Fangzipeng herd was monitored using field surveys only (since additional GPS collars were not available).

We also monitored three wild giant pandas (two adult females—Mei Mei and Zhong Zhong and one adult male—Chuan Chuan) using the same type of GPS collars. These pandas occupied an area in close proximity to the Yusidong herd (Fig. 1). While these pandas constitute a small sample, like many other endangered species (Gill et al. 2008; Miller et al. 2010), it is not feasible for the government to give permits to study many individuals using GPS collars. Nevertheless, this is the first spatially explicit account of sympatric panda and horse behavior using high accuracy GPS collar telemetry. The use of wild pandas for this project was approved by the State Forestry Administration of China. The China Conservation and Research Center for the Giant Panda (CCRCGP) was responsible for all animal care procedures. Efforts were made to limit disturbance to animals to short periods required for initial anesthetization and collar deployment. To keep the time period constant across individuals, we restricted the data used in this analysis to a one-year period (between 6/15/2011 and 6/15/2012 for all pandas and horses except Mei Mei, a female panda monitored from 6/15/2010 to 6/15/2011).
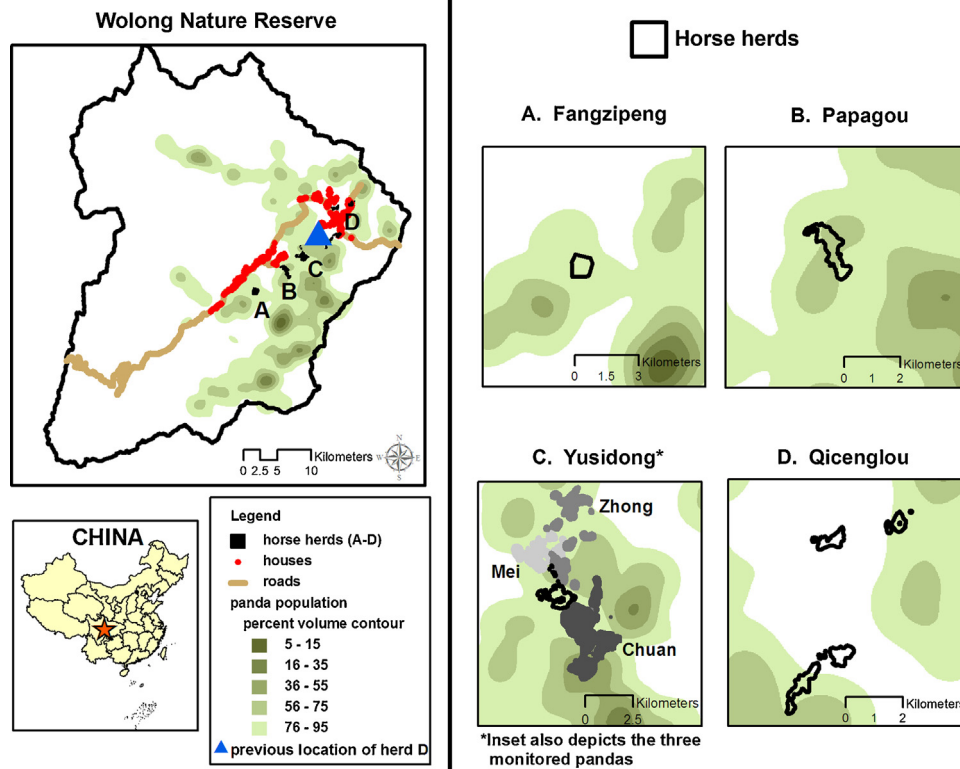
Fig. 1. Distribution of four domestic, free-ranging horses and pandas studied in Wolong Nature Reserve, China. The polygons represent the home ranges derived using the biased random bridge model (Benhamou 2011) with the exception of the Fangzipeng herd in which the MCP method was used on transect data due to lack of available GPS collar data. The probability distribution of pandas across the Reserve was obtained by conducting a bivariate normal probability density estimation on giant panda signs obtained from the most recent census on giant pandas conducted in 2001 (State Forestry Administration 2006). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

All GPS collars were 12-channel GPS 4400M models (Lotek Engineering Inc., Newmarket, ON, Canada) and were scheduled to record fixes every 4 h. Fix acquisition rates of the collars were 84, 99, and 90% for the Yusidong, Qicenglou, and Papagou horse herds, respectively and 51%, 16%, and 54%, for Mei Mei, Zhong Zhong, and Chuan Chuan, respectively. The lower fix acquisition rate for pandas is largely due to their behavior (e.g., time spent sleeping or feeding while inclined on the back may block satellite reception). Before deployment, we performed field tests of the collars' fix acquisition rates ($n = 30$ plots), and all exhibited rates above 90%, with no detectable effects of landscape characteristics (e.g., topographic position, canopy cover). Tests of locational accuracy against a differentially corrected GPS unit showed that locations obtained by the GPS collars were 95% accurate within 60 m.

Data collection and analysis

Spatial distribution of horses

We assessed giant panda habitat suitability in areas occupied by horses. Habitat suitability (divided into four suitability classes) was obtained by a multiplicative function of elevation, forest cover, and slope (Liu et al. 1999). Pandas require forest, are limited to certain mid-range elevations (around 2000–3300 m in Wolong) due to bamboo growing patterns, and prefer gentle slopes (<45°) for ease of travel (Schaller et al. 1985). The forest cover layer was derived from a supervised classification of Landsat^{TM} imagery (30 m × 30 m resolution) from 2007 (Viña et al. 2011) into forest versus non-forest (with an 82.6% accuracy). The slope and elevation layers were obtained from a Digital Elevation Model (DEM) acquired by the National Aeronautics and Space Administration's (NASA) Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER)

(29 m resolution). We conducted spatial overlays to summarize the proportion of each horse home range within each panda habitat suitability class.

We assessed the spatial relationship between areas occupied by horses and the predicted probability distribution of pandas across the Reserve. Panda distribution prior to horse occupancy was estimated by conducting a bivariate normal kernel density estimation (Bailey & Gatrell 1995) (bandwidth $h = 1000$ m) on all panda signs surveyed during the most recent nation-wide giant panda census in 2001 (conducted prior to horse occupancy, State Forestry Administration 2006). In this survey, surveyors searched for panda signs along transects established along elevational gradients within 2–6 km² habitat blocks distributed across all panda habitat in the Reserve. We summarized the proportion of each horse home range within each percent volume contour of the predicted panda distribution (5–100% contours, with 5% representing the top 5% probability of occurrence).

Horse home ranges were estimated by constructing 95% probability distributions around the locations obtained from each of the GPS collars in each herd using the biased random bridge approach (Benhamou 2011). This approach uses a probability density function to predict an animal's probability of use of an area based on the angle of movement from one time point to the next using a biased random walk (Benhamou 2011). A biased random walk refers to the condition in which the distribution of angles is not uniform due to a preference on the part of the animal. In the case of the Fangzipeng herd (which was not monitored with GPS collars), we established a set of 5 transects (0.5–1 km each) running through an area of ca. 1 km² where we observed the herd to roam, and recorded the presence or absence of horse signs (e.g., feces or eaten bamboo) in 30 m × 30 m plots ($n = 49$) every 100 m along these

transects (for sampling details see Section "Impact of horses on bamboo and pandas"). We then created a minimum convex polygon (MCP) that covered 95% of the plots with horse signs to represent a rough estimate of their home range. Despite the lower accuracy of this method, we included the Fangzipeng herd due to the historical significance of its location as the core study region of decades-long giant panda research (Schaller et al. 1985). All home range analyses were conducted using the R software (R Development Core Team 2005) and the "adehabitatHR" package for R (Calenge 2011b).

Comparison of space use and habitat selection of horses and pandas

We compared the home ranges estimated for horses with those estimated for the three wild GPS-collared giant pandas in order to contrast how these two species use space. For the pandas, we used the same home range estimation method used in the first three horse herds (biased random bridge approach). We excluded the fourth herd (Fangzipeng) from this comparison due to unavailability of GPS collar data. We compared horses' and pandas' home range sizes using isopleths. We also compared the core area sizes, which were calculated using the core area estimation method outlined in Vander Wal and Rodgers (2012).

We then compared habitat selection by horses and pandas, using the k-select analysis method (Calenge et al. 2005). This multivariate method is an eigenanalysis of the marginality in the data. Marginality refers to the "squared Euclidean distance between the average habitat conditions used by an organism and the average habitat conditions available to it" (Calenge et al. 2005: 145). The eigenanalysis reveals the "linear combination of habitat variables for which the average marginality is the greatest" (Calenge et al. 2005: 143). The approach is particularly useful for identifying differences in habitat selection among individuals of a group, rather than averaging the variation across individuals (Calenge et al. 2005). We also performed randomization tests (with $n = 10,000$ randomization steps) to determine the significance of the results. At each step, the k-select analysis was repeated and the first eigenvalue of the observed data was compared to the randomized data set. This method tests whether the marginality vector for each animal is significantly different from what would be expected under a random use and also determines the effect of each variable on the overall marginality. The k-select analysis was conducted using the "adehabitatHS" package for R (Calenge 2011a).

We defined "available habitat" in our analysis as a single large area that encompassed the home ranges of all study animals. This area was delineated by the smallest polygon that enclosed locations of all study animals, expanded by a 500-meter buffer area to allow the inclusion of border effects. We defined "used habitat" as a random selection of one fix per day from all fixes obtained for each animal. This random selection was used to account for temporal autocorrelation and offset differences in GPS fix acquisition rates among individuals.

Variables included in the habitat selection analysis were slope, elevation, topographic position, solar radiation, forest cover and distance to nearest household. These variables were chosen due to their importance for panda habitat use as demonstrated in previous studies (Bearer et al. 2008; Hu 2001; Liu et al. 2011). Slope, elevation and forest cover were obtained as previously described. Topographic position was measured using the topographic position index (TPI), which is a measure of the difference between the elevation in a pixel and the average elevation in the surrounding pixels. The TPI was calculated on a 9-pixel neighborhood area (chosen to represent the smallest window around a given pixel) using the Land Facet Corridor Designer in ArcGIS (Jenness et al. 2011) based on the same elevation layer described previously (i.e., DEM derived from ASTER data). Solar radiation was calculated using the Area Solar Radiation tool in ArcGIS (assuming a 200 m sky size and

a year-long calculation using monthly intervals). Distance to nearest household was calculated using ArcGIS while using the DEM to calculate the surface distance between each pixel. Household locations were obtained by our research group in 2003 using GPS receivers (Chen et al. 2009; Linderman et al. 2005).

Impact of horses on bamboo and pandas

To assess the impact of horses on bamboo, we established plots (30 m × 30 m) every 100 m along transects throughout the home ranges of the horse herds in two of the sites studied (Fangzipeng $n = 49$ and Yusidong $n = 57$). Transects were selected according to a spatial orientation which would allow an even coverage of the affected area and also capture variations in elevation and vegetation cover. We visually estimated the percent cover of arrow bamboo (*Bashania fangiana*) (the only bamboo species present in these areas), eaten in each plot. We also counted the number of bamboo culms foraged in 1 m × 1 m subplots located at the center of all Fangzipeng plots ($n = 49$) and at the center of a random sample of the plots at Yusidong ($n = 10$). If a subplot had no bamboo, we left the entry blank (yielding a total of $n = 38$ subplots with bamboo). Consumption of bamboo by horses was visually conspicuous and readily distinguishable from those of other animals. For instance, horses foraged along the tops of bamboo culms and ate leaves growing from the top few nodes of the plant. Contrary to native ungulates and giant pandas, horses did not selectively choose individual bamboo culms but instead foraged on the majority of the culms located in a given area, thus giving all culms a stunted appearance.

To assess the impact of horses on panda habitat use, we conducted a temporal analysis of frequency of panda signs before and after horse occupancy. This analysis was only conducted for Fangzipeng, since this was the only area for which we had a repeated sampling dataset. We summarized the number of panda signs found in our repeated sampling transects in three visits prior to horse occupancy (November 2006, February 2007, and April 2007) and four visits after horse occupancy (January 2008, October 2008, June 2009, and October 2009) and performed a two sample *t*-test to determine whether there was a significant difference in the number of feces found in the two periods. Although the exact months in which sampling was conducted varied in the pre- and post-horse occupancy sampling periods, differences of only one month (e.g. October vs. November) are not believed to create a bias, since panda signs remain visible for several months. For all periods, we searched exhaustively for panda signs (feces or eaten bamboo) within 100 m on either side of each transect line. If multiple signs were observed in the same 30 m × 30 m plot, they were counted as a single observation. There was a lower search effort in the sampling periods in June 2008 and October 2009 (one day of sampling instead of two) due to a recent earthquake, whereby the same amount of area was surveyed but with less time spent in the search. Therefore, for these two sampling periods, we multiplied the number of panda signs by two prior to the analysis to account for the 50% lower search effort. The earthquake caused no damage to the Fangzipeng habitat area [i.e., 0% habitat loss; Ouyang et al. (2008)] and did not result in discernible avoidance by pandas (Zhang et al. 2011). During our long-term sampling of this study area, we did not observe or detect any other disturbance aside from horses that could conceivably alter panda habitat use.

Results

Spatial distribution of horses

Approximately 50% of three of the horse herd home ranges were located in highly suitable or suitable giant panda habitat (Fig. 2). All
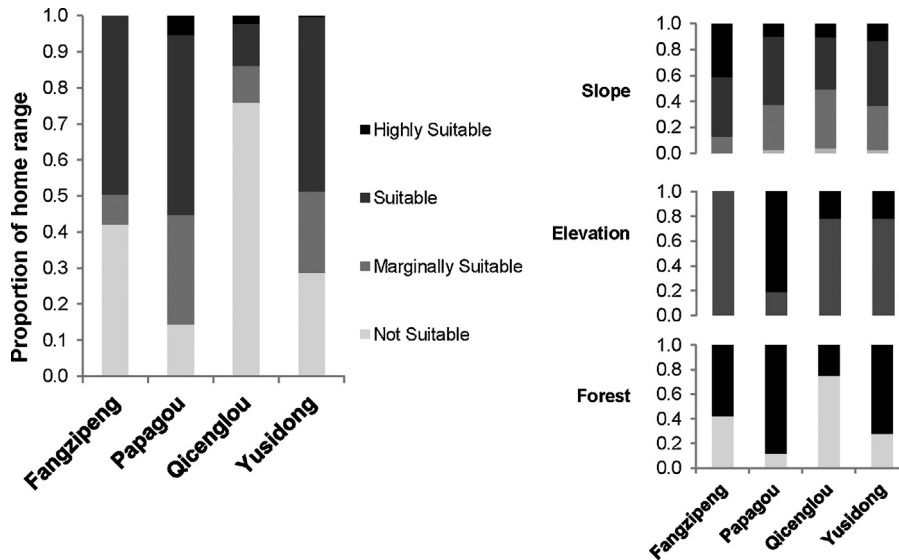
Fig. 2. Proportion of horse home ranges across giant panda habitat suitability classes. Data pertain to home ranges of four domestic, free-ranging horse herds inhabiting forested areas in Wolong Nature Reserve, China. Percent suitable habitat (a) is derived from a suitability index (Liu et al. 1999), which is a composite of forest cover, elevation and slope (each shown individually on the right). Forest was derived from supervised classification of Landsat^{TM} (2007) imagery and elevation and slope from a Digital Elevation Model (DEM) acquired by the National Aeronautics and Space Administration's (NASA) Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER).

herds were found at suitable elevations for panda inhabitance. With the exception of the Qicenglou herd, the majority of the horses' home ranges were located in forests (58–88%) with suitable slopes for the pandas (63–86%). Although the Qicenglou herd was distributed in comparably less suitable panda habitat than the other herds (mainly due to the existence of non-forest), the impact of this herd was the most widespread, as this herd was moved by the herders to four distinct locations over a three year period (see Fig. 1). All herds, except Qicenglou, were distributed completely within the predicted probability distribution of giant pandas. However, the herds never distributed within the central part of the panda distributions, as they were mainly distributed within the 75–85% percent volume contours (Fig. 3, for spatial distribution see Fig. 1).

Comparison of space use and habitat selection of horses and pandas

The utilization distributions of horses were smaller in area than those of pandas across all home range isopleths above 60 (Fig. 4). Panda home range sizes (the 95 level isopleths) were 2.2, 3.4 and 5.6 km^2 for Mei Mei, Zhong Zhong, and Chuan Chuan (the male), respectively, while horse home range sizes were 1.1, 1.0, and 1.6 km^2 for Yusidong, Papagou, and Qicenglou herds, respectively. Core areas were also generally smaller for horses ($Y = 0.3$ km^2, $P = 0.3$ km^2, and $Q = 0.6$ km^2) than pandas ($M = 0.6$ km^2, $Z = 0.9$ km^2, and $C = 1.4$ km^2).

Randomization tests revealed that the first eigenvalue obtained in the k-select analysis was significantly larger than expected under random habitat use ($\lambda_1 = 1.39$, $p < 0.0001$), making further analysis of habitat use patterns informative. Habitat use was significantly non-random for all horses and pandas (Table 2). All pandas and horses showed selection for gentle slopes and areas with high solar radiation (Table 2). All animals showed selection for higher elevations except the Qicenglou herd, which exhibited an opposite trend
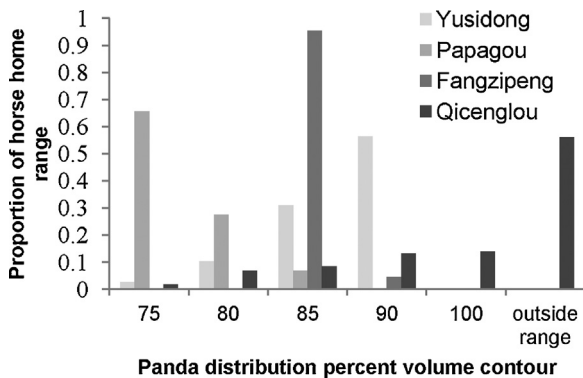

Fig. 3. Proportion of horse home ranges in each percent volume contour of the predicted probability distribution of giant pandas in Wolong Nature Reserve. The probability distribution was obtained by conducting a bivariate normal probability density estimation on giant panda signs obtained from the most recent census on giant pandas conducted across their entire range in 2001 (State Forestry Administration 2006). Percent volume contours ranged from 5 to 100% (with 5% representing the top 5% probability of occurrence), although no portion of any horse home range fell within the 5–70% range.
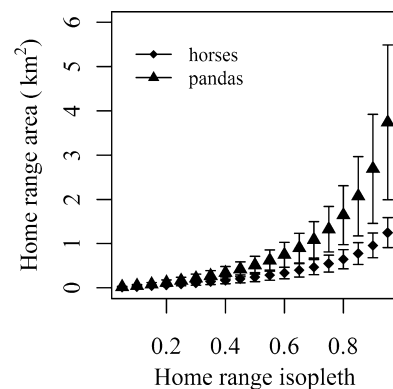

Fig. 4. Home range area obtained through home range isopleths for three domestic free-ranging horses and three wild pandas monitored using GPS collars in Wolong Nature Reserve. Home ranges were calculated using the biased random bridge approach (Benhamou 2011). Values depicted are the means and standard deviations.

Table 2
Results of the randomization test for the k-select analysis on habitat selection by pandas and horse herds. Tests were based on 10,000 randomization steps, at which the first eigenvalues of observed data were compared to those from randomized datasets. Marginality vectors for each variable represent differences between mean used and mean available habitats.

	Pandas			Horses		
	Mei	Zhong	Chuan	Papagou	Qicenglou	Yusidong
Tests of marginality						
Marginality	1.97*	0.83*	3.46*	1.59*	3.62*	2.01*
Selection of habitat variables (marginality vectors)						
Elevation	0.82*	0.53*	0.83*	0.46*	−0.88*	0.85*
Slope	−0.78*	−0.28*	−0.60*	−0.60*	−0.40*	−0.46*
Solar radiation	0.81*	0.51*	1.13*	0.81*	0.58*	1.03*
Terrain position	0.19*	0.38*	0.66*	0.35*	0.18	0.01
Forest cover	−0.14	0.22*	−0.26*	−0.15	−1.22*	−0.12
Distance to house	0.05	0.09	0.79*	−0.46*	−0.91*	0.00

* Significant at the 5% level after Bonferroni correction.

(i.e., selection for lower elevations). All pandas showed selection for areas of higher topographic position (e.g. mountain ridges), but only one of the three horse herds showed the same pattern. Only three subjects showed significant habitat selection with respect to distance to the nearest household, which included the male panda Chuan Chuan (positive) and two of the three horse herds (both negative). Results with respect to selection for forest cover were also mixed, as one panda selected positively for forest cover (Zhong Zhong), one horse herd and one panda (Chuan Chuan) selected against forest cover, and the rest displayed no selection.

With regard to the eigenanalysis, the first two eigenvalues captured the majority of the marginality in the data (Fig. 5a). The first axis represented mainly elevation, while the second axis captured mainly forest cover (Fig. 5b and c). As is evident from the configuration of the arrows representing each animal on the projection of the marginality vectors on the first factorial plane (Fig. 5d), the pandas had similar habitat selection patterns with one another as they selected for high elevation areas and high topographic position. One horse herd (Yusidong) had similar patterns as the pandas, and an almost identical niche as the panda Mei Mei. The Papagou

herd diverged slightly from the pandas by selecting more strongly for high solar radiation and low slope and less strongly for high elevation. The Qicenglou herd diverged strongly from all other animals by selecting against forested areas and for areas closer to the nearest household.

Impact of horses on bamboo and pandas

Horses had an impact on the arrow bamboo in both areas studied. At Fangzipeng, we estimated that the horses foraged more than 20% of the bamboo in 18 of the 49 plots, with 5 of those plots experiencing more than 75% bamboo foraged by horses (Fig. 6). At Yusidong, we estimated that horses foraged more than 20% of bamboo in 28 of the 57 plots and over 75% of the bamboo in 2 plots (Fig. 6). In the 1 m × 1 m subplots, horses either foraged over 90% of the available bamboo culms (52% of subplots) or less than 1% of the available bamboo culms (34% of subplots), with little moderate foraging in between these two extremes (i.e., remaining 12% of subplots). Horses also appear to have had a significant impact on panda habitat use, considering that the number of plots containing
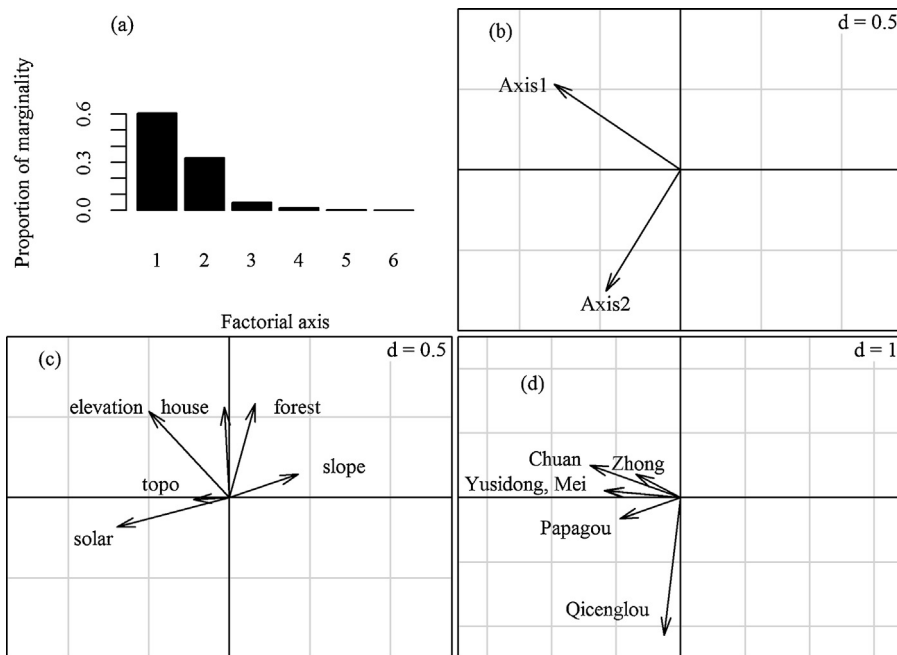

Fig. 5. k-Select analysis on marginality of habitat selection vectors among 3 wild giant pandas (Mei Mei, Zhong Zhong, and Chuan Chuan) and 3 horse herds roaming in giant panda habitat (Yusidong, Papagou, and Qicenglou). Plots include (a) bar chart of eigenanalysis showing proportion of marginality explained by each vector, (b) direction of the first two factorial axes, (c) variable loadings on the first factorial plane, and (d) marginality vectors for all 6 subjects on the first factorial plane. The notation "d" in (b)–(d) indicates the distance of each grid cell.
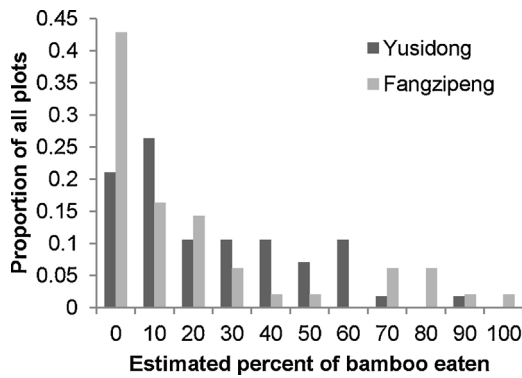
Fig. 6. Estimated percent of bamboo eaten by domestic, free-ranging horses in field plots (30 m × 30 m) distributed in two areas [Fangzipeng (n = 49) and Yusidong (n = 57)] of giant panda habitat in Wolong Nature Reserve, China.

panda signs in our repeated sampling prior to the introduction of the horses (2006 and 2007) at Fangzipeng was 5 to 10 times higher than the post-horse occupancy surveys in 2008 and 2009 (Fig. 7).

Discussion

This study documented an emerging threat to the endangered giant panda and its habitat: livestock grazing. Logistical constraints prevented us from following a greater number of pandas and horse herds; thus our inference space is relatively narrow and results should be interpreted with caution. However, our findings shed light on the potential consequences of this emerging conservation issue. Horses in particular may be poised to be incompatible with giant panda conservation goals due to their large food consumption rates and their ability to live for long periods of time un-monitored by humans in forested areas. Our results provide the first evidence to support this hypothesis by demonstrating horse use of suitable giant panda habitat, potential of some overlap with the niche of the giant panda, high bamboo consumption rates, and negative effect on panda occupancy.

One of our main findings was that horse herds engaged in forest encroachment are distributed in suitable panda habitat. The Fangzipeng area in particular is historically important for scientific research on the giant panda and has been portrayed as consistently harboring several pandas (Schaller et al. 1985). Fangzipeng supports at least two den trees that have been used by giant panda mothers to rear their young, not only in the past (Schaller et al. 1985) but also in recent years (according to our field observations) prior to horse occupancy. However, when we visited the den trees after horse occupancy, we saw only horse droppings where panda
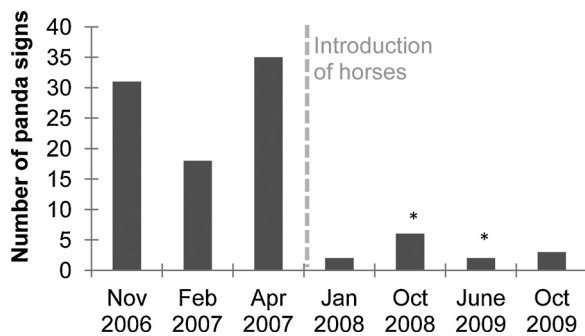

Fig. 7. Number of panda signs observed during repeated sampling in transects at Fangzipeng during three periods prior to horse occupancy and four periods after horse occupancy. Sampling periods denoted with a star (*) represent twice as many signs as were actually found during the survey (i.e., estimates were doubled to account for a 1/2 search effort performed during these periods).

droppings were once prevalent. Although we lacked a control site with which to compare the degree of decline in panda signs after horse occupancy, our results at Fangzipeng are important and useful to provide guidance for further research on the mechanisms (e.g., direct avoidance, competition for bamboo) behind the effects of horse occupancy on giant panda occupancy.

Our habitat suitability analysis also showed that the current methods used to classify and predict suitable panda habitat may be insufficient. Giant panda habitat suitability models often rely on binary classifications of forest versus non-forest as a primary measure to delineate areas suitable for panda inhabitance (Liu et al. 1999, 2004; Wang et al. 2010). Our findings suggest that it is also important to include other human disturbances in addition to timber harvesting (An et al. 2006; He et al. 2009; Linderman et al. 2006; Tuanmu et al. 2011), as current forested areas in otherwise suitable giant panda habitat may be subjected to threats such as livestock grazing that may only be detected using field surveys.

Our habitat selection analysis showed both similarities and differences in habitat selection by pandas and horses. Individual variation in selection patterns was also notable within both the pandas and horses. Areas most likely to be contested due to selection by both horses and pandas appear to be those with low slopes and high solar radiation. The Yusidong herd best demonstrated the potential for niche overlap between horses and pandas, while both seemed to group together in the k-select analysis due to their similar selection with respect to elevation, slope, and solar radiation. It is not surprising that this herd demonstrated the greatest similarity with the monitored pandas, as it is located in closest proximity to the monitored pandas compared to the other herds. On the other hand, the divergent pattern of the Qicenglou herd relative to the monitored pandas and its selection against forested areas suggests that there is potential to avoid niche overlap between horses and pandas if herders appropriately choose non-forested areas to allow their horses to roam and subsequently monitor them effectively.

Our field observations show that bamboo foraging by horses could potentially threaten the availability of food for the giant pandas, if horse populations are unchecked. This is a significant finding because in the past, it has generally been accepted that giant pandas have no strong competitors for their bamboo food source (Schaller et al. 1985; Taylor & Qin 1987). Other wild animal species that consume bamboo across the giant panda geographic range (e.g. tufted deer, sambar) do so in small quantities and as part of more varied diets (Schaller et al. 1985). Other species relying on bamboo such as the red panda select for different types of micro-habitats compared to giant pandas, displaying a degree of niche diversification (Zhang et al. 2006).

As non-ruminants, horses need to consume up to 10 kg of plant biomass a day, which is 60% larger than ruminants such as cattle, Menard et al. 2002). In our study areas, horses ate arrow bamboo, which provides around 0.4–0.9 kg of plant biomass per m^2 (Taylor & Qin 1987). However, horses only grazed the tops of bamboo stems and leaves, accounting for roughly 10% of each plant. At this rate, a herd of 20 horses could potentially graze on up to 20% of bamboo culms in a 1 km^2 area in a year. Although the daily consumption rate of horses is about the same as giant pandas, the level of intensity of foraging per unit of area by horses is significantly larger due to their higher densities, in addition to their smaller home ranges as compared to the pandas. Although exhibiting some overlap in their home ranges, pandas are solitary and are believed to be distributed at densities of about one individual per 2 km^2 in this reserve (or 19 pandas in a 35 km^2 area in one study, Schaller et al. 1985). Panda foraging itself does not significantly threaten bamboo populations (Pan et al. 2001), perhaps in part due to the adequate spacing of pandas, in addition to the fact that pandas alternate their foraging behavior to select for different bamboo plant parts and species throughout the year (Pan et al. 2001; Wei et al. 2011).

However, the nearly 50-fold higher density of horses introduced by humans presents a markedly higher amount of foraging pressure on localized bamboo patches. Further studies are needed in order to determine potential long-term effects of horse grazing on bamboo and ascertain whether horse foraging may promote or discourage new bamboo growth.

In addition to direct impacts from foraging, horse herding may also have other impacts on pandas that need to be further studied, including avoidance due to sound and odor disturbances. Other potential impacts to also explore in the future include disease transmission across the livestock–wildlife interface, a topic that has been understudied in pandas despite early warnings of potential risks (Hu 1981). Since we observed horse carcasses in close proximity to panda signs and horse feces in the pandas' water sources, this issue should be seriously considered in future research.

While a directive is in place requiring livestock to be kept within designated grazing areas inside of giant panda nature reserves, our observations [and those of others across the entire giant panda geographic range, State Forestry Administration 2006] suggest that this rule is not always operational on the ground. Indeed, in other areas of the giant panda geographic range exhibiting less management than Wolong and supporting higher numbers of livestock, the situation may be more serious (State Forestry Administration 2006). In order to better manage livestock management issues inside reserves, we propose that they be treated as part of a Coupled Human and Natural System (CHANS) so that the complex interactions between people and nature are fully appreciated (Liu et al. 2007). For instance, the financial needs of the local people should be taken into account, especially considering that animal husbandry serves as an important mechanism for combating poverty across western China and may be needed to fill an income gap created after timber harvesting was banned in the late 1990s (Melick et al. 2007). It may be possible to link livestock management efforts with other successful conservation incentive programs implemented across China (see Liu et al. 2008) by providing monetary incentives to local farmers for participating in conservation.

Our study is unique in that it captures the nature of a human disturbance toward the start of its emergence rather than after it has become a problem entrenched in a system. The value of such a study is that it can drive future management measures. For instance, after our concerns about the impact of horses were brought to the managers of Wolong Nature Reserve, the administration called for removal of horses from the reserve. This study thus demonstrates the importance of on the ground assessments of livestock impact on forests and direct ties to endangered species relying on such forests for their survival.

Acknowledgements

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