Giant panda distributional and habitat-use shifts in a changing landscape

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Abstract
Long-term data on populations, threats, and habitat-use changes are fundamentally important for conservation policy and management decisions affecting species, but these data are often in short supply. Here, we analyze survey data from 57,087 plots collected in approximately three-fourths of the giant panda's (Ailuropoda melanoleuca) distributional range during China's national surveys conducted in 1999–2003 and 2011–2014. Pandas associated preferentially with several ecological factors and avoided areas impacted by human activities, such as roads, livestock, mining, and tourism. Promise is shown by dramatic declines in logging rates, but is counterbalanced with recently emerging threats. Pandas have increasingly utilized secondary forest as these forests recovered under protective measures. Pandas have undergone a distributional shift to higher elevations, despite the elevational stability of their bamboo food source, perhaps in response to a similar upward shift in the distribution of livestock. Our findings showcase robust on-the-ground data from one of the largest-scale survey efforts worldwide for an endangered species and highlight how science and policy have contributed to this remarkable success story, and help frame future management strategies.

KEYWORDS
anthropogenic threat, conservation policy, giant panda, habitat use, population distribution
1 | INTRODUCTION

Species conservation may be experiencing a resurgence in conservation circles following new evaluations of their importance to ecosystem function (Hooper et al., 2012), and other values to scientific and lay communities (Gascon et al., 2015; Richardson & Loomis, 2009). What is needed is empirical evidence that the recipients of concerted conservation action benefit from on-the-ground conservation action. Evidence for improving conservation status for some key species is found in upgraded status for species listed on the International Union of Conservation for Nature (IUCN) Red List evaluation (Hoffmann et al., 2015). A recent prominent example is the dramatic turnaround in the status of the giant panda (*Ailuropoda melanoleuca*; hereafter “panda”), recently downlisted from Endangered to Vulnerable on IUCN’s Red List (Swaisgood, Wang, & Wei, 2016). Once nearly written off by pessimistic outlooks (Schaller, 1993), or perceived evolutionary obsolescence (Schaller, 1993), the data now indicate that panda numbers have been increasing for nearly two decades, supported by vast protected areas and recovering habitat (Swaisgood, Wang, & Wei, 2017). Reversals in conservation outlook will be easier for those species reaching critically low levels that can be shored up with conservation breeding and reintroduction or those species declining due to a few key threats that can be addressed. But reversals requiring governing bodies to marshal resources and policies across a large range, as in the case of the panda, will be an even more difficult milestone to attain. Thus, the panda makes an excellent case study revealing species conservation approaches required for success.

We know that the Grain-to-Green and National Forest Conservation Programs have had measurable impacts on forest cover in the panda’s range (Li et al., 2013; Liu, Li, Ouyang, Tam, & Chen, 2008), and have resulted in China becoming one of the few countries able to claim a net increase in forest cover (Food and Agriculture Organization of the United Nations, 2010). The creation of “panda reserves” has boosted protection of panda habitat by 54% in the past decade, an action associated with a 17% increase in panda population size (Sichuan Forestry Department, 2015, see Supporting Information Table S1). At the same time, pandas face emerging threats, such as continued habitat fragmentation and degradation from roads and other infrastructure development and anticipated impacts of climate change (Swaisgood et al., 2017; Xu et al., 2017). While habitat fragmentation and population subdivision are long-known threats to pandas (Wang et al., 2014), livestock encroachment is a relatively new problem (Wang, McShea, Wang, & Li, 2015) that has not been evaluated on a large scale. Less well understood are the current and future impacts of climate change. A number of climate change models project substantive impacts on pandas’ primary food source, bamboo, and a subsequent range constriction and significant panda population declines (Fan et al., 2014; Li et al., 2015; Songer, Delion, Biggs, & Huang, 2011; Tuanmu et al., 2013; Zang et al., 2017).

Here, we asked the question: What does panda recovery look like on the ground? Using one of the largest endangered species habitat data sets available, we quantified emerging threats, evaluated how policies are associated with changing circumstances for pandas and their habitat, and further defined biological and human disturbance variables that influence panda habitat use and distribution. We did this using data collected throughout the panda’s range in Sichuan Province during the third (1999–2003) and the fourth (2011–2014) national surveys.

2 | METHODS

2.1 | National survey data

We analyzed data collected from SFA’s third and fourth national surveys to estimate panda population size (State Forestry Administration, 2006; Sichuan Forestry Department, 2015). The methodology was nearly identical in each survey, and none of the small deviations impacted our analysis, unlike the first and second survey methods, which were substantially different and therefore omitted from our analysis. Our analyses focused on Sichuan Province, comprising 78.6% of the total panda habitat and 74.4% of the total population (Figure 1). Details of panda sign survey can be found in Zhang et al. (2011) and in Annex A.

2.2 | Panda habitat selection

Using an information theoretic approach we built separate sets of candidate models. The biological model included biotic and abiotic factors, whereas the disturbance model included human activity factors (Supporting Information Table S2). For the assignment and transformation of all covariates involved in our models please see Annex B. To examine how habitat selection changed over time, we developed an identical constrained set of candidate models for both surveys. We determined the top model for each survey to be any model with an Akaike’s information criterion (AIC; Burnham & Anderson, 2002) weight ($w_i$) exceeding 0.90. We examined how the magnitude and direction of panda habitat selection changed over time by comparing the beta coefficients for each covariate between the third and the fourth surveys.

To determine the importance of including biological and human disturbance factors, we combined the top biological and human disturbance models and compared the log-likelihood improvement with a log-likelihood ratio test. To assess nonlinearity in panda habitat selection, we examined interactions between variables previously shown to be important to pandas (Hull et al., 2011), and nonlinear...
transformation of continuous variables. In the third survey, only elevation was recorded as continuous data, while all other values were recorded categorically in the field (Supporting Information Table S2). However, in the fourth survey, elevation, slope, tree diameter, tree canopy, shrub height, and shrub cover were recorded as continuous data in the field, allowing for an assessment of nonlinearity for each covariate. Finally, we compared the relative probability of livestock and bamboo presence from plot-level observations across the elevational gradient in both surveys to infer potential mechanisms for shifting panda habitat selection.

2.3 Statistical assessment

Comparisons of proportions of observations between the third and the fourth survey were conducted with a Z-test. Covariates for habitat selection models were screened for collinearity, but all had a Pearson’s correlation coefficient $|r_s| < 0.5$, and were therefore retained in the candidate models. We fit binary logistic regression models using a logit link and a binomial-error distribution to maximize log-likelihood values. We employed a generalized linear mixed-effects model, with a random factor to control for regional subdivision of the panda survey. Relative probability curves were calculated using a resource selection function approach (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). We adopted R v3.0.3 for all statistical analyses, using packages lme4 (https://CRAN.R-project.org/package=lme4), MuMIn (https://CRAN.R-project.org/package=MuMIn), and ROCR (https://rocr.bioinf.mpi-sb.mpg.de). We set $P$ to 0.05 for significance tests.

3 | RESULTS

3.1 Human disturbance model

Human disturbance decreased significantly from 59.20% (15,446/26,090) of plots in the third survey to 45.20% (14,019/30,997) in the fourth ($Z = 33.28, P < 0.001$). The proportion of disturbance categorized as livestock, road, farming, and other disturbances significantly increased, while the proportion of logging significantly decreased (Figure 2a).

The top habitat selection model in both surveys had an AIC $w_j < 0.90$, therefore the beta values were averaged from the top two models (Supporting Information Table S3 and S4). Besides, the results of models validation with goodness-of-fit measures please see Supporting Information Figure S1. Pandas avoided all types of human disturbance, with the
exception of herb and shoot gathering (Figure 3a). The magnitude of avoidance significantly increased for livestock and significantly decreased for logging across surveys (Figure 3a). A separate analysis at the plot-level demonstrated that pandas avoid plots with livestock signs (Supporting Information Table S7). Panda preference for nature reserves significantly decreased between surveys, and showed no significant preference in the fourth survey for protected areas (Figure 3a).

3.2 Biological model

The proportion of plots with bamboo present, containing primary forest and with large trees, significantly decreased from the third to the fourth survey, while shrubs increased in height (Figure 2b). The top habitat selection model in the third survey had an AIC $w_j > 0.90$ and beta value averaging was not required, while beta coefficients were averaged across the top three models from the fourth survey (Supporting Information Tables S5 and S6). Pandas preferred habitat with bamboo, gentler slopes, larger trees, and sparser shrub cover in both surveys (Figure 3b). The magnitude of preference significantly increased for bamboo between the two surveys, and significantly decreased for forest age and tree DBH (Diameter at Breast Height) (Figure 3b). Pandas showed no significant preference in the fourth survey for primary forest (Figure 3b).
3.3 Nonlinear effects

Combining the global biological and human disturbance models significantly improved fit in the third ($\chi^2 = 427.80$, $df = 11$, $P < 0.001$) and the fourth ($\chi^2 = 133.60$, $df = 11$, $P < 0.001$) surveys. Significant improvements in model likelihood occurred in the third survey for including interactions between elevation and livestock ($\chi^2 = 9.40$, $df = 2$, $P = 0.01$), tree DBH and forest age ($\chi^2 = 22.80$, $df = 1$, $P < 0.001$), elevation and bamboo ($\chi^2 = 7.40$, $df = 2$, $P = 0.02$), but not for livestock and bamboo ($\chi^2 = 0.40$, $df = 1$, $P = 0.53$). Interactions in the third survey suggested that in the presence of livestock and absence of bamboo, the relative probability of selection for pandas peaked at a lower elevation (Figure 5). The interaction between forest age and tree DBH was negative ($\beta = -0.46$, $SE = 0.09$), suggesting a weakening panda preference for large trees in primary forest. No significant improvements to model fit occurred for including any of the interaction terms in the fourth survey.

Examination of continuous covariates from the fourth survey indicated significant model improvement for nonlinear...
responses in preference. Pandas prefer gentle slopes less than 30°, but the preference peaked at 15° (Supporting Information Figure S2a). Pandas prefer larger trees and denser forest, but the preference increased asymptotically (Supporting Information Figure S2b,c). Similarly, pandas prefer shorter shrubs with sparse cover, but the preference asymptotically decreased (Supporting Information Figure S2d,e).

4 | DISCUSSION

Our findings from this large-scale range-wide survey broadly support previous studies of panda habitat selection, demonstrating a preference for bamboo presence, gentle slope, sparse shrubs, and large trees (Liu et al., 2016; Shen et al., 2008; Zhang et al., 2011), important considerations when preserving...
or restoring habitat. China’s protection and restoration policies are associated with a 14% expansion in panda habitat and a 17% increase in panda population between the third and the fourth surveys (Supporting Information Table S1; Sichuan Forestry Department, 2015), and our data reveal the on-the-ground changes that may support these changes. Tree size and age became less important in predicting habitat use from the third to the fourth survey. In the fourth survey pandas were equally likely to use primary and secondary growth forests, in contrast to findings from the third survey in which pandas showed a strong preference for primary forest (Zhang et al., 2011). Now nearly half of panda habitat use occurs in secondary forest. We suggest that early successional growth is less suitable to pandas; however with time these forests are recovering and becoming more suitable, supported by our results indicating that tree DBH has increased in secondary forests. That recovery is taking place even before old-growth forest can be reestablished is encouraging. This finding is a strong endorsement of China’s forestry policies, such as the logging ban and reforestation programs (Liu et al., 2008, 2016; Loucks et al., 2001; Xu et al., 2017), and suggests that having set these ecological processes in motion, habitat will continue to improve.

Human disturbance is playing an increasing role on panda landscapes, with significant increases in livestock, roads, farming, and other disturbance activities, coupled with decreasing logging. With the exception of logging, these changes in human-use patterns are consistent with a
moderating economy that emphasizes commercial extraction over local use and consumption. More worrisome, livestock, roads, and farming increased, and pandas showed strong avoidance to these disturbances when selecting habitat (Figure 3a). Thus, dramatic declines in logging show great promise for improved panda habitat, but a suite of emerging threats may cause new problems. Livestock encroachment is the most common and rapidly growing threat, confirming results from data collected over much smaller scales within a single reserve (Zhang et al., 2017), indicating for the first time a prevalent rangewide threat from livestock.

We also found a significant increase in the mean elevation of panda-occupied habitat. In the decade between the two surveys, we found an 80 m upward shift in elevation (from 2,596 ± 353.40 m to 2,676 ± 395.27 m), a more rapid elevational shift than the median climate-mediated elevational shifts estimated at 11 m per decade (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011). However, there was no upward migration of the bamboo food source on which pandas depend, suggesting that pandas are not tracking changes in their foraging habitat. Livestock overlap with pandas was primarily at the low and high end of pandas’ elevational range (Figure 4), and there were similar upward shifts by both livestock and pandas. Further, panda sign was less frequent at plots used by livestock, suggesting that pandas avoid livestock or habitat impacted by livestock (Supporting Information Table S7). These results suggest that livestock reduce habitat suitability for pandas, presumably by consuming or trampling bamboo. Taken together, the observed elevational shift in pandas may not be only caused by climate change, as the observed shift is more rapid than expected and other plausible and rapidly occurring disturbances, such as livestock grazing, also explain these results. It is now incumbent upon policy-makers to use a combination of enforcement and eco-compensation to discourage livestock grazing (Zhang et al., 2017) and other forms of disturbance. Habitat near the pandas’ upper elevational limit may become increasingly important in the future, requiring managers to target these areas for preservation and management.

Protected areas are a cornerstone of biodiversity conservation but do not always provide the benefits for which they are designed and credited (Mascia & Pailler, 2010; Rodrigues et al., 2004). Protected areas undoubtedly figured prominently in the panda’s ongoing recovery (Swaisgood et al., 2017). However, our findings indicate that while protected status predicted panda presence in the third survey, this preference has diminished as in the fourth survey pandas showed no preference for using habitat inside reserves. Much of the area outside reserves is comprised of recovering secondary forests, which may explain why pandas are making use of areas that have no formal protected status. Our data suggest that pandas colonizing areas outside reserves are also avoiding areas of high disturbance, such as roads and farming. Eco-compensation programs (Yang et al., 2013a, 2013b), which are vital for maintaining this recovery trajectory in these less regulated areas, should target the disturbance factors we have shown and associated with reduced habitat use (roads, livestock, farming, and tourism). While protected areas are of great value for pandas and sympatric species living under their umbrella (Li & Pimm, 2016), protected areas alone will not be enough to support panda recovery since many pandas live in areas that are not part of the reserve system. Given the large expansion in the reserve system to include 67 reserves and 1.4 million hectares of panda habitat, covering 54% of the panda’s range, future conservation efforts will likely focus on better management and policy inside and outside of reserves (Swaisgood et al., 2017; Wei et al., 2015). Future research should build on previous research identifying ecological factors and anthropogenic threats (Bearer et al., 2008; Li et al., 2017; Schaller, Hu, Pan, & Zhu, 1985; Wei et al., 2015) that limit panda population size, and can be addressed with improved policy and management.

Our findings demonstrate many positive changes in habitat, and provide support for the recent controversial decision by IUCN to downlist the panda from Endangered to Vulnerable (Kang & Li, 2016; Swaisgood et al., 2016, 2017; Xu et al., 2017), but also reveal the nature of emerging threats to panda populations. While some of these emerging threats have been identified previously (Xu et al., 2017), our contribution is novel in its incorporation of rangewide data that includes panda presence and habitat use patterns rather than relying solely on remote sensing of habitat, allowing stronger and novel conclusions regarding how changes in habitat influence pandas’ decisions to use habitat.

That management actions and policy decisions have led to the notable on-the-ground changes for pandas shown here, even in the globe’s most populous nation, gives hope that conservation action with other, less well tended, species conservation can also achieve success. The lessons learned here include commitment to the collection of long-term data to monitor population and habitat changes and the political will to establish protected areas, enforce regulations, and implement practical eco-compensation programs. Add to these government actions a vibrant international conservation science community helping to inform and guide policy and management decisions (Liu et al., 2016; Swaisgood et al., 2017; Wei et al., 2015) and we have the main ingredients for a successful species conservation program. These efforts earned the panda a rare position in species conservation, joining the ranks of those species which have become less endangered (Hoffmann et al., 2015) in an era of defaunation. While these positive outcomes give reasons for hope, conservation efforts must continue to stay ahead of new threats lest the panda become endangered once more.
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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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