Old-growth forest is what giant pandas really need

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**Giant pandas (*Ailuropoda melanoleuca*) are an
iconic conservation species, but despite significant
research effort, do we understand what they really
need? Estimating and mapping suitable habitat
play a critical role in conservation planning and
policy. But if assumptions about ecological needs
are wrong, maps with misidentified suitable habi-
tat will misguide conservation action. Here, we use
an information-theoretic approach to analyse the
largest, landscape-level dataset on panda habitat
use to date, and challenge the prevailing wisdom
about panda habitat needs. We show that pandas
are associated with old-growth forest more than
with any ecological variable other than bamboo.
Other factors traditionally used in panda habitat
models, such as topographic slope, are less impor-
tant. We suggest that our findings are disparate
from previous research in part because our
research was conducted over a larger ecological
scale than previous research conducted over
more circumscribed areas within individual
reserves. Thus, extrapolating from habitat studies
on small scales to conservation planning on large
scales may entail some risk. As the Chinese gov-
ernment is considering the renewal of its logging
ban, it should take heed of the panda's dependency
on old growth.**

Keywords: conservation policy; ecological scale;
habitat suitability; giant panda

1. INTRODUCTION

The giant panda is at a high risk of extinction and
will require informed management for recovery.
Panda conservation science has come a long way in
recent years; now it is time to apply our increasingly
sophisticated knowledge of pandas to conservation
management strategies [1]. Although the giant
panda genome has now been sequenced [2], we are
still struggling to fully understand the panda's
ecological requirements.

Estimating and mapping suitable habitat play a criti-
cal role in conservation planning and policy, but if
assumptions about habitat suitability are wrong, conser-
vation action will be misguided [3,4]. Ecological scale,
perhaps the most fundamental concept in all of ecology
[5], intersects with conservation when research con-
ducted on one scale is used for conservation planning
on another scale [3]. For the iconic endangered giant
panda, models of habitat suitability have been used to
infer rates of habitat loss, estimate amount of suitable
habitat remaining inside and outside reserves, and
design reserve systems linked by ecologically relevant
corridors [6–8]. But maps and measures of habitat suit-
ability are only as good as the underlying biological
assumptions, which are sometimes influenced by the
scale over which data are obtained. Modellers of
panda habitat have not ignored the available ecological
data, but have been forced to rely on data collected
over limited temporal and spatial scales. What happens
if the resulting habitat models are wrong?

Here, we analyse the largest, landscape-level dataset
on panda habitat use, challenge prevailing wisdom
about panda habitat needs, and provide direction to
conservation policy and planning at the national
level. We use data collected by dozens of field teams
throughout Sichuan during the Chinese State Forestry
Administration's Third National Survey on the giant
panda, representing one of the most intensive efforts
to survey any endangered species. This massive under-
taking produced by far the largest dataset—in scope,
sample size and range—of habitat use by giant pandas.

2. MATERIAL AND METHODS

From 1999 to 2003, field observers recorded ecological variables
associated with panda signs, matched with control plots where panda
signs were not observed. The data included in our analysis were col-
lected across the giant panda range in Sichuan province, including 19
reserves in the four primary mountain ranges: Minshan, Qionglai,
Liangshan and Xiaoxiangling (figure 1; electronic supplementary
material). This multi-year survey—across seasons and much of the
landscape available to pandas today—avoids the potential limitations
arising from data collected over small spatial and temporal scales.

Details of the Third National Survey are available elsewhere [9].
The known and potential range of giant pandas was divided into sec-
tions measuring $2-6$ km^2 and field teams established transects along
altitudinal gradients, ensuring that each transect sampled all repre-
sentative habitat types. The presence of panda along transects was
determined by signs (primarily faeces, but also foraging sites and
dens) and vegetation was sampled in $20 \text{ m} \times 20 \text{ m}$ plots. A sign
more than 200 m from another sign merited establishing another
plot. Data collected for each plot included topography, altitude,
slope, forest type, forest age, tree diameter at breast height (DBH),
canopy coverage, shrub cover, shrub height and bamboo presence.
Control plots were established at every 200 m change in elevation
along the transect and following transitions between forest types, to
ensure that all habitat types encountered were sampled. After exclud-
ing marginal habitats, such as monocultured forests and data from
nine reserves with inadequate records, we had 4908 plots for analysis
(1116 panda sign plots and 3792 control plots).

We used an information-theoretic approach [10] to determine the
suite of factors that best predicted the presence of panda signs. Pear-
son's (for continuous variables) or Kendall's (for discrete variables)
correlation analysis was first conducted to test independence
between variables. For those variables with a correlation coefficient
above 0.5, we only kept the variable with clear biological meaning
in the subsequent analysis in order to weaken multi-collinearity.
We constructed a full model set, including global models with all
meaningful explanatory variables, and calculated the Akaike infor-
mation criterion (AIC) to evaluate model fit. Using the differences
in AIC values (Δi) between the lowest scoring model and each can-
didate model, we calculated the Akaike weights and evidence ratios
for each of the models.

Table 1. Summary of the top logistic regression model sets (evidence ratio greater than 10) predicting the presence of panda sign, out of a total of 256 models resulting from the full model set. The models are in descending order indicating the most to least supported based on Akaike information criteria (AIC). K, number of predictors in the model; ΔAIC, difference in AIC value from that of the best model; Wi, Akaike weight of the ith model, representing the probability that the ith model is the best model in the candidate group; W1/Wi, evidence ratio, comparing the model with the highest Akaike weight (w1) to the ith model (wi) in the candidate group.

model construction	K	AIC	ΔAIC	AIC weights (Wi)	evidence ratios (W1/Wi)
bamboo presence, slope, forest age, tree DBH, understory height	6	4830.85	0	0.214	1.00
bamboo presence, slope, forest age, tree DBH, understory height, shrub cover	7	4831.64	0.79	0.143	1.48
bamboo presence, slope, forest age, tree canopy, tree DBH, understory height	7	4832.37	1.52	0.099	2.14
bamboo presence, elevation, slope, forest age, tree DBH, understory height	7	4832.76	1.91	0.082	2.60
bamboo presence, slope, forest age, tree canopy, tree DBH, understory height, shrub cover	8	4833.23	2.38	0.065	3.29
bamboo presence, elevation, slope, forest age, tree DBH, understory height, shrub cover	8	4833.58	2.73	0.055	3.92
bamboo presence, elevation, slope, forest age, tree canopy, tree DBH, understory height	8	4834.31	3.46	0.038	5.64
bamboo presence, slope, forest age, tree DBH	5	4834.32	3.47	0.038	5.67
bamboo presence, elevation, forest age, tree canopy	5	4834.42	3.57	0.036	5.96
bamboo presence, forest age, tree DBH, understory height	5	4834.72	3.87	0.031	6.93
bamboo presence, elevation, slope, forest age, tree canopy, tree DBH, understory height, shrub cover	9	4835.19	4.34	0.024	8.76

3. RESULTS

Multiple models (i.e. 11 of the 256) had an evidence ratio less than 10 and differences between candidate models tended to be small (table 1). However, the first three models in table 1, including bamboo presence, slope, forest age, tree DBH and understory height, were approximately 1.5, 2.1 and 2.6 times more likely to explain the presence of panda signs than the models that included those same variables plus shrub cover, tree canopy and elevation, respectively.

Our analyses reveal presence of bamboo and forest age (old growth versus secondary growth) as the ecological variables best predicting panda habitat use. Of the top models (evidence ratios less than 10), bamboo and forest age are the only variables common to all models. Following model selection, we estimated the relative importance of each of the contributing variables by calculating the sum of the Akaike weights for all models that included the variable under consideration. Although the presence of bamboo ranked first, old-growth forest was essentially equivalent (Akaike weights = 1.010 and 1.009, respectively), followed closely by tree DBH (0.958), a measure that is undoubtedly related to forest age (as well as site productivity). Slope, a variable frequently used in habitat models for pandas [7,8], ranked much lower (0.844), no more important than understory height (0.824), which rarely factors into panda habitat suitability models. The remaining variables—shrub cover, elevation and tree canopy—had poor predictive power (less than 0.500).

4. DISCUSSION

As an obligate bamboo specialist, it is no surprise that bamboo predicts panda habitat use. But it is surprising that old-growth forest should attain the same level of importance as bamboo. Our data do not allow us to discern what draws pandas to advanced stages of forest succession. One possibility is that the bamboo that grows underneath old growth is more nutritious [11]. Another intriguing possibility is that only old-growth trees grow large enough to form cavities suitable for maternity dens [12]. This raises the question: are birth dens a factor-limiting panda population size in reserves with a history of logging [1]?

Despite numerous studies based on data collected over a limited scale—typically a portion of a single reserve [6,13–15]—previous research has not clearly identified this strong association with old-growth forests. Although one single-reserve study indicated a positive relationship between forest age and panda presence [13], old growth did not assume the primacy it did in our findings. Lack of robust range-wide data and conflicting evidence among several studies over smaller areas has meant that old growth has not figured prominently in habitat mapping, policy and planning. By contrast, our dataset represents more than 70 per cent of the panda's current range, which allows us to make inferences across the entire panda landscape. This underscores the importance of ecological scale in inferring habitat selection: old growth emerges as an important factor influencing panda habitat preferences only when data are collected over a large enough scale. Our fine-grained study over large extent captured habitat relations that were not fully understood previously. Now, maps and models of suitable panda habitat should be revised to give priority to old-growth forest.

Our data point to a need for habitat modelling to be more sensitive to the issue of ecological scale, especially when scaling up from data collected on localized scales to plan conservation practice over much larger scales. Appropriate conservation planning
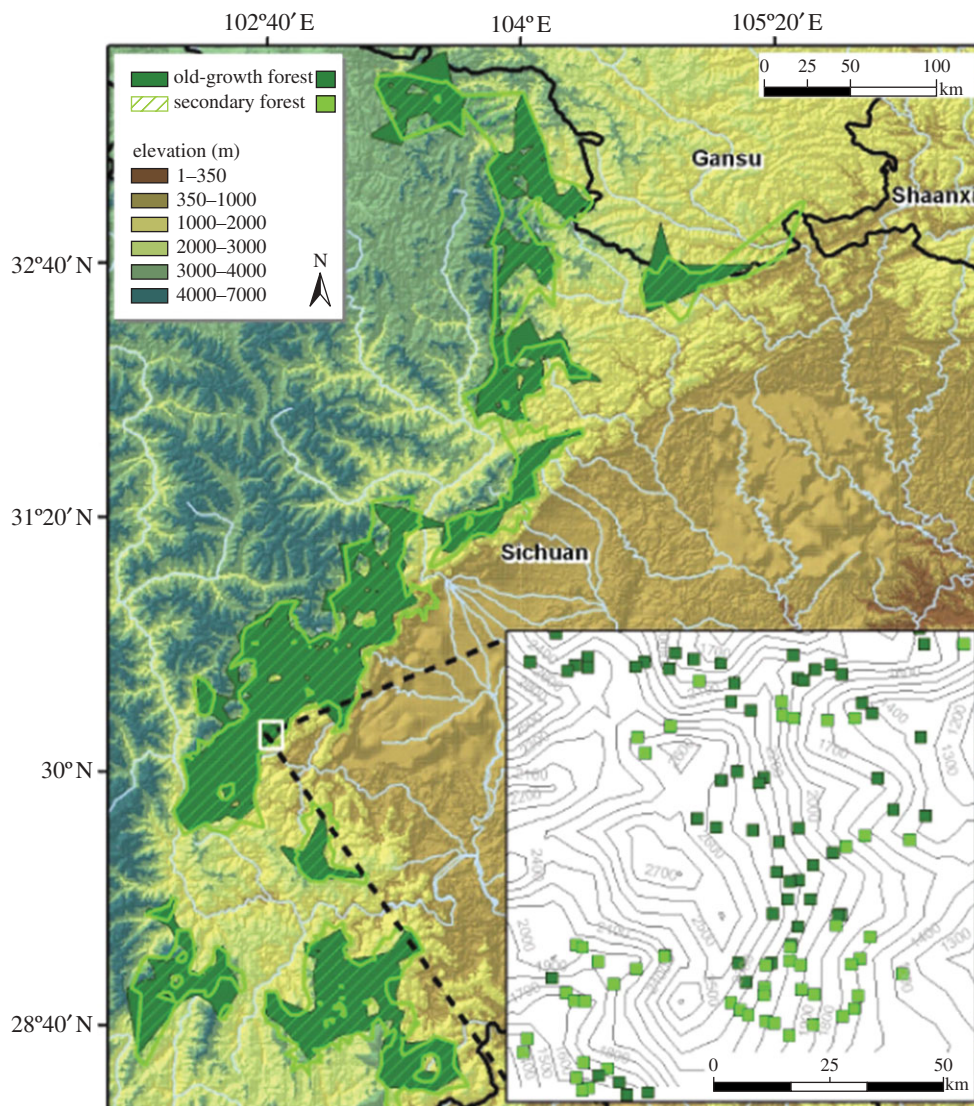
Figure 1. Distribution of old-growth forest (dark green fill) and secondary forest (light green stripe fill) in the mountain ranges of central China across 600 km of latitude. At regional scales there was a high degree of overlap between the two forest categories. At smaller local scales, the two forest categories were clustered in discrete patches (map inset: dark squares, old-growth forest 20 m × 20 m plots, light-green squares, secondary plots).

often requires this type of range-wide landscape scale approach. We recognize that scale-appropriate ecological research will not always be easy and may require substantial effort over time and space. However, there are at times no good substitutes to real effort. While such endeavours in ecology are increasingly rare in an era when quick empirical studies trump investment in long-term ecological research, the pay-off can be substantial and irreplaceable [16].

More than a decade ago the Chinese government implemented a ban on all logging throughout the panda's range, an action that curtailed significant losses to the forest ecosystem on which giant pandas and other wildlife depend [17]. This logging moratorium expires in 2010 and the government must decide whether to extend the ban [17,18]. It is critical for the long-term future of the panda to identify the ecological variables important for their persistence now, when the government still has time to consider these variables while devising its timber-harvest policy. As the Chinese government decides whether or not to lift the ban on logging, it should consider this: it

may be more cost-effective to protect the existing old growth than to open it up to logging while protecting an equivalent area of secondary growth forest.

1 Swaisgood, R. R., Wei, F., Wildt, D. E., Kouba, A. J. & Zhang, Z. 2010 Giant panda conservation science: how far we have come. *Biol. Lett.* **6**, 143–145. (doi:10.1098/rsbl.2009.0786)

2 Li, R. *et al.* 2009 The sequence and de nova assembly of the giant panda genome. *Nature* **463**, 311–317. (doi:10.1038/nature08696)

3 Hobbs, N. T. 2003 Challenges and opportunities in integrating ecological knowledge across scales. *For. Ecol. Manage.* **181**, 223–238. (doi:10.1016/S0378-1127(03)00135-X)

4 Orians, G. H. & Wittenberger, J. F. 1991 Spatial and temporal scales in habitat selection. *Am. Nat.* **137**, S29–S49. (doi:10.1086/285138)

5 Levin, S. A. 1992 The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* **73**, 1943–1967. (doi:10.2307/1941447)

6 Feng, T., Van Manen, F. T., Zhao, N., Li, M. & Wei, F. 2009 Habitat assessment for giant pandas in the Qinling mountain region of China. *J. Wildl. Manage.* **73**, 852–858. (doi:10.2193/2008-186)

7 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. (doi:10.1126/science.1058104)

8 Shen, G., Feng, C., Xie, Z., Ouyang, Z., Li, J. & Pascal, M. 2008 Proposed conservation landscape for giant pandas in the Minshan Mountains, China. *Conserv. Biol.* **22**, 1144–1153. (doi:10.1111/j.1523-1739.2008.01038.x)

9 State Forestry Administration. 2006 *The third national survey report on giant panda in China*. Beijing, China: Science Press.

10 Burnham, K. & Anderson, D. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.

11 Reid, D. G., Taylor, A. H., Hu, J. & Qin, Z. 1991 Environmental influences on bamboo *Bashania fangiana* growth and implications for giant panda conservation. *J. Appl. Ecol.* **28**, 855–868. (doi:10.2307/2404212)

12 Zhang, Z., Swaisgood, R. R., Wu, H., Zhang, Z., Li, M., Yong, Y., Hu, J. & Wei, F. 2007 Factors predicting den use by maternal giant pandas. *J. Wildl. Manage.* **71**, 2694–2698. (doi:10.2193/2006-504)

13 Bearer, S., Linderman, M., Huang, J., An, L., He, G. & Liu, J. 2008 Effects of fuelwood collection and timber harvesting on giant panda habitat use. *Biol. Conserv.* **141**, 385–393. (doi:10.1016/j.biocon.2007.10.009)

14 Linderman, M., Bearer, S., An, L., Tan, Y., Ouyang, Z. & Liu, J. 2005 The effects of understory bamboo on broad-scale estimates of giant panda habitat. *Biol. Conserv.* **121**, 383–390. (doi:10.1016/j.biocon.2004.05.011)

15 Schaller, G. B., Hu, J., Pan, W. & Zhu, J. 1985 *The giant pandas of Wolong*. Chicago, IL: University of Chicago Press.

16 Swaisgood, R. R., Terborgh, J. T. & Blumstein, D. T. 2010 Funding should come to those who wait. *Science* **329**, 276. (doi:10.1126/science.329.5989.276-a)

17 Morell, V. 2008 Letting 1000 forests bloom. *Science* **320**, 1442–1443. (doi:10.1126/science.320.5882.1442)

18 Loucks, C. J., Lu, Z., Dinerstein, E., Wang, H., Olson, D. M., Zhu, C. & Wang, D. 2001 Giant pandas in a changing landscape. *Science* **294**, 1465. (doi:10.1126/science.1064710)