

Balancing Panda and Human Needs for Bamboo Shoots in Mabian Nature Reserve, China

PREDICTIONS FROM A LOGISTIC-LIKE MODEL

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THE SCARCITY of the endemic giant panda (*Ailuropoda melanoleuca*) in China is a consequence of population decline and isolation, habitat degradation, and human interference (Schaller et al. 1985; Hu et al. 1990; Hu 2001). Mortality seems high even for an ursid: about 57% over the first year of life for cubs in the Qionglai Mountains (Wei and Hu 1994; Wei et al. 1997a). Conservation challenges and the unique biology of giant pandas have attracted worldwide attention. Their ecology has been studied in a number of habitats (Schaller et al. 1985, 1989; Pan et al. 1988; Hu et al. 1990; Reid and Hu 1991; Johnson et al. 1988; Wei et al. 1996a,b, 1997a,b, 1999a,b,c, 2000a,b; see also Long et al. [chapter 6], Yong et al. [chapter 10], and Liu et al. [chapter 11]).

To date, the only quantitative assessment of interactions between the panda and its food supply (bamboo) is that by Yuan et al. (1990) in the Qionglai Mountains. They modified Smith's (1979) dual logistic predation model to account

for two classes of predators and prey (bamboo). Our study further revises Smith's model to account for human harvest, so as to better understand the dynamic relationship between bamboo, pandas, and human harvest, and to provide an improved basis for conserving each species. Vital rates for bamboo in Mabian Dafenging Natural Reserve, in the Liangshan Mountains, were ascertained by a 1-year field survey.

STUDY AREA

The Liangshan Mountains are one of the main habitats of pandas in China (Hu and Wei, chapter 9). In 1978, to protect core habitats and their panda populations, the Chinese government established two adjacent refuges: Mabian Dafenging and Meigu Dafenging Nature Reserves. The fieldwork of our study was performed mainly in Mabian.

Mabian encompasses several habitat types that are separated altitudinally (table 13.1). Six

TABLE 13.1
Altitudinal Ranges of Vegetation Communities in Mabian Natural Reserve

ELEVATION (m)	HABITAT TYPE
<2000	Evergreen broad-leaved forest
2000–2400	Mixed broad-leaved and deciduous forest
2400–2800	Mixed coniferous and broad-leaved forest
2800–3700	Coniferous forest
>3700	Subalpine shrubs and alpine meadows

bamboo species (*Qiongzhusa macrophylla*, *Indocalamus longiauritus*, *Bashania fangiiana*, *Chimonobambus pachstachys*, *C. szechuanensis*, and *Yushania mabianensis*) occur in the reserve. Of these, *Q. macrophylla* (1900–2450 m) and *I. longiauritus* (2400–2900) constituted the main food of pandas. We analyzed the dynamic relationship between pandas and these two bamboo species.

METHODS AND MODELS

The methods used in this fieldwork have been described by Yuan et al. (1990) and Yang et al. (1994).

PREDATOR-PREY MODELS

Smith (1979) used a pair of logistic-like models to assess the dynamics of a single species of predator and prey with a constant per capita rate of predation:

$$\text{Prey: } dB/dt = (r_B/B_{\max})(B_{\max} - B)B - cP; \quad (13.1)$$

$$\text{Predator: } dP/dt = (r_P/P_K)(P_K - P)P, \quad (13.2)$$

where:

r = the density-independent (DI) rate of increase for each species: $r = (b_{DI} - d_{DI})$;

b_{DI} = maximum per capita birth rate (%);

d_{DI} = minimum per capita mortality rate (%);

B and P = densities per km² of prey (tons of bamboo) and predators (number of pandas);

K = equilibrium density (of bamboo or pandas), the density where reproduction is exactly balanced by mortality;

B_{\max} = bamboo density so high that bamboo reproduction ceases (at K , reproduction $\neq 0$ unless mortality = 0);

P_K = equilibrium size for a predator population governed solely by prey supply; and

c = mean consumption rate of prey per predator (e.g., tons of bamboo/year/panda).

Additional terms can be added to the logistic-like submodels to account for multiple predator or prey species. For example, Yuan et al. (1990) used the cP term for pandas and added a second term i to represent a constant percentage (i) loss of bamboo to predation by insects and rats.

$$\text{Prey: } dB/dt = [(r_B/B_{\max})(B_{\max} - B)B] - [iB + cP], \quad (13.3)$$

where the term $[(r_B/B_{\max})(B_{\max} - B)B]$ represents predation-free dynamics of the prey and the term $[iB + cP]$ represents the impact of predation.

This revised predation model was applied to data from Wuyipeng, Wolong Nature Reserve, to explore the dynamic relationship between pandas and two local bamboo species, *Fargesia robusta* and *B. fangiiana*, whose vital rates were determined by fieldwork (Yuan et al. 1990).

To apply this model to Mabian Natural Reserve, further revision was needed to account for the harvest of bamboo shoots by local residents. Shoot harvesting is permitted by the local gov-

TABLE 13.2
 Statistical Results from Bamboo Plots in Mabian Natural Reserve

PARAMETERS	QJONGZHUEA MACROPHYLLA		INDOCALAMUS LONGIAURITUS	
	AVERAGE	STANDARD DEVIATION	AVERAGE	STANDARD DEVIATION
A: Density before increasing (culms/m ²)	18.35	10.28	16.55	8.93
B: Number of shoots (culms/m ²)	4.37	3.48	4.02	3.90
C: Density after increasing (culms/m ²) = (A + B)	22.72	13.32	20.57	12.35
D: Shooting rate = (B/A)	0.238	0.215	0.243	0.223
E: Loss by insects and bamboo rats (culms/m ²)	2.29	0.943	2.21	0.824
F: Loss rate (%) by insects and bamboo rats = (E/C)	0.101	0.078	0.108	0.065

ernment and the Reserve administration. Historically, the harvest quota has been set by the local government without consideration of the population densities of bamboo or pandas. To investigate impacts of shoot harvesting on the bamboo growth and the local panda population, a new term h , representing a constant annual amount (tons) of bamboo harvesting, was added to the model of Yuan et al. (1990):

$$\text{Prey: } dB/dt = [(r_B/B_{\max})(B_{\max} - B)B] - [iB + cP + h]. \quad (13.4)$$

EQUILIBRIUM DENSITY OF PANDAS

All of the above equations are variants of the Verhulst-Pearl logistic. In a logistic model, there are two possible equilibria: 0 and K (P_K in the case of pandas and B_K in the case of bamboo). Our long-term goal is to determine P_K for Mabian pandas and the corresponding bamboo densities. We make the simplifying assumption that P_K is determined only by the supply of food (bamboo). The value of P_K would be no greater than the highest panda density that could be supported by the bamboo crops without pandas overgrazing the bamboo, and thereby decreasing future bamboo productivity. The overall rate of consumption by pandas (cP) is assumed to be directly

related to panda density; the per capita rate (c) is assumed to be constant. Other assumed constants are (1) the percentage of the bamboo crop lost to consumption by other predators (mainly rats and insects = i ; so total loss is iB) and (2) the annual number of tons harvested by humans (h).

RESULTS AND DISCUSSION

BAMBOO

To estimate vital rates for bamboo, 1-m² plots were established in stands of *Q. macrophylla* ($N=100$) and *I. longiauritus* ($N=80$), distributed randomly with regard to the elevation, slope gradient, aspect, bamboo density, and other habitat variables. Rates of shoot production, density-independent mortality, and bamboo consumption by pandas and other predators were recorded for each sample plot (table 13.2).

RATE OF INCREASE

By definition, the mean geometric rate of change in population size over time interval t is calculated as:

$$r_{0-t} = [\ln(B_t/B_0)]/t = [\ln(B_t) - \ln(B_0)]/t,$$

where B_0 and B_t are bamboo densities at times 0 and t , and t is the survey duration (1 year). Using the data in table 13.2:

$$Q. \text{ macrophylla: } r_Q = \ln(22.72) - \ln(18.35) \\ = 0.214 = 21.4\%/year;$$

$$I. \text{ longiauritus: } r_I = \ln(20.57) - \ln(16.55) \\ = 0.218 = 21.8\%/year.$$

MAXIMUM BAMBOO DENSITY

In our study area, sympatry by these bamboo species was low enough for interspecific density interactions to be ignored. Within each species, however, shooting rate was negatively related to culm density (C culms/km²), as expressed in the following regression equations. C_{max} was approximated by extrapolating the value of C at which S (shooting rate in culms/km²/yr) = annual culm production = 0:

$$Q. \text{ macrophylla } (N = 100 \text{ plots}): \\ S_Q = 0.376 - 0.0108C_Q \quad (R_Q = -0.60);$$

$$C_{Qmax} = 3.48 \times 10^7 \text{ culms/km}^2;$$

$$I. \text{ longiauritus } (N = 80 \text{ plots}): \\ S_I = 0.495 - 0.0153C_I \quad (R_I = -0.75);$$

$$C_{Imax} = 3.24 \times 10^7 \text{ culms/km}^2,$$

where R is the correlation coefficient.

The averages of the culm sizes was computed to be:

	WEIGHT (g)	HEIGHT (cm)	BASAL DIAMETER (mm)
<i>Q. macrophylla</i> ($N = 384$)	277.31	281.21	12.18
<i>I. longiauritus</i> ($N = 277$)	83.48	166.51	10.81

Two regression equations were derived between culm weight (W) versus height (H) and base diameter (D):

$$Q. \text{ macrophylla } (N = 127): \\ W_Q = -417.19 + 1.2970H_Q + 27.07D_Q;$$

$$I. \text{ longiauritus } (N = 73): \\ W_I = -306.40 + 1.8781H_I + 7.72D_I.$$

Converting culm numerical density (culms/km²) to biomass density (tons/km²): maximum biomass densities were calculated as:

$$C_{max} \text{ (culms/km}^2) \cdot W \text{ (g/culm)} \times 10^6 \\ = B_{max} \text{ (tons/km}^2);$$

$$Q. \text{ macrophylla:} \\ B_{Qmax} = 3.48 \times 10^7 \cdot 277.31 = 9650.39;$$

$$I. \text{ longiauritus:} \\ B_{Imax} = 3.24 \times 10^7 \cdot 83.84 = 2716.42.$$

Using equation 13.4, tons of culms/km² are calculated:

$$Q. \text{ macrophylla: } r_B / B_{Qmax} = 0.214/9650.39 \\ = 2.22 \times 10^{-5} \text{ tons/km}^2;$$

$$I. \text{ longiauritus: } r_B / B_{Imax} = 0.218/2716.42 \\ = 8.03 \times 10^{-5} \text{ tons/km}^2.$$

RATES OF BAMBOO CONSUMPTION

Mabian Natural Reserve is home to eight pandas. During our year of observations, they spent approximately 213 days in *Q. macrophylla* and 137 days in *I. longiauritus* (Yang 1993). Number of culms eaten/day/panda was estimated as 707 ($N = 9$ scats) for *Q. macrophylla* and 722 ($N = 3$) for *I. longiauritus* (Yang 1993), based on the number of culms utilized and scat deposited by pandas on the tracking line (calculated culms/scat) and on the 120-scat/day rate observed by Hu et al. (1990).

Annual numbers of bamboo culms consumed are estimated as:

$$N = (\text{days/year eating culms}) \cdot (\text{culms/day/panda}) \\ = \text{culms/year/panda};$$

$$Q. \text{ macrophylla:} \\ N_Q = 213 \cdot 707 = 15.1 \times 10^4;$$

$$I. \text{ longiauritus:} \\ N_I = 137 \cdot 722 = 9.9 \times 10^4.$$

Then, mean rates of bamboo consumption were estimated as:

$$(\text{g/culm}) \cdot (\text{culms/year/panda}) \\ = \text{tons/year/panda};$$

Q. macrophylla:

$$c_Q = 277.21 \cdot 15.1 \times 10^4 = 41.76;$$

I. longiauritus:

$$c_I = 83.48 \cdot 9.9 \times 10^4 = 8.29.$$

RATES OF CONSUMPTION OF BAMBOO BY INSECTS AND RATS

These losses were estimated (table 13.2) at $i_Q = 10.1\%$ and $i_I = 10.8\%$.

RATE OF LOSS TO HARVEST BY HUMANS

This rate (h) was estimated as a multiple of the weight of shoots sold in the local market. Over two successive years, we estimated that 20,000 kg and 25,000 kg of shoots were harvested from approximately 7.52 km² of *Q. macrophylla* around our field station. The mean of 22,500 kg was used to estimate $h_Q = 2.99$ tons/km². Shoots of *I. longiauritus* are so slender and distributed at such a high altitude (>2600 m) that they were not harvested; $h_I = 0$.

BAMBOO GROWTH EQUATIONS

Using equation 13.4, we calculate that:

Q. macrophylla:

$$\begin{aligned} d_{B_Q}/dt &= [(0.214/9650.39) \cdot (9650.39 - B)B] \\ &\quad - [0.101B_Q + 41.76P + h] \\ &= [0.113B_Q - 2.22 \times 10^{-5}B_Q^2] - [41.76 \cdot 3.03 + h] \\ &= [0.113B_Q - 2.22 \times 10^{-5}B_Q^2] - 127 - h; \quad (13.5) \end{aligned}$$

I. longiauritus: $dB_I/dt = [(0.218/2716.42)$

$$\begin{aligned} &\quad \cdot (2716.42 - B)B] - [0.108B_I + 8.29P + h] \\ &= 0.110B_I - 8.03 \times 10^{-5}B_I^2 - 25.1 - h. \quad (13.6) \end{aligned}$$

PANDAS

RATE OF INCREASE

From equation 13.2, it can be seen that this logistic-like model is just a rearrangement of that applied to panda population dynamics by Yuan et al. (1990). Based on the age structure of the Mabian panda population (Yang 1993; Yang et al. 1994) and age-specific birth rates of pandas elsewhere (Wei et al. 1989), the birth rate (b) for our population was estimated as 0.193 cubs/panda/year (i.e., 19.3%) for the current age-sex

ratio. The mortality rate (d) observed by Wei et al. (1989) was 17.4%/year. For the purposes of this preliminary modeling, these rates and ratios are assumed to remain constant, on average, over the foreseeable future. (Ideally, later iterations of the model will address changes in vital rates and in age-sex ratios.)

We used the observed mean rate of increase:

$$r'_p = b - d = 0.1931 - 0.174 = 0.019$$

to approximate r_p , the intrinsic (density-independent) rate of increase, in the absence of any other basis for predicting how much higher r_p would be. Although the logistic model assumes intraspecific density effects even at $P = 2$, in reality, such effects may not begin for Ursidae until their density approaches K (Taylor 1994).

This value of r_p would be required for calculating the relationships between the dynamics of panda, bamboo, insect, and rat populations. However, at this early stage of modeling, we ignore dynamics in panda population density and analyze sustainable bamboo harvest by people only at equilibrium density for the panda population.

PREDATOR-PREY EQUILIBRIA

PANDAS

Studies at Wolong Nature Reserve showed that the mean size of a giant panda's core area was 33 ha. Most of the panda's nutrition came from its core area (Schaller et al. 1985). Overlap between core areas was negligible. Hence, mean density of these pandas was estimated as:

$$1/33 \text{ ha} = 1/0.33 \text{ km}^2 = 3.03/\text{km}^2.$$

This is assumed to approximate equilibrium density at Wolong, and serves as a first approximation for equilibrium density in our study area. Note that this is more than six times the present density of 0.48/km² (Yang et al. 1994).

BAMBOO

The assumed density-dependent relationship between bamboo abundance and the addition of

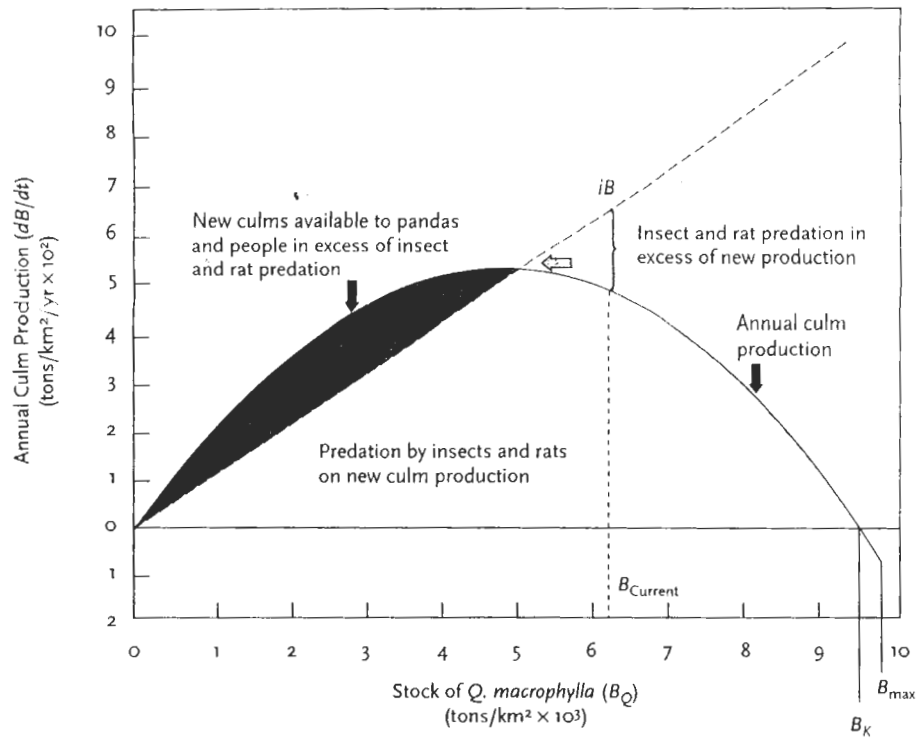


FIGURE 13.1. Bamboo culm biomass available for human harvest at various densities of bamboo, rats, and insects. B_K = equilibrium bamboo density (reproductive rate exactly balanced by mortality rate); B_{max} = the density above which bamboo reproduction ceases, despite continuing mortality. Consumption by insects and rats is represented by iB , rising as a constant proportion of stock density. The relationship shown here for *Q. macrophylla* is similar for *I. longiauritus*.

new culms (reproduction) is parabolic—rising at a decreasing rate as the bamboo stock increases from low to moderate densities, then decreasing as stock density continues rising toward carrying capacity B_K (figure 13.1). Culm consumption by insects and bamboo rats is represented by a diagonal line iB with a y -intercept at the origin, rising as a constant proportion of stock density. At the current stock density $B_{Current}$ of 6293 tons/km² for *Q. macrophylla*, insects and rats are consuming more of this bamboo than new culm production can replace—depicted at the far right of figure 13.1 by the area below the diagonal line but above the parabola. This excessive predation by insects and rats, coupled with bamboo consumption by pandas and human harvesting, tends to decrease overall bamboo stock density, as indicated by the gray arrow at the left. Once bamboo density falls well

below about 50% of B_K (i.e., in the darkly shaded area under the parabola but above the diagonal line), culm production would be high enough, and predation by insects and rats low enough, to leave sufficient “surplus” to meet the needs of giant pandas and people without continuing to reduce bamboo density. A new bamboo equilibrium could be created at any bamboo stock density within the shaded range.

In figure 13.2, the shaded area in figure 13.1 is plotted separately, whereupon the diagonal line in figure 13.1 becomes horizontal, running along the x -axis in figure 13.2. As can be seen most clearly in figure 13.2, the amount of bamboo available for pandas and humans would be maximized near 25% of B_{max} , in contrast to total culm production, which is maximized near 50% of B_{max} . The amount of bamboo (cP) needed by an equilibrium density of pandas (P_K) (i.e., cP_K)

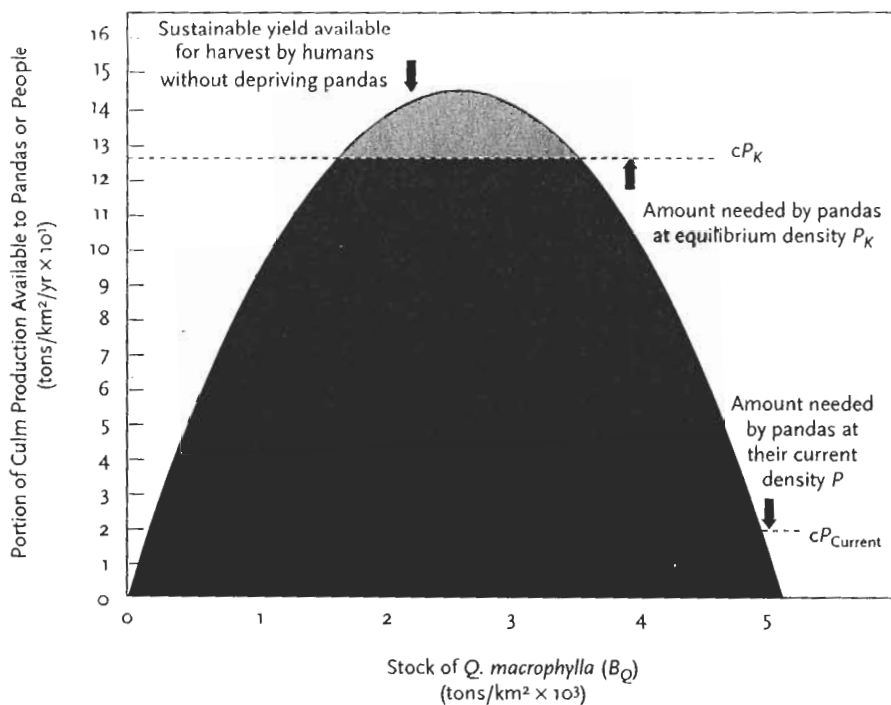


FIGURE 13.2. Sustainable culm harvest by people and pandas, in excess of predation by insects and rats. The entire parabola is equivalent to the shaded area in figure 13.1, where the diagonal iB in that figure runs horizontally along the origin in figure 13.2. The lightly shaded area here is the amount of bamboo culms available for harvest by humans at an equilibrium panda population density. The relationship shown here for *Q. macrophylla* is similar for *I. longiauritus*.

is represented by a horizontal line bisecting the parabola in figure 13.2. Once panda density reaches equilibrium, there would be only a narrow range of bamboo densities in which people would be able to harvest even moderate amounts of bamboo culms without causing the stock density to decline, which would be a problem only at stock densities below 25% of B_{max} .

From equations 13.5 and 13.6, the maximum allowable human harvest of culms is calculated in two steps. First, the maximum value of dB/dt is calculated for each equation by differentiating it with respect to t and setting the resultant equation equal to 0. This yields the bamboo stock density at which dB/dt is maximized. That maximum is then calculated. Second, from that stock density we subtract total bamboo consumption by rats, insects, and an equilibrium population of pandas. Total available bamboo

minus the amount consumed by animals is h_{max} , the maximum sustainable harvest by humans:

	B AT MAX dB/dt (tons/ km^2)	MAX dB/dt (tons/ km^2 / year)	MAXIMUM SUSTAINABLE HARVEST (tons/ km^2 / year)
<i>Q. macrophylla</i>	2250	144	17.4
<i>I. longiauritus</i>	685	37	12.0

ECOLOGICAL IMPLICATIONS AND CONSERVATION STRATEGIES

MEETING THE NEEDS OF PANDAS

The equilibrium density/ km^2 of pandas (3.03) is more than six times the current density (0.48) at Mabian (Yang et al. 1994), whereas the corresponding equilibrium densities/ km^2 of bamboo

are about 60–70% of current levels: 5088.7 tons of *Q. macrophylla* and 1411.95 tons of *I. longicauritus* (Yang 1993). Increasing panda density/km² to 3.03 would tend to reduce bamboo supply to these new equilibrium densities. Bamboo supply thus appears more than adequate to support a several-fold increase in the panda population, so long as losses to rats, insects, and human harvest do not increase dramatically.

MEETING THE NEEDS OF HUMANS

The maximum shoot harvesting that will not disrupt the dynamic equilibrium between the panda and the bamboo is h_{\max} . Once h_{\max} is exceeded, the combined predation by insects, rats, and pandas would tend to depress bamboo populations to the point that the pandas would eventually starve.

Earlier in the chapter, for each species of bamboo we estimated potential rate of increase, density dependence, and predation loss to insects, rats, and pandas. For pandas, we estimated low-density rates of birth, death, and population increase corresponding to the assumed equilibrium size. Based on those figures, we calculated maximum sustainable human harvest levels of 17.4 tons/km² for *Qiongzhusua* and 12.0 tons/km² for *Indocalamus*. Both are higher than the current harvest of 2.99 tons/km² for *Qiongzhusua* alone. By definition, so long as the harvest level remains below h_{\max} for each bamboo species, harvesting should not prevent an increase in the panda population to equilibrium size, much less jeopardize permanent survival of the panda or either species of bamboo.

Years of observation may be required to verify that these model outputs are basically correct, much less to refine them. One approach to refinement is to devise more realistic models—for instance, models that take into account variations over time in (1) vital rates for pandas and bamboo (e.g., as influenced by weather), and (2) in predation by insects and rats. We also need models which more closely mimic population dynamics of rats, insects, and ursids—especially models of response to changes in food supply and competition, such as those derived by String-

ham (1983, 1985) for the grizzly bear (*Ursus arctos*). A second way of refining these results would be through cautious adaptive management; for instance, by setting substantially lower quotas and noting responses by pandas and each species of bamboo. This would require continued field study of not only pandas and bamboo, but also the majority of factors that control their vital rates, such as weather and predation on bamboo by insects and rats. Finally, it is essential to keep in mind that these figures for allowable harvest levels of bamboo address only the impacts of lowering the bamboo supply. They do not address the impacts of harvesting itself—for instance, disturbance of the pandas or degradation of their habitat.

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