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Giant panda (*Ailuropoda melanoleuca*) population dynamics and bamboo (subfamily Bambusoideae) life history: a structured population approach to examining carrying capacity when the prey are semelparous

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Abstract

The giant panda, *Ailuropoda melanoleuca*, is a highly specialized Ursid whose diet consists almost entirely of various species of bamboo. Bamboo (Bambusoideae) is a grass subfamily whose species often exhibit synchronous semelparity. Synchronous semelparity can create local drops in carrying capacity for the panda. We modeled the interaction of pandas and their bamboo food resources with an age structured panda population model linked to a natural history model of bamboo biomass dynamics based on literature values of bamboo biomass, and giant panda life history dynamics. This paper reports the results of our examination of the interaction between pandas and their bamboo food resource and its implications for panda conservation. In the model all panda populations were well below the carrying capacity of the habitat. The giant panda populations growth was most sensitive to changes in birth rates and removal of reproductive aged individuals. Periodic starvation that has been documented in conjunction with bamboo die-offs is probably related to the inability to move to other areas within the region where bamboo is still available. Based on the results of this model, giant panda conservation should concentrate on keeping breeding individuals in the wild, keep corridors to different bamboo species open to pandas, and to concentrate research on bamboo life history. © 1999 Published by Elsevier Science B.V.

Keywords: Giant panda; *Ailuropoda melanoleuca*; Bamboo; Population dynamics; Population viability analysis; China; Life history; Leslie matrix

1. Introduction

Giant pandas, *Ailuropoda melanoleuca*, (hereafter, pandas) live in the bamboo forests of six

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isolated mountain ranges in southwestern China (Reid, 1994). Approximately 99% of their diet is bamboo (Bambusoideae; Schaller et al., 1985). Many of these bamboo species sexually reproduce by synchronous semelparity, i.e. the bamboos of a given species within a given region flower at the same time and then die. If the particular bamboo species is one that pandas locally depend upon, there can be a great reduction in local carrying capacity. For example, in the mid 1970s several species of bamboo flowered and died around the same time in the Min Mountains and many pandas starved (Johnson et al., 1988).

While neonates may experience predation, adult pandas have virtually no natural enemies. Most adult deaths result either from direct poaching or accidental killing in snares and traps set out for other species (Reid, 1994). Therefore, the primary environmental threats to pandas are loss of current bamboo forest habitat and periodic drops in carrying capacity caused by die-offs of preferred species.

We are interested in the implications of the bamboo's life history characteristics for panda conservation biology. In this paper we present an age structured model of panda population dynamics in which the survivorships and fecundity rates (collectively, 'vital rates') are density dependent on bamboo biomass. We then use sensitivity analysis and population viability analysis on the model to explore the interaction of bamboo life history and panda population dynamics.

2. Methods

2.1. Model description

We created the model with version 4.0 of STELLA (High Performance Systems, 1992). This model is a revision and reanalysis of the model presented by Carter and Wang (1993), and is available for inspection (Carter et al., 1997). The model is composed of three submodels, one for panda populations, one for bamboo species, and a linking model. The model time-step is 1 year, we used Euler's approximation (High Performance Systems, 1992), and we restricted panda populations to be integers.

2.1.1. Giant panda submodel description

The regional panda populations are reproductively isolated, and subpopulations within a region may be isolated as well (Reid, 1994). In this model we treat each region as one large population, but we combine the two smallest panda populations in the neighboring Daxiangling and Xiaoxiangling Mountains in a population we call the Xiangling population. We combined these two populations because the data available on bamboo distribution are presented that way (Wang, 1989). We modeled each region as a closed population using an age structured approach (Table 1) with vital rates from life tables in Wei et al. (1990) and Wei and Hu (1994). Like the life tables, the model uses two-year age-classes. We constrained the stocks representing each age-class to a 'first-in, first out' protocol so that yearly cohorts did not become mixed during the 1-year time-step.

In the wild, females take 2 years to raise a single young to independence. If her young dies in the first year, she may have a second young the following year (Johnson et al., 1988). Our model simulates this compensatory reproduction by replacing a fraction of the young that have died in year 1 with new young the following year (Eq. (1)). Thus, the infant survival rate and reproductive rate are inversely proportional.

Table 1
Giant panda life history table^a

Age-class	Survivorship	Fecundity
0:1	0.41 ^b	0
2:3	0.95	0
4:5	0.98	0
6:7	0.96	0.35
8:9	0.9	0.7
10:11	0.83	0.7
12:13	0.64	0.7
14:15	0.72	0.7
16:17	0.72	0.7
18:19	0.62	0.5
20:21	0.5	0
22:23	0.25	0
24:25	0	0

^a This table is based on Wei et al. (1990) and is the table on which Leslie matrix sensitivity analysis was performed. The time-step in this model is 2 years.

^b The fecundity rates used were from Wei and Hu (1994).

$$C_{t+1} = (D_t^*f) \quad (1)$$

where C_{t+1} is the number of compensatory young born the second year, D_t is the number of 1 year olds that died in their first year, and f is the compensatory fraction. Unless otherwise noted, default value for f was 0.5, i.e. half the females whose young died in the first year had new young the following year.

We modeled both sexes of the population and modified age specific reproduction by calculating the number of available females using a sex ratio. The sex ratio was fixed for the length of a simulation and the default sex ratio was 1:1 (Wei et al., 1990; Zhou and Pan, 1997).

2.1.2. Bamboo submodel description and linking equations

The bamboo populations pandas feed upon are distributed in monospecific patches in the understory of mixed deciduous and coniferous evergreen Montane and sub-Alpine forests (Reid et al., 1991; Taylor et al., 1991; Taylor and Qin, 1993). These bamboo species have many synonyms and different authors have used various Latin binomials for the same species (e.g. Reid et al., 1991). The names used in this paper were checked against the synonym list compiled for the European Bamboo Society by Masman (1995).

The bamboo life history submodel was a three-stock, conservative-flow model that moved each species of bamboo through its life cycle, with the time from last flowering and die-off to regrowth cycles species dependent, and varying between 10 and 100 years. The year last flowered, when known, was set for each species so that model bamboo flowering cycles were synchronized with natural bamboo flowering cycles. Although pandas are known to eat over 30 species of bamboo (Wang and Hu, 1989), only 12 were used in the model (Appendix A). Pandas tend to focus their feeding efforts on one species at a time with distinct seasonal preferences as to species and part of plant eaten (Schaller et al., 1985). The 12 bamboo species selected for use in the model were chosen based on the panda's food preference, number of regions the bamboo species occurs in, and the bamboo species' importance regionally as

measured by estimated standing crop (Wang, 1989). Not all species used in a region are regularly eaten, but all consumed species were counted towards the regional carrying capacity since pandas have been observed using alternative species when preferred species were unavailable (Johnson et al., 1988). Furthermore, different pandas in the same subpopulation may differ in their bamboo preferences (Schaller et al., 1989). When information for a species' life history timing was unknown, we used a known cycling time for the genera, or if unavailable, we randomly assigned cycling times between 20 and 50 years.

Our model assumes that the density dependent changes in the vital rates occur at levels of the population near or above carrying capacity on a per capita basis (Fowler, 1981). If the bamboo available to a population is less than the minimum carrying capacity, the linking equation proportionately lowers survivorship and fecundity for all age-classes in that population using Eq. (2).

$$\text{If: } b_{rt} \div n_{rt} \leq m$$

$$\text{Then: } k_r = (b_{rt} \div n_{rt}) \div m \text{ and } A_{rt} = A_0^*k_r;$$

$$\text{Else: } A_{rt} = A_0 \quad (2)$$

where b_{rt} is the bamboo biomass (in kilograms) available for region r at time t , n_{rt} is the total panda population for region r at time t , m is the minimum amount of bamboo biomass needed per panda per year (4566 kg/yr; Reid et al., 1989), k_r is the carrying capacity for region r , A_{rt} is the density dependent Leslie matrix at time t for region r , and A_0 is the initial Leslie matrix.

2.2. Model analysis methods

We used three different approaches to analyze model behavior: sensitivity analysis of the panda model using eigenvalue and parameter adjustment methods; panda population viability analysis (PVA), where we simulated periodic drops in carrying capacity; and sensitivity analysis of the linked panda and bamboo biomass submodels. In general, simulations were run for each regional population from 200 to 1000 years. Before running simulation analyses, a simulation run of 500 years was made to determine the stable age-class

distribution for the base line panda population model. That distribution was used at the beginning of all subsequent simulation experiments.

2.2.1. Sensitivity analysis of the giant panda population dynamics model

The panda population dynamic submodel can be simplified to a Leslie matrix model when compensatory reproduction and density dependent interactions are ignored. We analyzed the simplified model using techniques outlined by Caswell (1989). This analysis involved determining the unique dominant eigenvalue λ for the matrix which has identity with the intrinsic growth rate $\lambda = e^r$ so that $r = \ln \lambda$. We then computed the rate of change in the intrinsic growth rate for a given change in survivorship or fertility rate (Eq. (3)).

$$\frac{\partial \lambda}{\partial F_i} \approx \frac{\lambda(F_i + h) - \lambda}{h} \quad \text{and} \quad \frac{\partial \lambda}{\partial S_i} \approx \frac{\lambda(S_i + h) - \lambda}{h}, \quad (3)$$

where F_i and S_i are the fertility rates and survivorship rates for age-class i , and h is an arbitrary but small number. In our calculations we set $h = 10^{-5}$ and changed F_i to $F_i + h$ in the Leslie matrix and then computed the new dominant eigenvalue. The eventual rate of convergence to the stable age distribution is governed by the damping ratio ρ , which is defined to be $(\lambda \div |\lambda_2|)$, where λ_2 is the eigenvalue(s) of the second largest absolute magnitude (Caswell, 1989). We then computed the rate of change of the damping ratio with respect to fertility and survivorship using Eq. (4):

$$\frac{\partial \rho}{\partial F_i} \approx \frac{\rho(F_i + h) - \rho}{h} \quad \text{and} \quad \frac{\partial \rho}{\partial S_i} \approx \frac{\rho(S_i + h) - \rho}{h} \quad (4)$$

In order to test the sensitivity of the model to the compensatory reproduction fraction and the sex ratio, we held other model parameters constant and varied the compensatory birth rate and sex ratio. We then calculated the growth rate at the end of the simulation.

2.2.2. Population viability analysis

In the PVA the panda population model was run unlinked from the bamboo model. We ran two kinds of PVA. In PVA 1 we examined the viability of populations in the baseline model's under non die-off conditions by randomly varying vital rates from 5 to 20% each year (Eq. (5)).

$$A_t = A_0^* v_t; \quad 0.8 \leq v_t \leq 1.2 \quad (5)$$

where A_t is the Leslie matrix at time t , A_0 is the initial Leslie matrix with initial vital rates (Table 1), and v_t is the random variation in vital rates at time t . We ran each PVA scenario 20 times for 200 years for each regional population and examined the percentage of runs in which the regional population of a given size went extinct. Extinction was defined as a regional population less than two.

In PVA 2 we examined the potential for extinction under a variety of 'die-off' scenarios. As in the PVA 1, vital rates were randomly varied during nondie-off years in a range not greater than 20% above or below the standard vital rates. Then, to simulate the reduction of carrying capacity that results from a bamboo flowering and die-off we reduced the carrying capacity a fixed amount (carrying capacity reduction, CCR) for three years (Tian, 1990). We varied the number of years between the start of bamboo die-offs (years between crashes: YBC) from 20 to 100 years. Each run of a given CCR–YBC combination was run 20 times for 200 years for each population. The percentage of runs in which the population went extinct and the percentage of runs that experienced an overall decline were noted for each initial population size–CCR–YBC combination (Appendix B). A population was considered to have experienced a decline if there were fewer individuals at the end of the run than at the beginning of the run.

2.2.3. Sensitivity analysis of giant panda–bamboo biomass model

These simulations were run for 1000 years, and the last 200 years were used to compile results. To test the sensitivity of the model to our biomass estimates, we ran the model from 100 to 10% of estimated biomass availability. To test the importance of each bamboo species for each region, we ran the model with each species removed one at a time. To assess the importance of alternative species for regional population dynamics, we ran the model with only the two most important species available (as determined from the removal experiment) and with the two most important species removed.

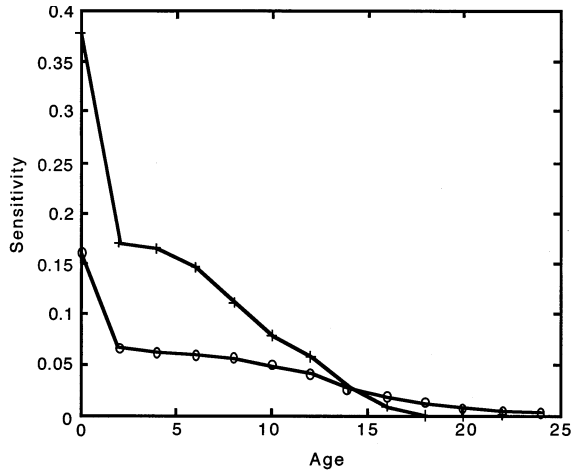


Fig. 1. Sensitivity of the Leslie matrix λ to changes in fertility and survivorship rates in different age-classes. 0, fertility; +, survivorship.

3. Results

3.1. Sensitivity analysis of panda population matrix

Our analysis of the base Leslie matrix found the unique dominant eigenvalue $\lambda = 1.0185762$. Following Caswell (1989) we calculated the intrinsic growth rate $r = 0.00921$ per capita per year. This means that under these constant vital rates the population will double its size in approximately 76 years.

Fertility and survival rate sensitivities were decreasing functions of age. Survival sensitivities were larger than fertility sensitivity at the beginning of the life cycle but eventually declined more rapidly and crossed the fertility curve (Fig. 1). The sensitivity of λ to changes in fertility rates varied by as much as three orders in magnitude between the first and the last age-class. The model was most sensitive to changes in vital rates in the early reproductive age-classes, least sensitive to changes in vital rates in the oldest age-classes, and intermediate in sensitivity to changes in vital rates of the juvenile age-classes. Fig. 1 also indicates that for age classes below 14 years a change in the survivorship rates affect the intrinsic growth rate of the population more than a similar change in

the fertility rates. However, for age classes between 16 and 25 years the opposite is true.

In our model $\lambda_2 = 0.4780621 + 0.62285234i$. The sensitivity of r to fertility and survivorship is shown in Fig. 2. The damping ratio was higher (i.e. convergence to a stable age-class distribution was faster) when the fertility rate was increased in the 2–11 and the 18–25 year old age-classes, and was lower (i.e. convergence to a stable age-class distribution was slower) when the fertility rate was increased in the 12–17 year old age-classes. The damping ratio would decrease most rapidly when the survivorship was increased for the 10–11 year age-class and was insensitive to changes in survivorship in the 18+ year old age-classes, i.e. the nonreproductive age-classes. An increase in the damping ratio dampens the oscillatory behavior of the population in a shorter time period. Similarly, a decrease in the damping ratio has the opposite effect.

Thus the age-class distribution was most affected by changes in the 10–11 year old class.

The growth rate was sensitive to the compensatory reproductive rate and was related to it by Eq. (6).

$$r_c = -0.02591388 * f + 0.0917463 \quad (6)$$

$n = 11, r^2 = 0.9989762$

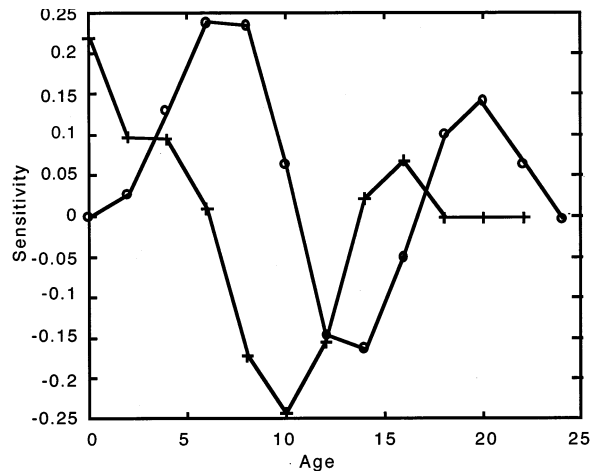


Fig. 2. Sensitivity of the damping ratio ρ to vital rates. 0, fertility rate; +, survivorship.

Modifying the sex ratio to increase the proportion of females proportionally increased the fecundity rate. Lowering the proportion of females had the opposite effect.

3.2. Population viability analysis

In PVA 1 we found all panda populations experienced growth during the 200 year period when a 20% random variance was added to the vital rates. Thus, panda populations were viable under a moderate amount of environmental stochasticity.

PVA 2 was conducted for six different CCR and five different YBC (Appendix B). The minimum viable population size, defined here as no extinctions in 200 years for 20 simulations, varied with the CCR-YBC combination. The probability of extinction increased with (1) decreasing population size, (2) increasing die-off severity, and (3) decreasing years between die-off (Fig. 3). Interestingly, larger populations were more likely to experience a decline than smaller populations under the same scenarios (Fig. 4). The relationship between percent extinction, YBC and CCR, is not linear (Fig. 5).

3.3. Panda bamboo interaction

3.3.1. Bamboo availability

The reported population statistics are for the last 200 years of a 1000 year simulation (Table 2). The Qionglai population, unlike the others, exhibited two distinct and alternating long-term carrying capacity levels of approximately 1400 and 3000 individuals that alternated every 200–300 years (Fig. 6). All initial panda populations were well below model carrying capacity and took more than 300 years to build to levels where bamboo dynamics became important. When the bamboo availability was reduced to 30% of the original value, all population averages were still one standard deviation or more above initial population sizes (Table 3). At reductions of 10–20% of estimated bamboo biomass, the Qinling and Min average population sizes were a standard deviation less than the initial population and the

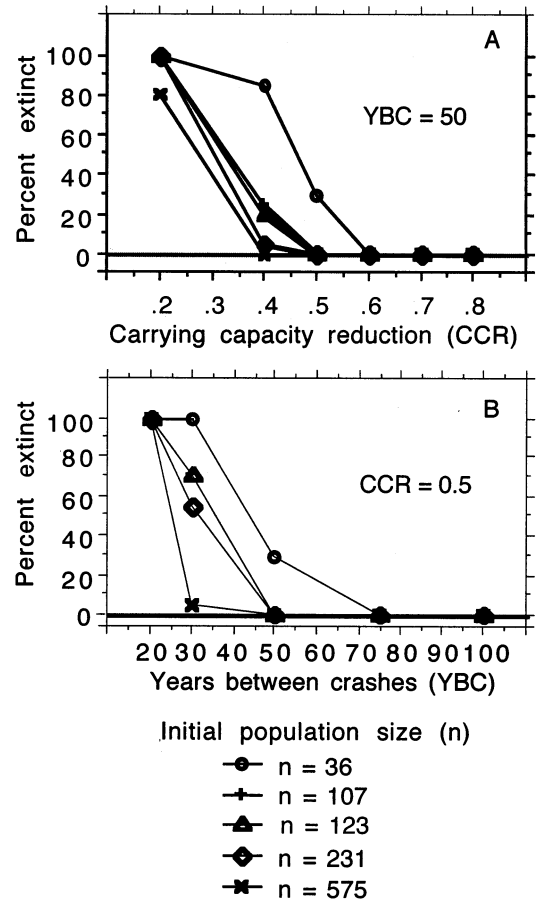


Fig. 3. Effect of population size, CCR, and years between crashes on extinction. (A) shows the percent of runs where extinction occurred (out of 20 runs) for a given CCR with years between crashes held at 50 years for all runs. (B) shows the percent of runs where extinction occurred (out of 20 runs) for a given CCR of 50%.

Qionglai population was within a standard deviation. Carrying capacity in the model never dropped below 0.5 for the Xiangling, Liang and Min populations. It regularly dropped below 0.5 for the Qinling and Qionglai populations (Fig. 7). As bamboo availability was reduced, the patterns of carrying capacity remained the same except that the start of the first drop occurred at earlier dates with reduced available biomass levels (Fig. 8).

3.3.2. Species removal

Table 4 lists the percent reduction in average population size when that species is removed. The Qinling population showed the greatest sensitivity to the loss of one species (*Fargesia robusta*). The Liang and Min populations were the least sensitive to the loss of any one species. Thus the sensitivity to species diversity varied among the regions in the model.

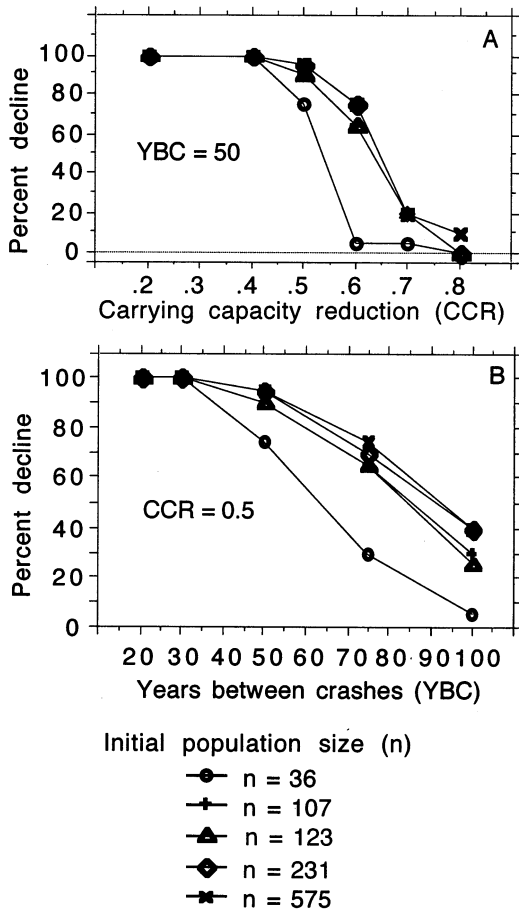


Fig. 4. Effects of population size, years between crashes, and CCR on probability of decline. (A) shows the percent of runs where declines occurred (out of 20 runs) for a given CCR with years between crashes held at 50 years for all runs. (B) shows the percent of runs where declines occurred (out of 20 runs) for a given CCR of 50%.

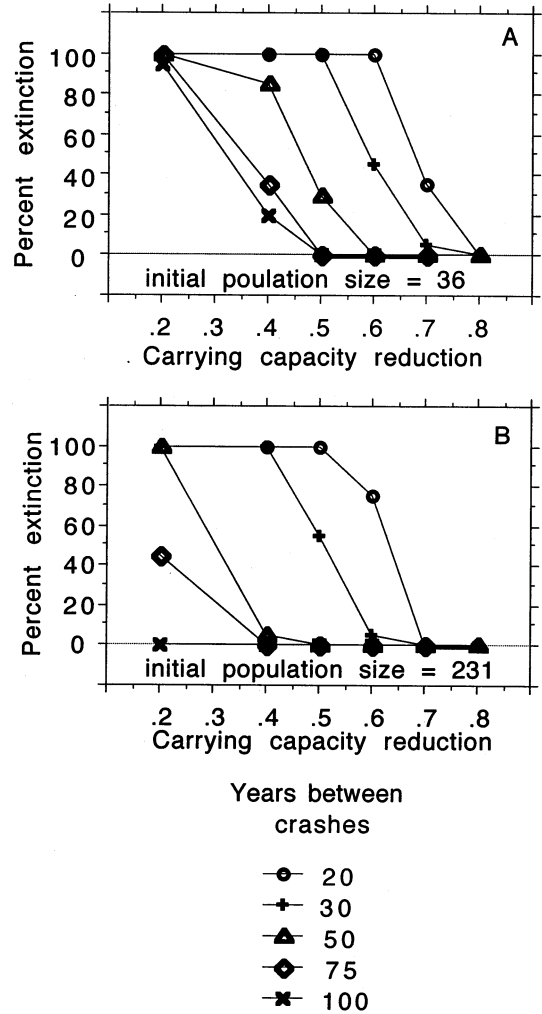


Fig. 5. Relationship between CCR, years between extinction, and extinction probability. The initial population size was 36 in (A) and 231 in (B). While carrying capacity and percent extinction were clearly related, the relationship is a nonlinear one.

3.3.3. Two important species

When simulations were run with only the two most important bamboo species in a given region all populations were reduced in size when compared to simulations in which all species were used (Table 5). Liang, Min, and Xiangling had population averages a standard deviation or more larger than their initial populations. The Qinling and Qionglai populations were within a standard deviation of their initial population sizes.

When simulations were run excluding the two most important bamboo species in a given region, some populations showed increases above initial levels while others went extinct (Table 6).

There were no clear patterns as to which regions experienced population loss or gain when the two most important species of bamboo were either used alone, or removed. Thus the degree to which the most regionally important species are crucial for panda survival in any given region varies (Table 7).

4. Discussion

4.1. Data sources

The panda life history data we used had several problems associated with it. First, the model was very sensitive to survivorship. Although the survivorship rates in the 0:1 age-class reported by Wei and Hu (1994), Wei et al. (1990) (42.86 and 40.7%, respectively) were within 3% of each other, this difference nearly doubled the growth rate ($r = 0.0096$ vs. 0.0051) from our previous model (Carter and Wang, 1993). Zhou and Pan (1997) reported even higher survivorships in this age-class. While no estimation errors have been published, 3% is probably well within the measurement error.

Second, the drop and rise in survivorship between the age-classes 12:13 and 14:15 has no known basis in natural history and is most likely an artifact of small sample size (Xia and Hu, 1990), the implications of which were explored in

Carter and Wang (1993). Therefore, high parameter sensitivity and probable error in estimates make any accurate projections of panda population unreliable.

Zhou and Pan (1997) found sex specific differences in survivorship based on the fact that females are often forced to emigrate. Functionally, in our model, female emigration is equivalent to reducing the sex ratio in favor of males, which effectively reduced fertility rates.

Data for the important bamboo species were difficult to come by. While there has been some excellent work done on the community ecology of the bamboo forest pandas inhabit, there is still little published documentation on the life cycle parameters for many of the bamboo species pandas depend upon. Pandas eat different portions of different species of bamboo and vary preferences with the season. Although detailed estimates of regional bamboo biomass exist (Wang, 1989), populations and individuals in a region show local differences in preferences. Finally, the ability to switch to an alternative species of bamboo in the event of a die-off of currently preferred species is limited by a local population's ability to migrate within a region. These facts, taken together, make our regional estimates of panda carrying capacities imprecise.

4.2. Giant panda submodel

Results of the eigenvalue analysis were in agreement with the more ad hoc analysis in Carter and Wang (1993). First, the population was most sensitive to mortality in the reproductive age-classes,

Table 2
Summary of the standard model's panda population projections by region^a

	Liang	Min	Qinling	Qionglai	Xiangling
Initial population	231	575	108	123	36
Mean	3973.85	3754.09	920.39	2326.87	700.3
Median	4004.5	3558	930	2105.5	712
S.D.	685.95	753.60	266.79	1008.76	180.03
Min.	2306	2610	347	806	305
Max.	5564	5690	1434	4134	1165

^a Statistics are for the last 200 years of a 1000 year simulation. The standard model was run with 100% bamboo availability and a compensatory reproductive rate of 0.5.

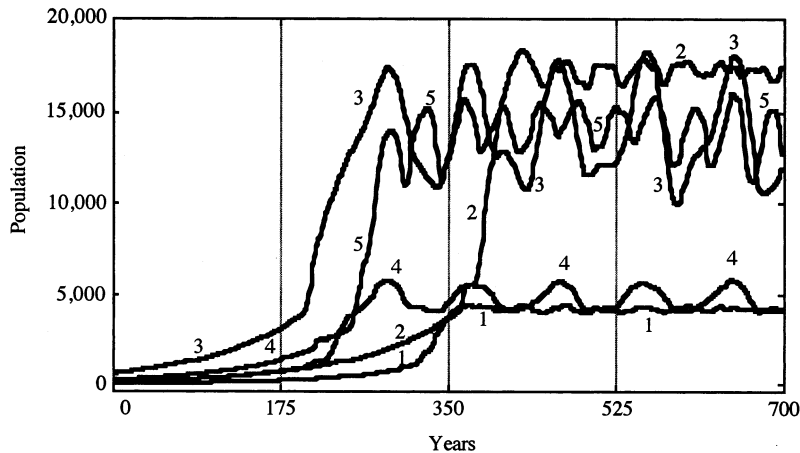


Fig. 6. Standard panda–bamboo biomass simulation. Key: 1, Xiangling; 2, Liang; 3, Min; 4, Qinling; 5, Qionglai. All populations grew above currently reported giant panda population estimates.

followed by pre-adult age-classes. The model was not sensitive to losses in post-reproductive age-classes. There are reasons, however, to believe that even the oldest females could be reproductively capable and, depending on their fertility rate, this fertility could have a significant positive affect on the population growth rate (Carter and Wang, 1993). Another important factor in the panda growth rate is the extent to which females experience compensatory reproduction. Even a small increase in compensatory reproduction could have a significant effect on the population growth rate. The extent to which compensatory reproduction occurs needs to be quantified.

The implications of the population dynamics analysis for conservation and management of panda populations are clear. In those instances where pandas are to be removed from the wild, only the oldest individuals should be taken since their removal will have the smallest detrimental effect on the population growth rate. Finally, while the vital rates project a growing population, that growth rate is rather low and very sensitive to any additional mortality in the reproductive age-classes. In their previous study, Carter and Wang (1993) found that the removal of only one individual from the juvenile or reproductive age-classes every 2 years can cause a decline in all but the largest of the existing panda populations. Therefore management options that carry any

risk to animals in these age-classes, such as the transfer of individuals between regions in order to bolster smaller populations or to prevent inbreeding depression, should be undertaken with great scrutiny. Furthermore, the capture of animals for use in zoos and captive breeding programs is problematic since most of the animals collected are young, and captive breeding programs have been generally unsuccessful, with the result that there are more deaths than births in captivity (Hunter, 1991).

There are no set criteria for conducting PVA (Boyce, 1992). In general, the goal of PVA is to establish the likelihood that a population will persist for an arbitrarily chosen time period and usually involves establishing a minimum viable population size (MVP) (Gilpin and Soulé, 1986). There are two aspects, stochastic and genetic, to establishing a MVP. A stochastic MVP is concerned with how stochastic properties of the environment affects a species long term survival. A genetic MVP is concerned with the problems of maintaining a viable population in the face of inbreeding depression. Our analysis is a stochastic MVP.

Carter and Wang (1993) first addressed the question of panda population viability with a deterministic model of panda dynamics combined with bamboo life history characteristics. In that paper they explored the impacts of poaching,

population transfers, carrying capacity, and the sensitivity to parameter estimations. A PVA that was much broader in scope but covered panda population dynamics in less detail was presented by Reid (1994). Reid covered the life history dynamics using generalized population growth rates and qualitatively examined factors controlling the metapopulation dynamics of pandas. It is not clear if Reid created a mathematical model of panda population dynamics. Wu et al. (1996) created a Lotka–Volterra predator–prey model of linked panda–arrow bamboo dynamics for the Wolong Natural Reserve (Qionglai Mountains). Their model used generalized population growth rate and examined one species of bamboo and the impact of periodic bamboo die-off on panda population dynamics. A PVA for a panda subpopulation in the Qinling Mountains was conducted by Zhou and Pan (1997). Their model used a Leslie matrix approach, assumed populations were at carrying capacity, did not consider the effects of bamboo die-offs, and did not directly tie in carrying capacity to bamboo availability. They examined in detail the impact of life history attributes, such as emigration, in their analysis. Here we have attempted to model the global noncaptive panda population by using a modified Leslie matrix approach and by adding carrying capacity in the form of bamboo availability. Our analysis focused on a formal sensitivity analysis of the base Leslie matrix, a PVA of a stochastic

model with die-offs and the examination of potential bamboo dynamics.

We had no information with which to gauge year to year variability of the bamboo forest habitat in non die-off years. However, research indicates that pandas, unlike other bears, store little or no fat and are adapted to food resources and environmental conditions that are generally constant and dependable year round (Schaller et al., 1989). Therefore our estimate of interannual variation as 20% was probably high. Under the standard model and PVA 1, pandas have a positive growth rate high enough that they can tolerate random year to year changes in vital rates of 20% or more. Thus, in non die-off years, all wild panda populations should be growing.

Since periodic die-off of key bamboo species are the main non anthropogenic threat to panda populations, our PVA approach examined a range of die-off scenarios for each of the known panda populations. Furthermore, we have no direct estimates of the total drop off in panda carrying capacity for a region, though it has been reported that bamboo die-offs were able to reduce the available biomass of a key species by more than 80% (Reid et al., 1989). The actual MVP probably varies for each region's populations depending upon which species and alternative species are available and the relative timing of their flowering. Thus, rather than present a MVP estimate, a range of minimums can be selected given a range

Table 3
Population estimates by region^a

Region	N_0	30% Availability 0 Comp. repro.		30% Availability 0.5 Comp. repro.		10% Availability 0 Comp. repro.		10% Availability 0.5 Comp. repro.	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Liang	123	1059	137.1	1222	160	353	45.8	407	53.5
Min	575	967	146.4	1104	236.3	322 ^b	48.9	369 ^b	79.6
Qinling	108	224	30.7	287	61	74 ^b	10.5	96 ^b	20.2
Qionglai	232	596	322.6	725	352.8	198 ^b	107.4	243	116.7
Xiangling	36	174	36.7	224	44.8	58	12.6	75	15

^a Estimates based on average of last 200 years of a 700 year simulation. Estimates were made at 30 and 10% of estimated bamboo biomass available to the regional population (% availability) and at 0.0 and 0.5 compensatory reproductive rates (comp. repro.). The mean and the standard deviation (S.D.) around the mean values are presented. N_0 is the initial population size.

^b Population sizes lower than initial.

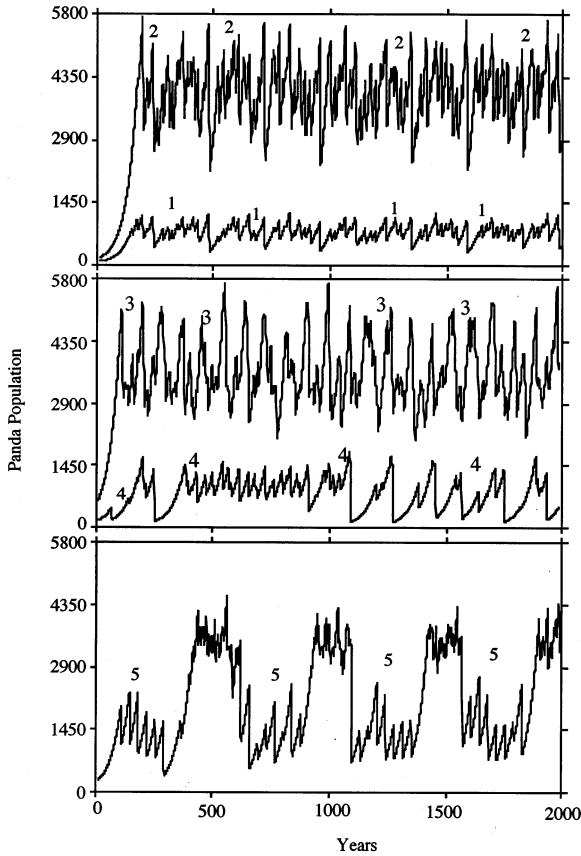


Fig. 7. Carrying capacity k for the standard model runs for 1000 years. Compensatory reproduction was set at 0 and bamboo availability at 1. The carrying capacity of the population dropped to less than 1 when food per panda was below the minimum needed to fully support all pandas. The smaller the k the greater the food stress. k equal to 1 indicates the population is not under food stress and the population is density dependent.

of reductions in carrying capacity, lengths of time between carrying capacity drops, and acceptable probability of extinction (Appendix B).

For intermediate ranges of CCR–YBC combinations, the probability of decline increased with population size even as the probability of extinction went down. We hypothesize that this is an artifact of random behavior near a minimum. We can view the population trajectory as a drunken walk along the edge of a cliff, where we mark the distance from the edge over time. The closer to the edge the walker starts (small initial popula-

tion) the greater the probability the walker will fall over the edge (extinction). If the walker doesn't fall over the edge, chances are the walker will be farther away from the edge at the end of the walk than at the beginning. Conversely, the walker who starts farther from the edge has a greater potential for being closer to the edge at the end of the walk without going over.

4.3. Giant panda–bamboo model

All regional panda populations are well below crash level carrying capacities in our model. Tian (1990) and Carter and Wang (1993) both estimated that the Qinling population could support many more pandas than its current level. On the other hand, Zhou and Pan reported that, based on home range sizes, pandas were at carrying

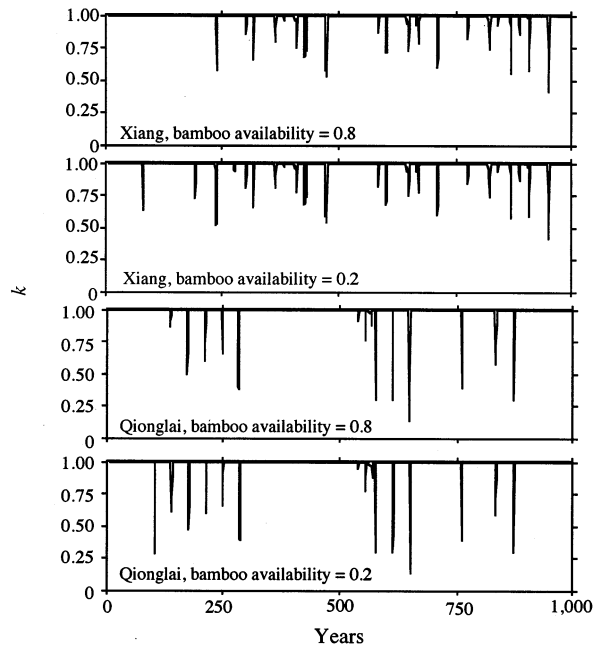


Fig. 8. Effect of reduced food availability on carrying capacity k . Compensatory reproduction is 0.5 for the Xiangling region. The carrying capacity of the population dropped to less than 1 when food per panda was below the minimum needed to fully support all pandas. This carrying capacity k less than 1 is a measure of the severity of food stress in the model population. 0.2 = 20% of bamboo availability levels in the standard model, 0.8 = 80% of bamboo availability levels of the standard model.

Table 4
The importance of individual bamboo species for regional panda populations^a

Species\region	Compensatory reproduction = 0					Compensatory reproduction = 0.5				
	Liang	Min	Qinling	Qionglai	Xiangling	Liang	Min	Qinling	Qionglai	Xiangling
<i>B. fargesii</i>		16	87				14	80		
<i>B. fangiana</i>	4	1		16	7	4	1		9	8
<i>C. pachystachys</i>	29			29	38	27			21	36
<i>F. denudata</i>		48					45			
<i>F. ferax</i>	48				74	42				67
<i>F. nitida</i>		14	67	8			14	34	5	
<i>F. robusta</i>		5	96	89			5	93	87	
<i>F. rufa</i>		33					30			
<i>F. scabrida</i>		6		1			6			
<i>Q. opienensis</i>	41				4	33				2
<i>Y. chungii</i>		1	4	59			2	4	48	
<i>Y. confusa</i>	20				36	21				32

^a The percentage of the average population size for the last 200 years of a 700 to 1000 year simulation, divided by the average population of the model with all bamboo species used, subtracted from one. Those species whose removal did not reduce a regions population are blank. Simulations were run at both 0 and 0.5 compensatory reproductive rates. Genera key: B, *Bashania*; C, *Chimonobambusa*; F, *Fargesia*; Q, *Qiongzhuca*; Y, *Yushania*.

capacity in their analysis of another population in the Qinling mountains. We had to reduce our estimates of available biomass to 20% or less of the original values to produce reduced populations sizes, and even then, some populations continued to grow. Why are our estimates of potential panda populations so high? First, anthropogenic sources of population losses could be a significant factor reducing the populations (Carter and Wang, 1993; Reid, 1994). Second, we may overestimate the availability of the bamboo biomass in a region since regional figures for bamboo do not indicate how much of the total regional bamboo is actually accessible. Panda did starve during the die-offs in the Min Mountains

during the bamboo die off event between 1975 and 1976 (Schaller et al., 1985) and outside the Wolong Reserve in the Qionglai Mountains between 1980 and 1983. During the die-off in the Wolong Reserve, pandas moved to adjacent areas with alternative bamboo resources as preferred species became unavailable (Johnson et al., 1988). When multiple bamboo species flowered and died at the same time in the Min Mountains, alternative species may not have been available. This model, however, indicates that the more likely cause of starvation was the inability of individuals to gain access to other bamboo forests in the same region where alternative bamboo resources were available. Therefore, the establishment of

Table 5
Simulations using only the two most important species^a

	Liang	Min	Qinling	Qionglai	Xiangling
Initial	231	575	108	123	36
Mean	1772.41 ^b	2058.03 ^b	153.05	125.48	277.02 ^b
S.D.	177.28	211.78	72.21	12.68	58.14

^a The top two species were those that accounted for the largest drop in average biomass production in a 200 year period. The simulations were run at 100% and compensatory reproduction set at 50%. The initial, mean, and standard deviation (S.D.) are presented for the last 200 years of the 1000 year simulation.

^b Means one or more standard deviations larger than initial.

corridors between current panda habitat and areas where alternative, but currently unused, bamboo species exist might be a useful strategy for panda conservation.

The k value in our bamboo analysis was equal to our CCR value in our PVA. While a CCR value of 0.4 and YBC of 20 resulted in extinction of all populations in our PVA model, the panda populations in our bamboo reduction simulations never suffered extinction, even when the k regularly dropped below 0.5 for Qinling and Qionglai. An important difference between the two analyses is that most extinctions in the PVA occurred during the first 100 years of the simulation. This difference indicates that our PVA approach seems to overestimate the population's susceptibility to bamboo crashes since it reduces the vital rates without regard to actual carrying capacity. The k analysis, however, does indicate that the Qinling and Qionglai populations have more frequent and larger drops in k than the other three populations.

The bamboo species removal experiment indicated that the loss of individual species did not result in an additive loss in carrying capacity. For example, the removal of any of the bamboo species *Bashania fargesii*, *Fargesia nitida*, or *Fargesia robusta* each results in a greater than 50% reduction in 200 year average biomass in the Qinling population. A bamboo species' importance in determining the long term average population size for a region is therefore related as much to the synchronization between species life history as it

is to the available biomass of the particular species involved. This finding is in agreement with our previous study (Carter and Wang, 1993) where we varied the relative timing and cycle length of the flowering periods of the bamboo species used by giant pandas.

The dependence of the different panda populations on their two major species of bamboo varied. When only two species were used, Liang, Min, and Xiangling populations still experienced significant growth while Qinling and Qionglai did not show significant growth. When only minor species were used, Qinling's population went extinct, Min's population declined, and the other populations showed significant increases. Again, this points out that it is not the number of species that a population depends upon, but the synchronization of their life history that seems to dominate long-term survival for pandas. It should be noted that one of the populations with the greatest potential for growth in this model was the smallest, the Xiangling region.

In many ways our model is liberal with respect to panda population dynamics. First, our compensatory growth rate adjustment significantly increased the panda growth rates. Second, while the bamboo biomass is unaffected by the panda population, a potential negative feedback in the system is ignored (Tian, 1990). Finally, the model assumes that all the bamboo within the region is accessible. It has been hypothesized that the pandas response to periodic die-offs of preferred bamboo species was to switch to another species.

Table 6
Simulations excluding the two most important species^a

	Liang	Min	Qinling	Qionglai	Xiangling
Initial	231	575	108	123	36
Mean	405.36 ^b	477.82 ^c	0 ^c	309.49 ^b	62.66 ^b
S.D.	124.46	283.14	0	109.78	7.44
Max	738	796	0	522	78
Min	236	283	0	124	48

^a The top two species were those that accounted for the largest drop in average biomass production in a 200 year period. The simulations were run at 100% and compensatory reproduction set at 50%. The mean, standard deviation (S.D.), maximum (max.), and minimum (min.) presented are for the last 200 years of the 1000 year simulation.

^b Means one or more standard deviations larger than initial.

^c Means within a standard deviation or less of the initial value.

Table 7
Summary of bamboo removal experiment^a

	Liang	Min	Qinling	Qionglai	Xiangling
2 Top species only	+	+	0	0	+
2 Top species excluded	+	0	–	+	+

^a Values based on mean population size for the last 200 years of a 1000 year simulation. ‘+’ indicates a standard deviation or more increase above initial regional panda population levels. ‘0’ indicates that changes were within a standard deviation of initial levels. ‘–’ indicates that populations were a standard deviation or more below initial levels.

However, because of human activity this may no longer be possible (Johnson et al., 1988).

5. Conclusions

While data may be sparse with respect to important aspects of panda conservation biology, our analysis indicates that the panda populations could be significantly higher than present. Currently low population levels are probably the result of direct removal of pandas from the population or prevention of migration to other suitable habitats because of human activities and infrastructure. To reduce the population level impacts, a policy discouraging panda removal from the wild for zoos and breeding programs should be considered. The removal of only a few sub- or young adult individuals can eliminate population growth in panda populations. Currently plans are being made to create corridors between panda populations. Additional corridors should be considered between areas already occupied by pandas and suitable but currently unused bamboo forest. These two policies would allow panda populations to grow to their potential. All strategies should be long-term since most populations do not begin to reach carrying capacity for 200–300 years. By using the best available data, our simulations indicate that the smallest population, the Xiangling, has a more robust growth potential than the much larger Qinling and Qionglai populations.

Finally, more research is needed into the timing of the life history dynamics of bamboo species

pandas use for food. Future modeling efforts should probably focus on the spatial distribution of food resources, barriers on the landscape, and finer grain population models.

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Appendix A. Bamboo species used in the model

The species used were determined by panda feeding preference within a region, biomass availability, and wide dispersal (Wang, 1989). Sources used to estimate life span and year of last flowering included Campbell and Qin (1983), Schaller et al. (1985), Reid et al. (1989) and Hu (1990).

Species	Cycle length	Years since last flowered	Regions	Sources
<i>Bashania fargesii</i> ^c	23	30	Min, Qinling, Qionglai	4, 9, 12, 13, 14
<i>Bashania fangi</i> ^{cf}	45	15	Min, Xiangling, Liang	1, 2, 3, 5, 6, 7, 10, 11, 13
<i>Chimonobambusa pachystachys</i>	16	5	Min, Qionglai, Xiangling, Liang	1, 13
<i>Fargesia scrubrida</i> ^f	50	23	Min, Qionglai	2,8, 11, 13
<i>Fargesia denudata</i> ^f	40	23	Min,	9, 13
<i>Fargesia ferax</i>	40	8	Xiangling, Liang	13
<i>Fargesia nitida</i> ^{cf}	90	7	Min, Qinling, Qionglai	12, 13
<i>Fargesia robusta</i> ^f	37	23	Min, Qinling, Qionglai	1, 2, 3, 4, 5, 6, 7, 12, 13, 14
<i>Fargesia rufa</i>	15	14	Min	13
<i>Qiongzhusia opienensis</i>	20	0	Xiangling, Liang	13
<i>Yushania chungii</i> ^{cf}	20	24	Min, Qinling, Qionglai	1, 2, 13
<i>Yushania confusa</i>	22	10	Xiangling, Liang	13

Key: c is cycle length reported; f is year of last flowering reported; (1) Campbell and Qin, 1983; (2) Campbell, 1984; (3) Johnson et al., 1988; (4) Pan and Lu, 1993; (5) Reid et al., 1989; (6) Reid and Hu, 1991; (7) Reid et al., 1991; (8) Schaller et al., 1985; (9) Schaller et al., 1989; (10) Taylor and Qin, 1993; (12) Tian, 1990; (13) Wang, 1989; (14) Zhou and Pan, 1997.

Appendix B. Population viability analysis of panda population under a variety of CCR and YBC

Each of five initial populations sizes were simulated 20 times for 200 years, the percentage of runs in which extinction occurred (% ext: final popula-

tion < 2) and the percentage of runs where declines occurred (% red: initial population > final population) were recorded. A 0.2 CCR is equivalent to the carrying capacity 20% of base line, and a 0.8 CCR is a carrying capacity 80% of base line. When not experiencing a CCR there was a stochastic 20% variation in year to year carrying capacity.

CCR	Initial population	YBC									
		20		30		50		75		100	
		% ext	% red	% ext	% red	% ext	% red	% ext	% red	% ext	% red
0.20	36	100	100	100	100	100	100	100	100	95	100
	107	100	100	100	100	100	100	80	100	5	95
	123	100	100	100	100	100	100	75	100	0	95
	231	100	100	100	100	100	100	45	100	0	95
	575	100	100	80	100	80	100	5	100	0	95
0.40	36	100	100	85	100	85	100	35	85	20	45
	107	100	100	25	100	25	100	0	100	0	40
	123	100	100	20	100	20	100	0	100	0	40
	231	100	100	5	100	5	100	0	100	0	45
	575	100	100	0	100	0	100	0	100	0	45

Appendix 2 (Continued)

0.50	36	100	100	30	75	30	75	0	30	0	5
	107	100	100	0	90	0	90	0	65	0	30
	123	100	100	0	90	0	90	0	65	0	25
	231	100	100	0	95	0	95	0	70	0	40
	575	100	100	0	95	0	95	0	75	0	40
0.60	36	100	100	0	5	0	5	0	5	0	0
	107	95	100	0	65	0	65	0	20	0	15
	123	95	100	0	65	0	65	0	20	0	15
	231	75	100	0	75	0	75	0	20	0	15
	575	35	100	0	75	0	75	0	25	0	20
0.70	36	35	95	0	5	0	5	0	0	0	0
	107	0	100	0	20	0	20	0	0	0	0
	123	0	100	0	20	0	20	0	0	0	0
	231	0	100	0	20	0	20	0	0	0	0
	575	0	100	0	20	0	20	0	0	0	0
0.80	36	0	20	0	0	0	0	0	0	0	0
	107	0	85	0	0	0	0	0	0	0	0
	123	0	85	0	0	0	0	0	0	0	0
	231	0	85	0	0	0	0	0	0	0	0
	575	0	90	0	10	0	10	0	0	0	0

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