

THE INFLUENCE OF DISPERSAL ON THE METAPOPOPULATION
VIABILITY OF GIANT PANDA (*ALIUROPODA MELANOLEUCA*)
IN THE MINSHAN MOUNTAINS

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Giant Panda *Aliuropoda melanoleuca* is a rare ancient animal native to China, and its population in the Minshan Mountains in China has been divided into six subpopulations that are almost disconnected from each other. The six sub-populations are named respectively BH sub-pop, ZZWG sub-pop, MS sub-pop, BCH sub-pop, QFS sub-pop and GGS sub-pop. It is crucial and urgent to find ways to conserve these isolated subpopulations. In this study VORTEX software is used to model the dynamics of the Giant Panda population over the next 100 years in the Minshan Mountain as a metapopulation (named Minshan meta-pop). Results are as follows: (1) If there were no dispersers, BH sub-pop, ZZWG sub-pop, QFS sub-pop and GGS sub-pop would become extinct within 100 years, and the population size of MS sub-pop and BCH sub-pop would increase within 100 years. (2) If there were immigrants the four little sub-populations (BH sub-pop, ZZWG sub-pop, QFS sub-pop and GGS sub-pop) would retain more than 90% of their current genetic diversity over the next 100 years, even if the dispersal rate was just 1%. (3) High dispersal rate was not of benefit to population growth and maintenance of genetic diversity in the metapopulation. (4) In the polygynous system of the Giant Panda, the male plays an important role in dispersal. Limiting the dispersal of females and increasing the successful dispersal of males could promote the development of the metapopulation. (5) Altering the age of dispersers had almost no impact upon the dynamics of metapopulations. (6) In order to ensure that this metapopulation will survive for 100 years, the minimum effective viable population size (N_e) should be 40 breeding individuals or 100 total individuals with a stable age distribution. Finally, we put forward some specific recommendations in light of the current situation faced by Giant Pandas in the Minshan Mountains, such as constructing “corridor belt” to link large and small populations and analyzing the sensitivity of Giant Panda population.

Key words: Giant Panda, metapopulation, Population Viability of Analysis, VORTEX, dispersal

INTRODUCTION

The Giant Panda (*Aliuropoda melanoleuca*) is a rare mammal native to China and has been endangered because of habitat fragmentation, bamboo die-off, disease, environmental variations and so on. The conservation of this endangered species is attracting worldwide attention. Today it is listed as a Category I species

on the Nationally Protected Animal List in China, and it is also listed by the Convention on International Trade in Endangered Species (CITES) as an Appendix I species. Up to now, it can only be found on five mountains (i.e. Qinling, Minshan, Qionglai, Liangshan and Xiangling). The total population is estimated at about 1,500 (The Third Giant Panda Survey 2002). Several populations have been living in isolation with little gene exchange. Of the five populations, the one in the Minshan Mountain is the biggest isolated population, and the Minshan Mountains are widely acknowledged as a hot spot of biodiversity in Southwestern China. Furthermore, the Minshan's Giant Panda population has been divided into six subpopulations with little genetic exchange due to traffic, land reclamation, logging, and so on (HU 2000). The corresponding distribution is seen in Figure 1. Could these subpopulations survive unless dispersal occurs? If not, could they survive long-term as a metapopulation? How does the dispersal influence population viability? Therefore it is crucial to understand how to estimate the viability of these isolated populations and to know about whether they can survive for long. Population Viability Analysis (PVA) is one method for estimating the extinction risk and the effective population size of endangered species, by modeling the effects of demographic stochasticity, environmental stochasticity, natural catastrophes, genetic stochasticity, environmental spatial structure, population spatial structure, variety of landscape structure, and influences of management measures on the endangered population. PVA is designed to suggest management strategies that will benefit populations or metapopulations (SHAFFER 1981, BOYCE 1992, LI 2003). Since the advent of PVA, it has become a popular approach in biological conservation research. Because biodiversity has been threatened seriously, the urgent search for tools to evaluate extinction risk has promoted the theoretical development and application of PVA. In recent years, literature on PVA has increased exponentially; its contents are related to vertebrates, especially mammals and birds, its use also extends to invertebrates and plants, and have been used for decision-making on their conservation (DENNIS *et al.* 1991, FRYE 1996*a, b*, MENGES 2000, COULSON 2001, REED *et al.* 2002, ELLNER *et al.* 2002, BROOK *et al.* 2002, LI 2003). However, because PVA includes many stochastic factors, many people have different viewpoints on its ability some doubt the utility of risk estimates derived from PVA (ELLNER 2002, LUDWIG 1996*a, b*, 1999, FIEBERG *et al.* 2000, CAUGHLEY 1994). But BROOK *et al.* (2000) conducted a retrospective test of PVA based on 21 long-term ecological studies and, contrary to recent criticism, they found that PVA predictions were surprisingly accurate. Furthermore, the predictions of five PVA software packages (INMAT, GAPPS, RAMAS/Stage, RAMAS/Metapop and VORTEX) were highly concordant. Thus they conclude that PVA is a valid and sufficiently accurate tool for categorizing and managing endangered species. More-

over, they believe that PVA is the best available method for guiding management decisions, especially when data are limited (BROOK *et al.* 2002). There have been more PVA studies on Giant Panda than on other mammals in China. VORTEX software has been used to model the dynamics of the Giant Panda over the next 100 years in Wuyipeng, Wolong National Nature Reserve (WEI 1994); in Foping, Shanxi province (LI 1997); in Yele Nature Reserve (GUO 1999); and in Tangjihe Nature Reserve (ZHANG 2002). Doubtlessly, these studies offer some good recommendations, but they mainly focus on small, isolated habitats, and predict extinction risk in small, isolated populations. They didn't consider the effect of dispersal on populations. Furthermore, up to now, there has been no detailed data on dispersal of the Giant Panda. PVA can and should be used to predict the dynamics of the larger Giant Panda metapopulation consisting of several, perhaps weakly linked populations located in several mountain ranges (HU 2000). At the same time, in a relatively large range, we need to know how dispersal influences each isolated small population, whether any modes of dispersal are beneficial to these isolated small populations, and which mode of dispersal benefits these small populations most. We know the Minshan Giant Panda population had been divided into six isolated subpopulations with little genetic exchange by traffic, land reclamation, logging, and so on. In this essay, the authors treat the Minshan Giant Panda population as a metapopulation to model its dynamics and study how dispersal affects the viability of these subpopulations by testing variations in dispersal rate, age, survival rate, and sex, so as to gain some new ideas for the reconstruction of Giant Panda habitat and provide new insights for formulating conservation strategies for the Giant Panda and biodiversity on a large scale.

METHODS

Various PVA packages are now available, each with differing capabilities. These include the individual-based programs GAPPS and VORTEX, and the matrix-based packages INMAT, RAMAS ® Metapop, and RAMAS ® Stage. All are suitable for population risk assessments, although each was designed with slightly different objectives in mind, reflected in their structure, capabilities, and assumptions. These simulation programs provide a convenient tool for building predictive models based on characteristics of life history, deterministic factors, and stochastic processes that together control the dynamics of natural populations. Different PVA programs have been shown to give divergent predictions in previous comparative studies (MILLS *et al.* 1996, BROOK *et al.* 1999). However, these findings were based on analyses from a single species, and the differences arose because the input was not completely standardized across programs. In other words, the underlying deterministic models were not exactly matched, and nonstandard factors such as inbreeding depression and stochastic breeding structure were included (BROOK *et al.* 2000). Furthermore, the predictions of five PVA software packages (INMAT, GAPPS, RAMAS/Stage, RAMAS/Metapop and VORTEX) tested by Brook were highly concordant (BROOK *et al.* 2002). Among these five PVA software pack-

ages, RAMAS/Metapop and VORTEX can be used to model metapopulations. However, RAMAS/Metapop does not consider the inbreeding depression of population. In this essay, we select VORTEX9.41 to analysis the viability of six isolated subpopulations. First, we identify those subpopulations that can't survive for long, and then we search for models of dispersal that maximize metapopulation persistence.

Estimation of parameters in VORTEX9.41

Initial reproductive ages: According to observations of the wild Giant Panda population, the initial reproductive age of females is age 8 and males is age 7 (WEI & HU 1994). **Maximum age of reproduction:** The average longevity of the wild Giant Panda is about 20 (WEI & HU 1994). Here, we assumed its maximum age of reproduction is 20 and assumed all adults can breed. **Maximum number of progeny per year:** We assume each female can produce up to two offspring per year, in keeping with the only available data (HU 1985).

Reproductive rates: We assume that 62.5% of females breed each year, with 93.3% producing one offspring and 6.7% producing two offspring (WEI & HU 1994). **Sex ratio at birth:** 1:1 males to females. **Density dependence in reproduction:** There is no evidence that reproductive rates are density dependent in wild Giant Pandas, so this parameter was omitted here. **Mortality rates:** Based on observed data (WEI & HU 1994), we assumed age- and sex-specific mortality rates as shown in Table 1.

Inbreeding depression: There are no data on inbreeding depression in the Giant Panda. This parameter was omitted here. **Initial population size:** Data from 2001 to 2003 indicated that the size of the Minshan Giant Panda population was 600 ± 104 . For the purposes of this modeling effort model, we assumed that the Minshan Giant Panda population size was 600. Because of traffic, land reclamation, logging, and so on (HU 2000), the Minshan Giant Panda population had been divided into six subpopulations with little genetic exchange. We assumed that the sizes of these six subpopulations were as follows: (1) Baihe subpopulation (BH sub-pop), $N = 10$, inhabited the middle of Yanziyagou and Zhimagou, in Jiuzhaigou county; (2) Zezhawagou subpopulation (ZZWG sub-pop), $N = 10$, inhabited Zezhawagou, Rizhaigou, Zhongzhagou, Xiarcunzhai and Zharugou; (3) Minshan subpopulation (MS sub-pop), $N = 360$, inhabited the southeast of the middle and upper reaches of Baishui River; (4) Baicaohe subpopulation (BCH sub-pop), $N = 180$, inhabited the middle and upper reaches of Xutang River, Tumen River, Baicao River and Qingpian River; (5) Qianfoshan subpopulation (QFS

Table 1. Mortality of wild Giant Pandas at different ages

Age	Mortality rates (%)	
	Female	Male
1	40.00(10.0)	40.00(10.0)
2	9.67(3.0)	9.67(3.0)
3	3.14(2.0)	3.14(2.0)
4	1.52(1.0)	1.52(1.0)
5	1.55(1.0)	1.55(1.0)
6	1.57(1.0)	1.57(1.0)
7	1.60(1.0)	1.60(1.0)
8	–	3.45(2.0)
Adults	13.33(3.0)	14.16(3.0)

sub-pop), $N = 30$, inhabited the southeast of Tumen River and the upper reaches of Chaping River and Niujiaodong River; and (6) Guangguangshan subpopulation (GGS sub-pop), $N = 20$, inhabited the upper reaches of Shiting River, Baishuihe River and Baisha River. The corresponding distribution is shown in Figure 1.

Carrying capacity: Here we selected the area of bamboo to estimate the value of K because wild Giant Panda only eat bamboo. According to previous surveys (HU 1990) the total area of bamboo in this region was $1,950.46 \text{ km}^2$, of which 423.38 km^2 of bamboo have recently died off, and the highest recorded density of Giant Pandas was 3.03 individuals per km^2 . So we estimated the value of K (carrying capacity) of the entire Minshan Giant Panda population was $(1,950 - 423) \times 3.03 = 4,627$. The total area of habitat in the Minshan Mountains was $6,127.55 \text{ km}^2$ (HU 1990), and then, we calculated that there was 0.25 km^2 of bamboo per km^2 of habitat $((1950.46 - 423.38) / 6127.55 = 0.25)$. So

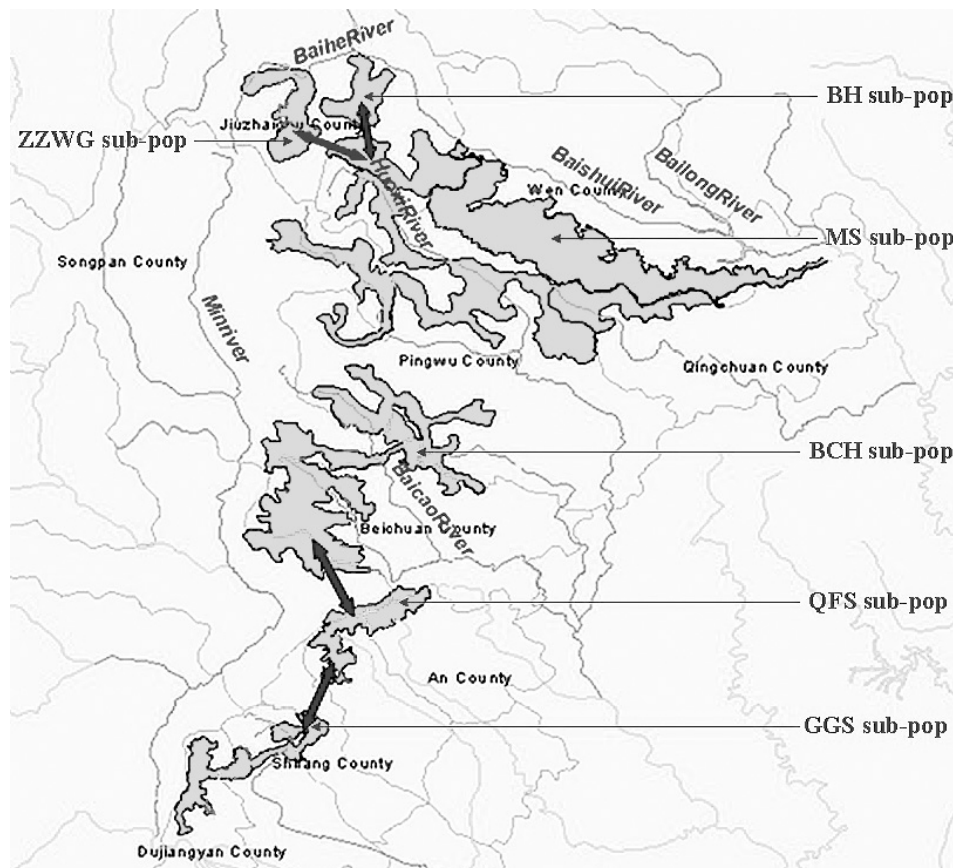


Fig. 1. The distribution of each subpopulation and the suggested “corridor belts” within the Minshan metapopulation. ZZWG sub-pop, BH sub-pop, MS sub-pop, BCH sub-pop, QFS sub-pop and GGS sub-pop are abbreviations for Zezhawagou subpopulation, Baihe subpopulation, Minshan subpopulation, Baicaohe subpopulation, Qianfoshan subpopulation, and Guangguangshan subpopulation, respectively

Table 2. The distribution of five treatment with different parameters of dispersal

		The probability of disperser survival					
	group	1	0.9	0.8	0.7	0.6	0.5
Dispersal rate	1%	①	①	①	①	①	①
	2%	②	②	②	②	②	②
	4%	③	③	③	③	③	③
	8%	④	④	④	④	④	④
	16%	⑤	⑤	⑤	⑤	⑤	⑤

Figures represent five groups respectively. In group ①, when the dispersal rate is equal to 1% values of the probability of disperser survival are 1, 0.9, 0.8, 0.7, 0.6, 0.5 respectively as in groups ②③④ and ⑤

the value of K of each subpopulation was estimated as follows: K_{BH} 121; K_{ZZWG} 106; K_{MS} 2,836; K_{BCH} 1,133; K_{QFS} 204; K_{GGS} 227.

Catastrophe: In this study we assumed only one kind of catastrophe, bamboo die-off, which has a great impact on the Giant Panda, and occurs once in about every sixty years (LI 1997), i.e., its frequency was 1.67%.

Dispersal: We varied dispersal in order to learn how it affects population dynamics by simulating dynamics under different dispersal rates, different probabilities of disperser survival and different dispersal ages. We selected five groups of data to explore the effect of dispersal on population dynamics (Table 2).

Iterations: We allowed 1000 iterations per set of parameter values.

The number of years to predict: Each simulation was run for 100 years.

RESULTS

Dynamics of each subpopulation without dispersal

Without dispersal, the values of the stochastic population growth rate (stoc-r) would be negative for four of the six sub-populations. The values of stoc-r for sub-pops BH, ZZWG, QFS and GGS would be, respectively, -0.021 , -0.023 , -0.014 and -0.018 . Corresponding values for relative genetic diversity would be 0.5047, 0.6163, 0.7166 and 0.6793. Over the next 100 years, all four sub-populations would lose much more than 10% of their current genetic diversity and each would face a probability of extinction much higher than 2%. It is generally agreed that any long-term population management strategy should aim for an annual extinction probability less than 2%, while maintaining more than 90% of current genetic diversity (JIANG 1997). Only two sub-populations would have non-negative values of stoc-r and acceptable maintenance of genetic diversity over the next 100 years: Minshan (stoc-r = 0.003, relative diversity = 0.9788) and BCH (stoc-r = 0.000, relative diversity = 0.9536). If no large variation occurs in the environment, these two subpopulations could survive indefinitely (Table 3).

Table 3. Dynamics of six subpopulations without dispersal

	stoc-r	SD(stoc-r)	PE	GeneDiv	SD(GD)	N-all	SD(N-all)
BH sub-pop.	-0.021	0.144	0.9	0.5047	0.1325	0.94	2.92
ZZWG sub-pop.	-0.023	0.142	0.94	0.6163	0.0915	0.82	3.75
MS sub-pop.	0.003	0.044	0	0.9785	0.0062	504.97	238.97
BCH sub-pop.	0	0.049	0	0.9536	0.02	213.51	110.97
QFS sub-pop.	-0.014	0.1	0.44	0.7166	0.1423	14.99	21.73
GGs sub-pop.	-0.018	0.118	0.68	0.6793	0.1535	6.21	15.25

Note: stoc-r, SD, PE, GeneDiv and N-all are abbreviations of stochastic population growth rate, standard deviation, probability of extinction, gene diversity, and final average population size, respectively, with the same meanings in later tables

Population dynamics with different dispersal rates and probabilities of disperser survival

We modeled the dynamics of the Minshan metapopulation under several different dispersal rates (1%, 2%, 4%, 8%, 16%) combined with several different probabilities of disperser survival (1, 0.9, 0.8, 0.7, 0.6, 0.5). The results indicate that the genetic diversity of BH sub-pop increased to over 90% if the dispersal rate were just 1% and was relatively insensitive to higher rates of dispersal. At the dispersal rates of 1% and 2%, the BH sub-pop keeps increasing even if the probability of survival of dispersers is only 0.5 (Fig. 2). The genetic diversity of the larger MS sub-pop shows little variation with respect to dispersal rate (Table 4). However, metapopulation size can decline as a result of dispersal, through disperser mortality. Unless the probability of survival of dispersers is quite high (greater than 0.9), even a low dispersal rate (2%) can result in the decline of Minshan metapopulation size (Fig. 3). Therefore we must find a trade-off between the dispersal rate and the probability of survival of dispersers so that we can not only guarantee the maintenance of genetic diversity but also ensure the rise in the size of the metapopulation.

At the same time, we want to ask how local population sizes, combined with dispersal, affect metapopulation dynamics. To answer this question, we simulated a metapopulation consisting of six very small sub-populations (each $N=10$), with a dispersal rate of 1% and 100% survival of all dispersers. The result shows that all six of these subpopulations would die in 100 years. So we can see that the factors facilitating small population development (population growth and maintenance of genetic diversity) are not just the exchange of genes, but also the absolute population size. MS sub-pop and BCH sub-pop have a relative larger population size than the other four subpopulations and they contribute more individuals to those small

Table 4. Comparison of genetic diversity maintained under different dispersal rates, assuming 90% survival of dispersers

	no disperser	dispersal rate				
		1%	2%	4%	8%	16%
BH sub-pop	0.5047	0.9558	0.9611	0.9562	0.9329	0.8105
MS sub-pop	0.9785	0.9696	0.9678	0.961	0.9359	0.8534

subpopulations even when they have the same dispersal rate, so it is possible for the smaller populations to increase continuously. On the contrary, MS sub-pop and BCH sub-pop have negative values of stoch-r when dispersal is greater than 2%, even if the Minshan metapopulation shows an increasing trend (Table 5).

Effects of the sex of dispersers on metapopulation dynamics

We explored the effect of the sex of dispersers by allowing only males, only females, or both sexes to disperse. Assuming a 90% survival rate for dispersers and a 2–8% dispersal rate, female-only or male-and-female dispersal results in metapopulation decline while male-only dispersal results in a positive metapopulation growth rate (Fig. 4). Assuming 4% dispersal and a 100% survival rate for dispersers, results are the same as above (Fig. 4).

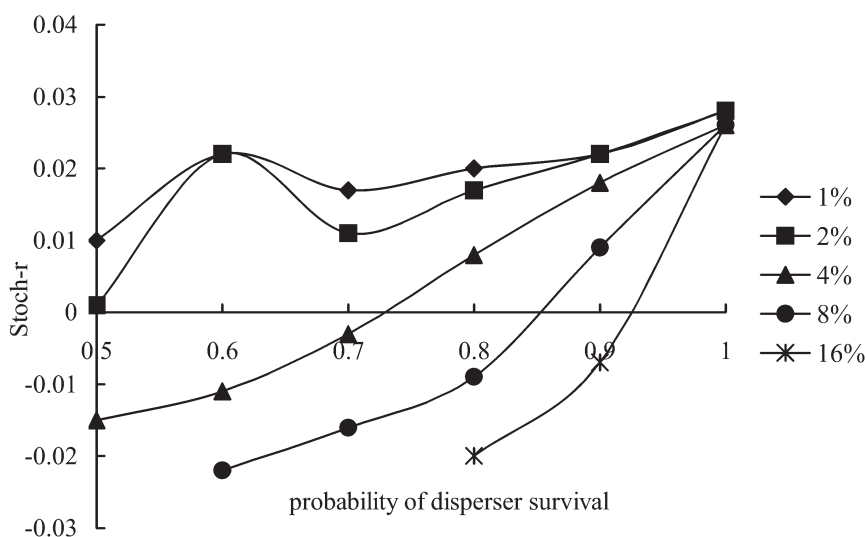
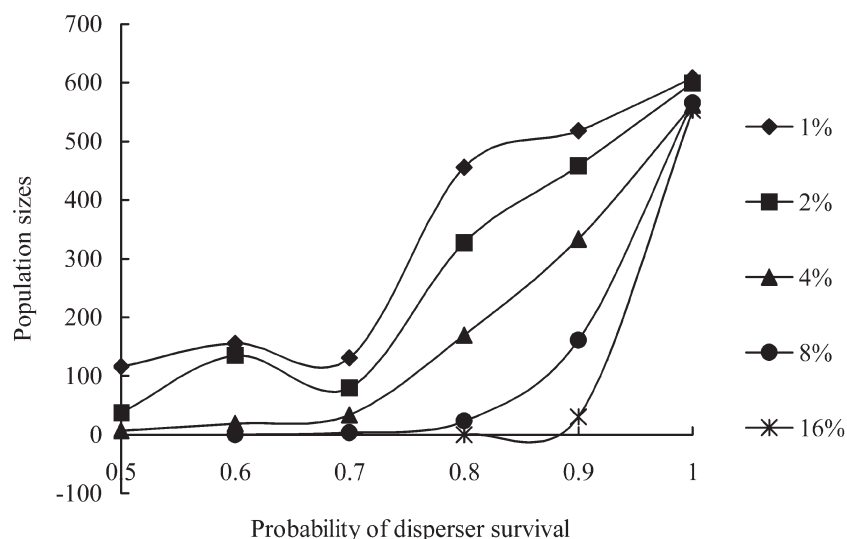
**Fig. 2.** Stoch-r of Baihe subpopulation with different dispersal rate and probability of disperser survival. Curves 1%, 2%, 4%, 8%, 16% represent different dispersal rates

Table 5. Hypothetical dynamics of a Giant Panda metapopulation consisting of six, initially very small populations, simulated for 100 years, assuming 1% dispersal

Population	Initial pop. size	stoc-r	SD(r)	PE	N-all	SD(Nall)	GeneDiv	SD(GD)
sub-pop01	10	-0.018	0.165	0.91	1.27	4.69	0.6851	0.1411
sub-pop02	10	-0.018	0.163	0.89	1.27	4.29	0.7043	0.172
sub-pop03	10	-0.017	0.168	0.88	1.01	2.95	0.6648	0.1387
sub-pop04	10	-0.019	0.163	0.95	0.5	1.86	0.651	0.1231
sub-pop05	10	-0.02	0.163	0.93	0.77	3.6	0.6782	0.1035
sub-pop06	10	-0.02	0.154	0.89	1.54	4.92	0.673	0.1123
Metapop	60	-0.032	0.098	0.73	6.36	14.08	0.7319	0.1306

Effects of the age of dispersers on metapopulation dynamics

Changing the range of ages of dispersing males, from 2–22 years to 2–6 years of age, brought about little change in the population dynamics under the same condition of dispersal rate and probability disperser survival. The values of stoc-r under these two scenarios are respectively 0.002 (SD 0.033) and 0.003 (SD 0.036), which do not differ according to Z test ($Z = 0.0205$, $P > 0.05$). Since the assumption of the model was that all of the adults can breed, changing the dispersal age has nearly no influence on the population (Fig. 5).

**Fig. 3.** Minshan metapopulation size in 100 years, assuming different dispersal rates and probabilities of disperser survival. Different curves correspond to different dispersal rates, as shown in the legend

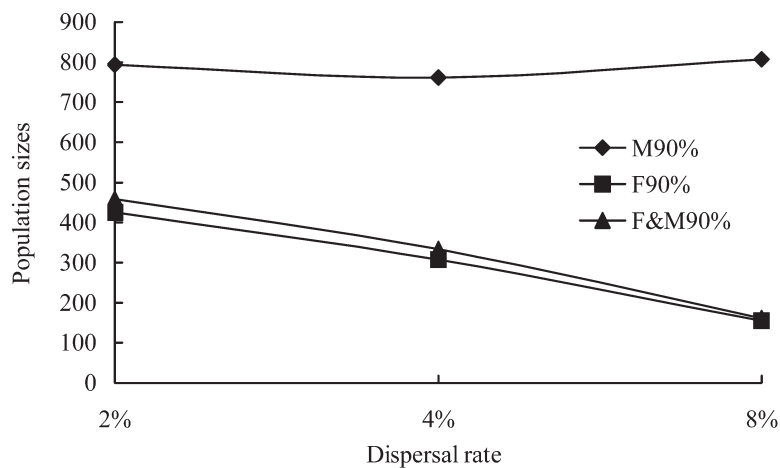


Fig. 4. Population size of different sexes dispersing with 90% survival of dispersers in 100 years. M90%, F90% and F&M90% indicate dispersal of only males, only females, or both sexes, respectively

The Minimum Viable Population (MVP) for the Giant Panda

It has been theorized that the effective population size (N_e) can not be less than 50 individuals to ensure population survival over the short term and N_e can not be less than 500 to ensure survival over the long term (FRANKLIN 1980). But there are no “magic” numbers for population survival (SIMBERLOFF 1988). Now

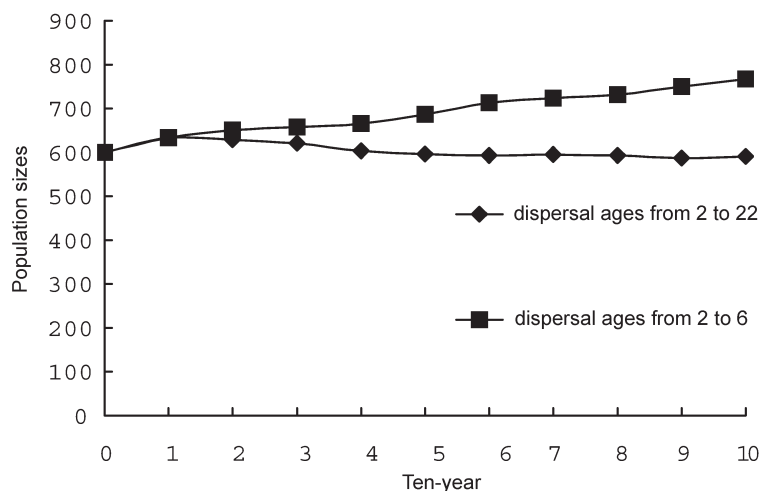


Fig. 5. Population dynamics in 100 years when changing range of dispersal ages, assuming only males to disperse

Table 6. Population dynamics with different initial population size

Initial pop.	size(N0)	stoc-r	SD(r) PE	N-all	SD(Nall)	GeneDiv	SD(GD)
50	-0.006	0.077	0.08	39.61	32.66	0.817	0.091
60	-0.006	0.074	0.05	53.32	45.39	0.8376	0.0863
70	-0.004	0.068	0.04	63.47	46.57	0.8622	0.0733
80	-0.004	0.063	0.01	71.08	51.99	0.8836	0.0597
90	-0.003	0.061	0	93.08	61.71	0.891	0.079
100	-0.002	0.059	0.01	105.15	74.53	0.9086	0.0456
110	-0.002	0.057	0	121.26	82.38	0.9194	0.0384
120	0	0.055	0.01	142.4	88.32	0.9311	0.0385
130	-0.001	0.054	0.02	148.49	93.19	0.9356	0.0291
140	0.001	0.051	0	173.49	89.16	0.9443	0.0195

researchers hypothesize that the minimum viable population (MVP) is determined by three basic elements (SHAFFER 1987): (1) any stochastic effects on the population; (2) the duration of the conservation project; (3) the degree of population security desired. Only the first element can be determined with certainty; the second and third elements are influenced by the social economy. Because the time limit and viability criterion are changeable, and because different species have different population traits, genetic characteristics, ecological environments and degrees of threat, there is no universal MVP can be fit to each species. Under the condition that the probability of extinction (PE) of Giant Panda is lower than 0.02 and its genetic diversity (GeneDive) is higher than 0.9, we want to find a minimum viable population of Giant Panda that can survive for 100 years. In order to determine this MVP, we simply varied initial population size and simulated the dynamics of these populations for 100 years by use of VORTEX software. From Table 6 we selected the population size most fit for the criterion. The results show that when the population is initiated with at least 100 individuals not only its PE is lower than 0.02 (PE = 0.01) but also its genetic diversity is higher than 0.9 (GeneDive = 0.9086, SD = 0.0456). Assuming that the population is in stable age distribution, when 40 percent of all individuals should be breeding individuals, the minimum effective population size (N_e) of the minimum viable population should be at least 40 individuals.

DISCUSSION

For the Giant Panda, we find that the minimum viable effective population size is at least 40 breeding individuals. A population of this size should maintain a low probability of extinction ($P < 0.02$ over 100 years) and should maintain high

genetic diversity (> 90% of current diversity maintained over 100 years. Within the Minshan metapopulation, the size of BH sub-pop, ZZWG sub-pop, QFS sub-pop and GGS sub-pop are lower than this MVP. Assuming no dispersal, the four subpopulations will go extinct in 100 years. The size of N_e is important for the development of a population and it really decides whether the population will increase. It is not enough to just investigate the size of a wild population. We must also know about its population structure and age distribution. In this way we can correctly estimate whether the population will survive for long or go extinct soon. However, we know little about many population parameters of the wild Giant Panda at present, so more work should be done in this field. Results of the simulations show that a small population can increase if there are dispersers within the current metapopulation, even if the dispersal rate is 1%, so it is important to supply immigrant Giant Panda individuals to little populations. If the probability of survival of dispersers can not reach 100%, the Minshan metapopulation size will go down with the increase of the dispersal rate. Why? There may be two reasons. 1) If a significant fraction of dispersing individuals die, then an increase in dispersal rate increases the rate of population loss. 2) As dispersal increases, fewer individuals are located within breeding habitats, resulting in lower rates of reproduction, which is only hypothetical. It is meaning to explore the correlation between the dispersal time spent outside of breeding habitats and the reduced reproduction. Therefore importance should not be attached to increasing dispersal rate but to ensuring high probability of survival of dispersers. In the polygynous system of the Giant Panda, the male plays an important role in dispersal. To limit the dispersal of the female and increase that of the male can promote the development of the metapopulation. Probably a high proportion of male dispersal will not only guarantee genetic exchange, but also prevent the case in which the reproduction rate declines because females die during dispersal. Consideration should be given as to how to control the proportion of males vs. females dispersing among populations, even though it is difficult to do. From the 1950's to the present, the habitats of the Giant Panda have showed a high rate of decrease, and over 75 percent of the total habitat has been reduced during the past 50 years (HU 2000). In fact, it has been difficult for each subpopulation in the Minshan Mountains to have genetic exchange with other subpopulations. BH sub-pop, ZZWG sub-pop, QFS sub-pop and GGS sub-pop may soon be extinct, while MS sub-pop and BCH sub-pop may continue to survive. However, if habitat reduction continues and there is no dispersal among populations, MS sub-pop and BCH sub-pop might face extinction soon. Habitat restoration and construction of "corridor belts" may improve prospects for the Giant Panda and other conservation targets (HU 2000, SHEN *et al.* 2002). But with limited funds and time, measures can not to be taken in all directions. From

our simulation we can see that the main factor facilitating a small population's development is the absolute size of that small population, while dispersal among small populations does not enhance their size or persistence. According to this phenomenon, some criteria for the construction of "corridor belts" must be put forward. That is to say, we should first set up connections between a small population and a large population, which can quickly enlarge the small population. No time and funds need to be wasted to connect two small populations except when there is no bigger population nearby. To enhance the entire Minshan metapopulation, we may place emphasis on connecting BH sub-pop and MS sub-pop, ZZWG sub-pop and MS sub-pop, QFS sub-pop and BCH sub-pop. Because GGS sub-pop is located in the southern end of the Minshan Mountain, it can only be connected with QFS sub-pop for enhancing genetic diversity (Fig. 1). Simultaneously, "corridor belts" must fit the local environment of the Giant Panda.

Finally, there are many parameters of wild Giant Panda population growth which we know little about. This makes it very difficult to predict population dynamics by use of PVA. Thus, we must emphasize the need to collect population parameters for the wild Giant Panda effectively and accurately. However, given limited resources, we must also determine which parameters are most important to population growth. By analyzing the sensitivity of Giant Panda population growth to each population parameter in turn, we can determine how best to allocate limited resources.

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REFERENCES

- AKCAKAYA, H. R. & SJOGREN-GULVE, P. (2000) Population viability analysis in conservation planning: an overview. *Ecological Bulletins* **48**: 9–21.
- BEISSINGER, S. & WESTPHAL, M. I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**: 821–841.
- BOYCE, M. S. (1992) Population viability analysis. *Annual Review of Ecology and Systematics* **23**: 481–506.
- BROOK, B. W., CANNON, J. R., LACY, R. C., MIRANDE, C. & FRANKHAM, R. A. (1999) Comparison of the population viability analysis packages GAPPS, INMAT, RAMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*). *Animal Conservation* **2**: 23–31.

- BROOK, B. W. (2000) Pessimistic and optimistic bias in population viability analysis. *Conservation Biology* **14**: 564–566.
- BROOK, B. W., M. A. BURGMAN, & R. FRANKHAM (2000) Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. *Conservation Ecology* **4**(1): 6.
- BROOK, B. W., O'GRADY, J. J., CHAPMAN, A. P., BURGMAN, M. A., AKCAKAYA, R. & FRANKHAM, R. (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature* **404**: 385–387.
- BROOK, B. W., BURGMAN, M. A., AKCAKAYA, R., O'GRADY, J. J. & FRANKHAM, R. (2002) Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. *Conservation Biology* **16**: 262–263.
- BURGMAN, M. A. & LAMONT, B. B. (1992) A stochastic model for the viability of *Banksia cuneata* population: environmental, demographic and genetic effects. *Journal of Applied Ecology* **29**: 719–727.
- BURGMAN, M. A., FERSON, S. & AKCAKAYA, H. R. (1993) *Risk assessment in conservation biology*. Chapman and Hall, London.
- CHAPMAN, A. P., BROOK, B., BLUTTON-BROCK, T. H., GRENFELL, B. T. & FRANKHAM, R. (2001) Population viability analysis on a cycling population: a cautionary tale. *Biological Conservation* **97**: 61–69.
- COULSON, T., MACE, G. M., HUDSON, E. & POSSINGHAM, H. (2001) The use and abuse of population viability analysis. *Trends in Ecology and Evolution* **16**: 219–221.
- DENNIS, B., MUTHOLLAND, P. L. & SCOTT, J. M. (1991) Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* **61**: 115–143.
- ELLNER, S. P., FIEBERG, J., LUDWIG, D. & WILCOX, C. (2002) Precision of population viability analysis. *Conservation Biology* **16**: 258–261.
- FIEBERG, J. & ELLNER, S. P. (2000) When is it meaningful to estimate an extinction probability? *Ecology* **81**: 2040–2047.
- FRANKLIN, I. A. (1980) Evolutionary change in small population. Pp. 135–149. In: SOULE, M. E. & WILCOX, B. A. (eds) *Conservation Biology: An evolutionary ecological perspective*. Sunderland, Mass: Sinauer Associate.
- FRYE, R. J. (1996a) Population viability analysis of *Pediocactus paradinei*. Pp. 39–46. In: MASCHINSKI, J., HAMMOND, H. D. & HOLTER, L. (eds) *Southwestern rare and endangered plants*. Proceedings of the Second Conference. Fort Collins, Colorado.
- FRYE, R. J. (1996b) Environmental variability and population viability of a rare cactus. *Bulletin of the Ecological Society of America* **77**: 151.
- GUO, J. & HU, J. C. (1999) Population viability analysis for Giant Panda in Yele area. *Journal of Nanjing Forestry University* **23**(5): 27–31.
- HU, J. C. (1990) Giant Panda behaviour and carrying capacity following a bamboo die-off. *Journal of Sichuan Normal College* **11**(2): 103–113.
- HU, J. C., WEI, F. W., YUAN, C. G. & WU, Y. (1990) *Research and progress in biology of the Giant Panda*. Sichuan Publishing House of Science and Technology, Chengdu, China.
- HU, J. C. (2000) Review on the classification and population ecology of the Giant Panda. *Chinese Zoological Research* **21**(1): 28–34.
- JIANG, Z. G. (1997) *Conservation Biology*. Zhejiang Scientific and Technologic Press, China.
- LACY, R. C. (1997) Important of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* **78**: 320–335.
- LACY, R. C. (2000) Structure of the VORTEX simulation model for population viability analysis. *Ecology Bulletins* **48**: 191–203.

- LANDE, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**: 911–927.
- LI, C. B. (1997) *Research on the staple food bamboo of Giant Panda*. Guizhou Publishing House of Science and Technology, China.
- LI, X-H., LI, D-M. & LU, B-Z. (1994) Population viability analysis of *Nipponia nippon*. *Chinese Biodiversity* **2**(1): 69–77.
- LI, Y-M. & LI, D-M. (1994) Advances in population viability analysis. *Chinese Biodiversity* **2**(1): 1–10.
- LI, Y. M., GUO, Z. W., YANG, Q. S., WANG, Y. S. & NIEMELÄ, J. (2003). The implications of poaching for Giant Panda conservation. *Biological Conservation* **111**: 125–136.
- LUDWIG, D. (1996a) Uncertainty and the assessment of extinction probability. *Ecological Application* **9**: 901–918.
- LUDWIG, D. (1996b) The distribution of population survival times. *American Naturalist* **147**: 506–526.
- LUDWIG, D. (1999) Is it meaningful to estimate a probability of extinction. *Ecology* **80**: 298–310.
- MARRIS, W. E., BLOCH, P. L., HUDGENS, B. R., MOYLE, L. C. & STINCHCOMBE, J. R. (2002) Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecological Applications* **12**: 708–712.
- MENGES, E. S. & DOLAN, R. W. (1998) Demographic viability of population of *Silene regia* in mid-western prairies: relationship with fire management, genetic variation, geographic location, population size, and isolation. *Journal of Ecology* **86**: 63–78.
- MENGES, E. S. (2000) Population viability analysis in plants: challenges and opportunities. *Trends in Ecology and Evolution* **15**: 51–56.
- MILLS, L. S., HAYES, S. G., BALDWIN, C. J., CITTA, J., MATISON, D. C. J. & MURPHY, K. (1996) Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology* **10**: 863–873.
- QIN, Z. S. (1990) Bamboo food resources of Giant Pandas and the regeneration of the bamboo groves in Sichuan. Pp. 103–111. In: HU, J. C. (ed.) *Research and Progress on Biology of the Giant Panda*. Sichuan Publishing House of Science and Technology, Chengdu, China.
- RALLS, K., BALLOU, J. D. & TEMPLETON, A. (1988) Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* **2**: 185–193.
- REED, J. M., ELPHICK, C. & ORING, L. W. (1998) Life history and viability analysis of the endangered Hawaiian Stilt. *Biological Conservation* **84**: 35–45.
- REED, J. M., MILLS, L. S., DUNNING, J. B., MENGES, E. S., MCKELVEY, K. S., FRYE, R., BEISSINGER, S. R., ANSTETT, M. & MILLER P. (2002) Emerging issues in population viability analysis. *Conservation Biology* **16**: 7–19.
- SHAFFER, M. L. (1990) Population viability analysis. *Conservation Biology* **4**: 39–40.
- SHENG, G. Z., LI, J. Q. & ZHANG, M. R. (2002) Suggestions for restoration and reconstruction of degraded ecosystem in Giant Panda habitat. *Journal of Inner Mongolia Agricultural University* **23**(1): 36–40.
- SIMBERLOFF, D. (1988) The contribution of population and community biology to conservation science. *Annual Review Ecology and Systematics* **19**: 473–511.
- SONG, Y. L. (1996) Population viability analysis for two isolated Hainan Eld's deer populations. *Conservation Biology* **10**: 1467–1472.
- STACEY, P. B. & TAPER, M. (1992) Environmental variation and the persistence of small populations. *Ecological Applications* **2**: 18–29.
- TAYLOR, B. L. (1995) The reliability of using population viability analysis for risk classification of species. *Conservation Biology* **9**: 551–558.

- THOMPSON, P. M., WILSON, B., GRELLIER, K. & HAMMOND, P. S. (2000) Combined power analysis and population viability analysis to compare traditional precautionary approaches to conservation of coastal cetaceans. *Conservation Biology* **14**: 1253–1263.
- WEI, F. W. & HU, J. C. (1989) A study on the life table of wild Giant Pandas. *Acta Theriologica Sinica* **9**(2): 81–89.
- WEI, F. W. & HU, J. C. (1994) A preliminary analysis on population viability of Giant Pandas. Pp. 116–122. *In*: Chengdu zoo, Chengdu Giant Panda Reproduction Base (ed.) *Minutes of the international symposium in the protection of the Giant Panda*. Sichuan Publishing House of Science and Technology, Chengdu, China.
- WEI, F. W. & HU, J. C. (1994) A study on inbreeding of wild Giant Pandas in Wolong. *Acta Theriologica Sinica* **14**(4): 243–248.
- ZHANG, Z. J., HU, J. C., WU, H. & HOU, W. R. (2002) An analysis on population viability for Giant Panda in Tangjiahe. *Acta Ecologica Sinica* **22**(7): 990–998.
- ZHOU, Z. & PAN, W. (1997) Analysis of the viability of a Giant Panda population. *Journal of Applied Ecology* **34**: 363–374.

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