Insights into population dynamics of giant pandas gained from studies in North America

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Abstract Although population dynamics of giant pandas Ailuropoda melanoleuca remain poorly known, basic principles can be safely transferred from studies of, and experience with, similar species. Without minimizing the importance of continued study of demographics, genetics, and behavior of pandas, I offer the following generalizations from our understanding of carnivore population biology in North America. First, elasticity analyses confirm that pandas have evolved life histories that prioritize high survival of adult females. In comparison, reproductive rates are unimportant. Increases in survival of adult females will yield approximately 5 times the conservation benefit of proportional increases in reproductive output. Second, under circumstances likely to characterize most panda populations, survival rates of males (even adults) are also relatively unimportant. Thirdly, notwithstanding its well-deserved reputation as a slow breeder, giant panda populations are mathematically capable of growing surprisingly quickly, if habitats (and associated survival rates) allow. Finally, reintroductions of endangered species in western North America remind us of the critical role of maintaining large patches of unfragmented habitat. Wolves Canis lupus, extirpated from the western U.S. before the mid-20th century, have made a rapid and surprisingly painless recovery because wild areas and prey populations remained abundant. In contrast, black-footed ferrets Mustela nigripes, lost from the wild more recently, have encountered great difficulty in becoming reestablished, despite tremendous scientific efforts. It appears that ferrets may simply no longer have sufficient wild habitat (i.e., prey) to persist. The best science will not be capable of saving pandas if sufficient habitat is not available [Acta Zoologica Sinica 50 (4): 662 - 668, 2004].

Key words Giant panda, Ailuropoda melanoleuca, Elasticity, Population dynamics, Reintroduction, Survival

There is little doubt that the giant panda Ailuropoda melanoleuca is among the world’s most endangered species, and that preventing its extinction is a high priority. The task is multi-disciplinary, and will require energy and cooperation from experts, politicians, and non-governmental groups from a wide...
A variety of fields. Of course, the reason for the panda’s plight has little to do with the animals themselves, and much to do with humans: conserving pandas will fundamentally be a job that requires management of people and their activities. Pandas will be only too happy to do their own part.

That said, maintaining a healthy and vigorous panda population can, at least in theory, be reduced to the mathematics of ensuring that reproduction balances or, preferably, more than balances mortality. What humans do (or fail to do) can affect birth and death rates, but it is these rates that ultimately dictate whether any given panda population will increase, remain stable, or decline. In recent years, both theoretical and practical work has enhanced our understanding of these forces, and provided insights into the management and conservation of other wild populations. In this paper, I apply some lessons learned from other cases in North America to the population dynamics of giant pandas.

I have chosen four concepts that have recently been investigated or discussed in conservation of rare mammals in North America, all of which appear to have something to teach us about giant pandas. First, I briefly outline the concept of elasticity, arising from analysis of population matrices. I argue that elasticity analysis suggests that efforts focused on assuring high survival of reproductive females will be much more richly rewarded than will similar efforts placed on improving reproductive rates. Next, I reiterate a concept well-known to theoretical population biologists but often difficult to fathom for those of us more comfortable envisioning populations as aggregations of individual animals than abstracting them into life-tables or matrices: namely, that under a broad range of realistic circumstances, survival rates of males are irrelevant to population growth rate. Third, I attempt to lessen the pessimism that often surrounds discussion of the future of pandas by arguing that there is nothing inherent in their life-history strategy of low reproductive rates that dooms their populations to slow, or no increase. If adult female survival can be kept sufficiently high, even slow-reproducing pandas can increase rapidly enough to help themselves. Finally, I leave the theoretical world behind to provide an overview of some recent reintroductions of rare species in North America. Where natural habitat has been conserved, such reintroductions can succeed. However, where habitat reductions have been the primary reason for the species being rare and such reductions have not been reversed, even the most scientifically and carefully planned reintroductions have met with frustration. I conclude with some lessons for giant panda conservation.

1 Elasticity: investing conservation resources in panda reproduction is poor strategy compared with investing in panda survival

Elasticity analysis is an extension of the commonly-applied Leslie matrix that reveals the effect that a proportional change on a given life-history rate has on the population’s rate of increase \( \lambda \) (Benton and Grant, 1999; de Kroon et al., 2000). It measures how an infinitesimal change in an assumed fixed rate would affect population growth; it becomes less reliable if used to infer the relative effect of large changes on those rates. Formally, it is defined as:

\[
e_{ij} = \frac{a_{ij} \lambda}{\lambda} \frac{\partial \log \lambda}{\partial a_{ij}}
\]

where \( e_{ij} \) = elasticity of the element corresponding with the \( i \)th row and \( j \)th column, \( a_{ij} \) = the element corresponding with the \( i \)th row and \( j \)th column, and \( \lambda \) = the population’s finite rate of increase. Thus, under certain assumptions (Mills et al., 1999), it measures the “importance” of one life-history stage relative to another. Application of elasticity analyses to brown bear Ursus arctos populations in North America has generally revealed that adult (and in some cases, sub-adult) survival rates strongly influence \( \lambda \), whereas reproductive rates (or their constituent elements, probability of breeding and litter size) are relatively unimportant (Harris et al., 2004).

In general, it has been found that for long-lived species with low-reproductive rates, elasticity of survival rates is much greater than for reproductive rates (Taylor et al., 1987; Eberhardt et al., 1994; Hovey and McLellan, 1996; Boyce et al., 2001). Population information for giant pandas is still sparse and not necessarily reliable (Harris and Metzgar, 1993), but attempts have been made to use Leslie matrix and simulation models to project panda population growth rates. To conduct a preliminary elasticity analysis for giant pandas, I used 2 alternative life-table formulations: those from studies in Wolong Nature Reserve (Wei et al., 1989, 1997; Li et al., 2003) and the Foping Nature Reserve (Zhou and Pan, 1997; Pan et al., 2001, 2004). Although both survival/fecundity schedules were based on small sample sizes and may have been influenced by biases in data collection or interpretation (Harris and Metzgar, 1993), I assume here that they provide a reasonable approximation to panda life histories.

I used the life table and matrix projection modules of POPTOOLS (www.cse.csiro.au/cdg/popools/index.htm) to calculate deterministic (and therefore approximate only) estimates of \( \lambda \) and elasticities. (POPTOOLS is a set of functions that can be added to Microsoft Excel and which contains algo-
To generate elasticities for these 2 schedules of giant panda reproduction and survival, I first used POPTOOLS to transform reproductive rates (summarized by $m_x$) to the $F_i$ values required for a Leslie matrix (Taylor and Carley, 1988; Harris and Metzgar, 1993)

Elasticity analyses confirmed the importance of female survival and relative unimportance of reproductive rates in contributing to $\lambda$ for giant pandas. For the Wolong-based population matrix (Wei et al., 1989, 1997; Li et al., 2003), elasticities for survival rates ($s_x$) of subadults (ages 5-7) and adults (ages 8+) were 0.55 and 0.37, respectively, whereas elasticity of the $F_i$ (recruitment) was only 0.08. For the population matrix built for the Foping population (Zhou and Pan, 1997), elasticity for survival of subadult (cub5) pandas was 0.41 and for adults was 0.49, whereas for recruitment ($F_i$) it was only 0.10.

I also used life-table analysis to estimate the effect of increasing (and decreasing) isolated vital rates by 10% (Table 1). These results again demonstrated that proportional changes in panda reproduction (in this case, parameterized by $m_x$ rather than $F_i$) have minor influences compared to the same proportional change in survival. For example, if it were possible to increase reproductive output of a population similar to that modeled for Wolong by 10% over its documented value, $\lambda$ would increase by 0.7%. In contrast, if it were possible to increase survival of adults by 10% over its documented value, $\lambda$ would increase by 4.5%. For the Foping-based model (Zhou and Pan, 1997), the deterministic $\lambda$ associated with a stable age structure is 1.0396. With this growth rate, the population would double in 19 years. Were the reproductive rate ($m_i$) of 0.25/female cub/female/year reduced by 10%, such a population would still increase, albeit at a slower rate, and double in 25 years. However, were the high survival of 0.977 reduced by 10%, population trajectory would reverse, and in 19 years rather than be twice its initial size would instead be only half its initial size (Table 1).

Table 1 Vital rates summarized from 2 published life-history schedules of giant pandas (Zhou and Pan, 1997; Li et al., 2003), and sensitivities of the rates of increase ($\lambda$) to 10% increases and decreases in each rate separately (indicated in bold type)

<table>
<thead>
<tr>
<th>Li et al., 2003</th>
<th>Reproductive rate</th>
<th>Subadult female survival rate</th>
<th>Adult female survival rate</th>
<th>$\lambda$</th>
<th>Percentage change in $\lambda$</th>
<th>Doubling/halving time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Published rate</td>
<td>0.330</td>
<td>0.980</td>
<td>0.867</td>
<td>1.0046</td>
<td></td>
<td>153 +</td>
</tr>
<tr>
<td>Increased by 10%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproduction</td>
<td>0.363</td>
<td>0.980</td>
<td>0.867</td>
<td>1.0123</td>
<td>0.7% +</td>
<td>58 +</td>
</tr>
<tr>
<td>Adult survival</td>
<td>0.330</td>
<td>0.980</td>
<td>0.954</td>
<td>1.0502</td>
<td>4.5% +</td>
<td>15 +</td>
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<tr>
<td>Decreased by 10%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reproduction</td>
<td>0.297</td>
<td>0.980</td>
<td>0.867</td>
<td>0.9962</td>
<td>0.1% -</td>
<td>182 -</td>
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<tr>
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<td></td>
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<tr>
<td>Adult survival</td>
<td>0.330</td>
<td>0.826</td>
<td>0.867</td>
<td>0.9571</td>
<td>4.7% -</td>
<td>17 -</td>
</tr>
<tr>
<td>Zhou and Pan, 1997</td>
<td></td>
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<tr>
<td>Published rate</td>
<td>0.250</td>
<td>0.707</td>
<td>0.977</td>
<td>1.0396</td>
<td></td>
<td>19 +</td>
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<tr>
<td>Increased by 10%</td>
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<tr>
<td>Reproduction</td>
<td>0.275</td>
<td>0.707</td>
<td>0.977</td>
<td>1.0495</td>
<td>1.0% +</td>
<td>15 +</td>
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<tr>
<td>Subadult survival</td>
<td></td>
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<td></td>
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<td>Decreased by 10%</td>
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<tr>
<td>Reproduction</td>
<td>0.225</td>
<td>0.707</td>
<td>0.977</td>
<td>1.0290</td>
<td>1.0% -</td>
<td>25 +</td>
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<td>Subadult survival</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Adult survival</td>
<td>0.250</td>
<td>0.636</td>
<td>0.977</td>
<td>1.0185</td>
<td>2.0% -</td>
<td>39 +</td>
</tr>
<tr>
<td>Zhou and Pan, 1997</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Published rate</td>
<td>0.250</td>
<td>0.707</td>
<td>0.879</td>
<td>0.9658</td>
<td>7.1% -</td>
<td>19 -</td>
</tr>
</tbody>
</table>

Change is calculated as ($\lambda$original - $\lambda$modified)/$\lambda$original, expressed as a percentage. Also shown are the number of years required for a doubling (where $\lambda > 1$) or halving (where $\lambda < 1$) of the population (assuming no change in vital rates).

In general, then, reduction of mortality rates will reap conservation dividends roughly 5 times the size of proportional increase in panda reproduction. It is true that altering one life-history rate may be more diffi-
cult than altering another. Just because subadult or adult survival rates have higher elasticities than reproduction does not necessarily mean that improving survival will be easy or even possible (e.g., Li et al., 2000). However, reproductive rates of bears are usually relatively invariant within any given location, i.e., are not readily influenced by management, so this is probably not a situation in which relatively low elasticity misrepresents the potential for this life-history stage to contribute to population growth. I suspect that survival rates, particularly of adult females, would be quite high in the absence of humans. Thus, any reduction of artificial (i.e., human-caused) mortality or removal will reap large dividends.

2 Male survival may be unimportant for population growth

It is well known among managers of hunted populations usually unulates that populations are much more responsive to mortality of females than males. Less often appreciated by practitioners (even if well-known to mathematically-inclined theorists) is that, under a broad range of reasonable assumptions about how populations operate in the real world, the long-term trajectory of populations with a polygynous mating system is completely unaffected by the survival rate of males. That is, unless certain conditions apply, the rate of growth ($\lambda$) is entirely (not merely primarily) dictated by the survival and reproduction of the female segment of the population. As long as males are numerous enough to impregnate all the females available to breed in any year, their survival rate does not affect population trajectory. It is the survival rate of females that will determine how fast the population will grow.

This is easily shown mathematically but can still be difficult to embrace intuitively. Even if we have no problem understanding that females are the only animals that become pregnant, must not the mortality rate for males have some influence on $\lambda$, even if small? To see why it might not, I offer the following heuristic example (Fig. 1).

Imagine a highly-productive population of imaginary bears ($Ursus$ spp.) in which females produce, on average, 0.4 female cubs/year beginning in their 3rd year. After survival in the initial 2 years at 70% per year, constant annual survival is 0.92 for females and 0.85 for males until age 16, at which point survival declines. Such a population will increase at about 5.3% per year, and be about 55% females (Fig. 1A). Now imagine that annual survival of 2+ year-old males suddenly plummets from 0.85 to 0.50 (i.e., each year half the subadult and adult males die). It is natural to imagine that such high mortality for a long-lived animal would have a depresssing effect on the rate of increase. And indeed it does for a few years only, as the male : female ratio equilibrates to the new reality (Fig. 1B). But as soon as this equilibration has taken place, the overall population growth rate reverts to the original 5.3% per year (Fig. 1C). True, it does so from a lower overall level than would have been the case had annual male survival remained at 0.85 (the population now consists of about 65% females), but within a few years, the population is once again thriving (despite half the adult males dying each year). As long as there are sufficient males to impregnate all eligible adult females, cubs keep getting produced (5.3% more each year than the previous year), and half of these will be females (whose annual survival, in this hypothetical example, did not change). So the female portion of the population is entirely unaffected by the calamitous mortality affecting males, and the male portion of the population, after having its age-structure truncated by the increased mortality, follows along at the same 5.3% yearly increase (Fig. 2).

The irrelevance of males to $\lambda$ breaks down under 3 plausible scenarios that could apply to panda population dynamics. First, if the number of males becomes so low that females that are available for breeding are simply not bred, then clearly the number of males present matters. Such an effect, producing a positive correlation between population size and growth rate, could occur if survival of males is low enough that adults simply cannot find each other during estrous. Secondly, the simple model breaks down if reproductive rates or female survival is an inverse function of male density, i.e., if density-dependence (population growth a negative function of population size) is felt across gender lines. In this case, lower survival of males might actually lead to higher $\lambda$. Finally, mortality of males could affect $\lambda$ of the entire population if pandas practice infanticide, and if the probability of infanticide is, in turn, a function of social structure among males (Swenson, 2003).

In very small populations, or where males have become extremely rare, insufficient number of males is a true concern. Where pandas have been studied, however, there is little evidence that eligible females have lacked mates during the appropriate time of year (Pan et al., 2004). For most populations of bears in which anything about density-dependence can be determined, density is likely to affect growth rate only where populations are relatively dense, close to their ecological carrying capacity. There is now some evidence that where bears are totally protected from human exploitation, survival of cubs may decline (Miller et al., 2003). Whether this is a current concern for pandas is unclear. Finally, sexually-selected infanticide (Swenson, 2003) is a theoretical possibil-
Further, males make genetic, not merely demographic, contributions to populations. A highly imbalanced sex ratio, in which only a few males procure a highly disproportionate number of available mating opportunities, can dramatically decrease the effective population size \( N_e \), and thus increase the likelihood of inbreeding or genetic drift (Harris and Allendorf, 1989). As well, mortality of males may indicate undetected mortality of females, which as I argued above, is the driving force behind panda population trajectory. Thus, of course males are important.

But for populations facing an immediate demographic threat, i.e., that there simply aren’t enough animals to sustain themselves, the immediate task is usually to obtain population growth. That is, we desire to achieve \( \lambda > 1 \), the quicker the better. And for the immediate question of increasing \( \lambda \), as long as males are numerous enough to impregnate all females available to breed in any year, their survival rate is unimportant. It is the survival rate of females that will determine how fast the population will grow.

3 Does low reproductive rate doom panda populations to slow increase?

There is no question that pandas are relatively slow breeders, and that rates of increase of panda populations are therefore constrained. But a constrained or slow rate of increase does not necessarily mean that there is a “genetic problem” (Cao, 2004), that no increase at all is possible, or that, with truly effective measures in place, we cannot expect to see substantial increases. For example, when I combined survival rates used by Zhou and Pan (1997) with a mean reproductive rate of 0.25 female cub/adult female/year for females aged 5-19 (and half that for females aged 4), the expected growth rate was almost 4%/yr. Obviously this rate would only be achieved under conditions in which the available habitat was capable of supporting more than the existing population. But under such a growth rate, a population of 100 would increase to about 142 by the 10th year, and double in about 18 years.

4 If a panda population is lost, can it be successfully reintroduced using captive animals?

One rationale for emphasizing captive breeding of pandas is that they may eventually be released back into the wild. Experience with large mammal reintroductions in China is limited (Jiang, 2004). However, two recent carnivore reintroductions in the U.S. offer some useful lessons. Both the wolf \( Canis lupus \) and the black-footed ferret \( Mustela nigripes \) are con-
sidered endangered in the U. S., and receive federal protection. Both species were almost completely exterminated in the western states by the mid-20th century. However, the prey base for wolves (large artiodactyls, such as Odocoileus spp., Cervus elaphus, and Ales alces) had been well conserved, not only in national parks but also in publicly owned areas used for other resources and private lands. In contrast, rodents of the genus Cynomys—prey species upon which black-footed ferrets are wholly dependent—had experienced a dramatic decline, to the point where one species, C. ludovicianus, had even been categorized as worthy of endangered species protection itself. In the mid 1990s, U. S. federal agencies sponsored reintroductions of both wolves (in Yellowstone National Park, and in wilderness areas of central Idaho), and ferrets (in the best protected Cynomys spp. populations in Arizona, Montana, South Dakota, Utah, and Wyoming). Wolf reintroductions were conducted quickly and without much scientific preparation; wolf packs from Canada were captured by helicopter, and simply let go (in Idaho) or kept in on-site pens for a few months prior to release (in Yellowstone). In contrast, ferret reintroductions were preceded by years of careful captive breeding, and all reintroduced animals were carefully screened.

By 2002, it was clear that these 2 reintroductions had fared dramatically differently. Although wolves were feared and disliked by many rural residents, their populations had increased dramatically (U. S. Fish and Wildlife Service, 2003). In Yellowstone, 31 wolves introduced in 1995-1996 had by the year 2002 increased to 217. In Idaho, 35 wolves introduced during the same 2 years had increased to 263. Including wolves in Montana (some of which originated from residents), the total population in 2002 was approximately 663, and government officials had begun the process of changing their status from endangered.

In contrast, the ferret reintroduction programs experienced continual frustration. Despite exhaustive, research—researched captive breeding programs (Vargas et al., 2000), new populations formed from captive-bred individuals did not sustain themselves. At only 1 of 7 reintroduction sites in the U. S. had the ferret population increased. At the 6 other sites, the release of a total of 1,272 captive-reared ferrets (in addition to ferret kits born in the wild to these animals) had resulted in a total wild population of only 137 in the year 2002 (R. Matchett, U. S. Fish and Wildlife Service, Lewistown, Montana, USA, personal communication, 2003). The one successful population had among the largest Cynomys populations.

There are numerous possible reasons for the different outcomes of these 2 reintroduction programs. In particular, success in ferret reintroduction was complicated by the advent of plague Yersinia pestis, which had not been native to North America but by the late 20th century had become a major mortality factor for Cynomys spp. on which ferrets depend. Even accounting for the effects of plague, however, a strong correlation was found between survival rates of ferrets and the extent of their habitat (i.e., size of colonies of Cynomys spp.). In other words, where habitat for ferrets (Cynomys spp. populations) remained in large, relatively contiguous patches, the reintroduced ferret populations could succeed. Where wild habitat patches were small, the best laboratory science was incapable of overcoming those natural limitations. By contrast, wolves increased—despite local fears, occasional poisoning, and the removal each year of a number of livestock-killing wolves by federal agents—because their habitat (native ungulates) remained healthy. Wolves released were also wild animals, and had spent negligible time in captivity. In contrast, released ferrets (even those subjected to a pre-release "acclimatization" period) were all captive-born.

5 Implications for pandas

I conclude from these examples that emphasis on panda reproduction is misplaced. In general, it requires about 5 additional cubs to compensate for the loss of a single adult female. Put another way, efforts put toward allowing a given female to live in the wild until its natural death would produce 5 times more positive effect on a population than would producing a single additional cub. There has been too much em
phasis placed on the panda’s low reproductive rate (Cao, 2004). It certainly is low, but pandas have evolved a life-history strategy in which limited reproductive capability is balanced by relatively long lifespan.

Research on captive pandas is certainly valuable and has contributed important insights for conservation of wild populations. However, if reintroduction or augmentation of wild populations is envisioned, North American experience suggests that even the most rigorous captive rearing program may encounter frustration if wild habitats have become too limited. Focus on captive rearing is understandable: results may come relatively quickly, and one has the satisfaction of working with the animals themselves. But both theory and practice suggest that the largest contributions toward ensuring preservation of wild pandas will come from limiting human-caused mortality or removal of females, and ensuring that panda habitats remain as large and healthy as possible (Hu and Wei 2004). This will require creative and energetic efforts, because merely creating legal protection is evidently not sufficient (Liu et al., 2001, 2004); the social and economic conditions of local people also need to be addressed.

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References


