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# Allocating Scarce Resources for Conservation of Endangered Subspecies: Partitioning Zoo Space for Tigers

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**Abstract:** *All remaining subspecies of tigers (Panthera tigris) are endangered in the wild and space for captive breeding in western zoos is limited. How should this space be allocated to enhance survival and retention of genetic variation in the face of uncertainty about genetic relationships among tiger subspecies and about the future of tigers in the wild? We solicited expert judgments on subspecies population trends and on the ratio of effective to census size in captivity and analyzed different scenarios for dividing the 1000 captive spaces among four tiger subspecies. To maximize survival and retention of gene diversity in individual subspecies, it is best to divide the space equally among the four subspecies. To maximize retention of gene diversity for the species as whole, it is better to allocate more space to the subspecies that appears most variable on the basis of limited electrophoretic data (P. t. tigris). Allocating half of the captive space to tigris and dividing the remainder equally among the other three subspecies is a satisfactory compromise between species welfare and subspecies welfare that ensures survival of all four subspecies (at least in captivity) and retains about 80 percent of existing gene diversity within subspecies and about 93 percent of diversity for the species as a whole. Sensitivity analyses showed that our recommendations were robust to uncertainty about the demographic and genetic status of tiger subspecies. For other species with several endangered subspecies, such as rhinos, resource limitations*

**Resumen:** *Todas las subspecies que quedan del tigre (Panthera tigris) se encuentran en peligro de extinción en su estado salvaje y en el espacio para la crianza en zoológicos occidentales es limitado. ¿Cómo debería ser asignado este espacio para asegurar la sobrevivencia y la retención de la variación genética de la especie? El estado actual de las subspecies de tigres es incierto en lo que se refiere a las relaciones genéticas y al futuro de los tigres en estado salvaje. Nosotros solicitamos el juicio de experto 1) en la tendencia de poblaciones de subspecies, 2) en la relación entre el tamaño efectivo y 3) de los censos en cautiverio. También analizamos el escenario de dividir los 1000 espacios en cautiverio entre cuatro subspecies de tigres. Para maximizar la sobrevivencia y retención de la diversidad genética en subspecies individuales, es preferible el dividir el espacio de igual manera entre las cuatro subspecies. Para maximizar la retención de la diversidad genética para la especie como un todo, es mejor el asignar más espacio a las subspecies que aparecen más variables sobre las bases de datos electroforéticos limitados (P. t. tigris). Asignando la mitad del espacio en cautiverio a tigris y dividiendo el restante igualmente entre las otras tres subspecies es un compromiso satisfactorio entre el bienestar de la especie y de las subspecies que asegura la sobrevivencia de todas las cuatro subspecies (por lo menos en cautiverio) y retiene cerca del 80% de la diversidad genética existente dentro de las subspecies y cerca del 93% de diversidad para la especie como un todo. Análisis de sensibilidad mostraron que nuestras recomendaciones fueron sólidas a la incertidumbre acerca del estatus demográfico y genético de las subspecies de tigres. Para otras*

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may be too severe to permit an easy compromise between species and subspecies welfare and acquiring better genetic data becomes critical.

## Introduction

Many endangered species exhibit geographic variation formally recognized by subspecies designation. Modern taxonomists reserve subspecific names for geographically restricted populations that differ consistently over a number of characters (e.g., size, pelage, skeletal measurements). Many previously named subspecies, however, differ in only one or a few characteristics; these may not correspond to geographic distribution and may show little concordance with other variable traits (Wilson & Brown 1953). For other species, geographic variation with adaptive significance for local populations has no formal taxonomic designation. Whether recognized by taxonomy or not, the genetic basis and adaptive significance of differences among subspecies and geographic races are often unclear. Yet, conservation of intraspecific variation is an important part of efforts to preserve diversity (Chambers & Bayless 1983).

Resources for conserving diversity are limited (Soulé et al. 1986) and scarce resources must be allocated among a subset of the species and subspecies needing help. Because information on the population and genetic status of endangered species and subspecies is limited and the outcomes of management decisions uncertain, it is rarely obvious how to do this. The distribution of space for captive breeding of tiger (*Panthera tigris*) subspecies in North American and European zoos is a case in point. We will show how a combination of decision analysis, expert judgment, and sensitivity analysis can be used to extract the most from limited demographic and genetic data to guide managers of tiger subspecies in captivity.

## Current Status of Tigers

Tigers were once distributed throughout Asia. Eight or more subspecies were recognized on the basis of size, pelage, and skeletal dimensions (Herrington 1987). Habitat destruction and conflict with humans have reduced the wild population to five subspecies, all endangered. The map in Figure 1 shows the approximate distributions and current estimates of the numbers of each subspecies in the wild and in captivity (Seal et al. 1987). Because there are no short-term prospects for conserving *amoyensis* outside of China, we excluded this subspecies from our analysis.

especies, con varias subespecies en peligro, tales como rinocerontes, las limitaciones de recursos pueden ser demasiado severas para permitir un compromiso sencillo entre el bienestar de especies y subespecies y el adquirir mejores datos genéticos comienza a ser crítico.

The genetic structure of the surviving tiger subspecies is known only from limited electrophoretic analysis of blood proteins from captive tigers (Newman et al. 1985; O'Brien et al. 1987; S. O'Brien, unpublished data; Appendix). Genetic diversity in tigers is typical for mammals; the total expected heterozygosity, 0.036, is the same as the mean  $H$  from a survey of 46 mammalian species (Nevo 1978).  $F_{ST}$ , a measure of between-subspecies genetic divergence (Crow & Kimura 1970), is 0.073. The low  $F_{ST}$  value means that tiger subspecies differ very little genetically, less than one-third the divergence seen among human racial groups and less than half the separation among lion populations in Africa (O'Brien et al. 1987).

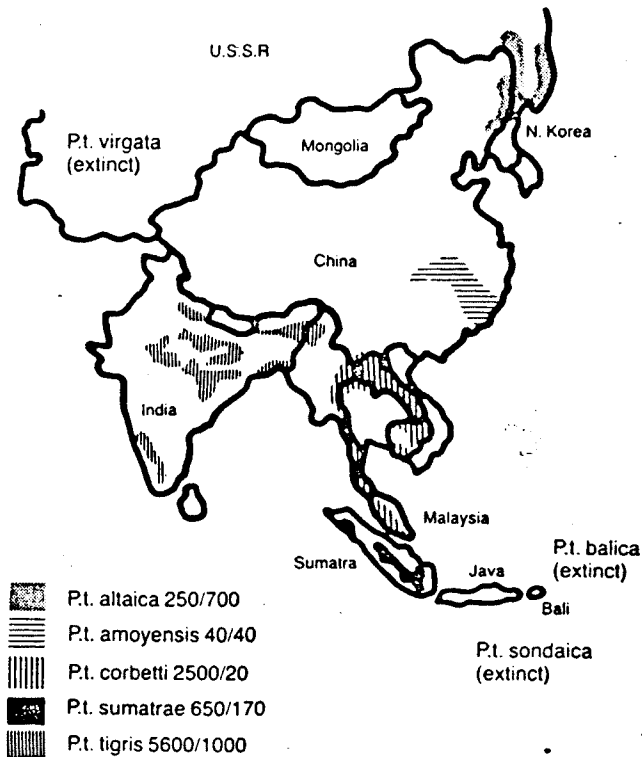


Figure 1. Current geographic distribution and population status of *Panthera tigris* subspecies. Estimated wild population/estimated captive population in zoos worldwide after Seal et al. (1987). (Map modified from R. L. Tilson and U. S. Seal, editors. 1987. *Tigers of the World*, with permission of Noyes Press, Park Ridge, New Jersey.)

## Captive Management of Tigers

The tiger Species Survival Plan (SSP) is a coordinated captive management program intended to maximize the contribution that western zoos can make to conserving tigers worldwide. A committee of experts recommends allocations of available space among tiger subspecies and prescribes schedules of breeding exchanges and demographic management to meet captive conservation objectives.

The representation of the four subspecies in the world captive population is far from equitable (Fig. 1). About 700 of the 1000 or so SSP spaces for tigers are occupied by *altaica* and most of the rest by *tigris* or *tigris*  $\times$  *altaica* crosses. This situation is partly the result of a conscious effort to use captive resources to bolster a subspecies severely imperiled in the wild, and partly the accidental outcome of the success of the captive breeding program for *altaica*. Recently, concern about threats to *sumatrae* in the wild prompted zoo managers to consider converting some spaces currently occupied by *altaica* to *sumatrae*. This suggestion accords with the conventional wisdom that captive programs should place highest priority on taxa that are least likely to survive in the wild.

But is this the best way to use zoo space for tiger conservation? All tiger subspecies are endangered in the wild, captive space is limited, and the taxonomic validity of and genetic relationships among subspecies are unclear. What is the best allocation of captive space among subspecies to support the overall goal of preserving tigers?

## Objectives and Criteria for Tiger Conservation

To optimally allocate captive space among tiger subspecies, we must identify specific conservation goals. We focused on three: (1) maximizing the number of subspecies surviving, whether in the wild or in captivity; (2) maximizing genetic diversity at the species level; and (3) maximizing genetic diversity at the subspecies level. We chose a 200-year time frame (about 32 tiger generations) to match the recommendation of Soulé et al. (1986) for long-term conservation plans.

The first objective assigns value to individual subspecies without regard for the taxonomic or genetic validity of subspecies designations. Maintaining individual subspecies focuses attention on geographic isolates, which helps to maintain the geographic distribution of tigers in the wild. Recognizing the uniqueness of tiger populations in their countries of origin motivates sociopolitical support for conservation programs that benefit not only tigers, but other species and habitats as well. The success of Project Tiger in securing reserves and

controlling poaching, especially in India (Panwar 1987), is a good example. The second objective ensures that the species as whole retains enough variation to maintain fitness in captive and wild environments (Ralls & Ballou 1983; Allendorf & Leary 1986). The third objective combines elements of the first two. It preserves variability in all four subspecies, but allows greater variability in one to be exchanged for lower variability in another.

Several metrics for assessing genetic variation have been proposed (e.g., total heterozygosity, allelic diversity, inbreeding coefficients), all of which have some drawbacks in calculation and interpretation (Hedrick et al. 1986; Fuerst & Maruyama 1986; Lacy 1987). We used the panmictic index ( $P_t$ ), which measures the fraction of initial heterozygosity retained at time  $t$ , to measure retention of gene diversity for individual subspecies and for the species as a whole (Crow & Kimura 1970; see Appendix for calculations).

## Allocating Captive Space

The problem then is to allocate the 1000 captive spaces among the four tiger subspecies in a way that best meets the objectives outlined above. Success in meeting the objective of subspecies survival requires that either the wild or the captive population (or both) remain large enough over the 200-year planning period to avoid extinction. Success in meeting the objectives for retention of genetic variation at the species and subspecies levels requires that the combined captive and wild populations of each subspecies have a genetically effective size as large as possible.

Effective population sizes in the wild and in captivity are influenced by both biological and sociopolitical events over which wildlife managers have only partial control. In the wild, effective population size depends on preservation of suitable habitat, mortality from natural and human causes, movements of tigers among isolated subpopulations, and other stochastic events. In captivity, effective population size depends on the allocation of captive space among subspecies, and on the ratio of effective to census size ( $N_e/N$ ) achieved through management of captive reproduction and mortality (Seal 1986).  $N_e/N$  in captivity depends partly on biological factors, such as the distribution of births and natural deaths, but also on institutional and sociopolitical factors, such as cooperation in breeding exchanges and public and professional reaction to culling captive tigers.

The decision tree in Figure 2 summarizes the factors affecting how well alternative allocations of captive space achieve tiger conservation goals. The decision node (square) represents the choice of captive popula-

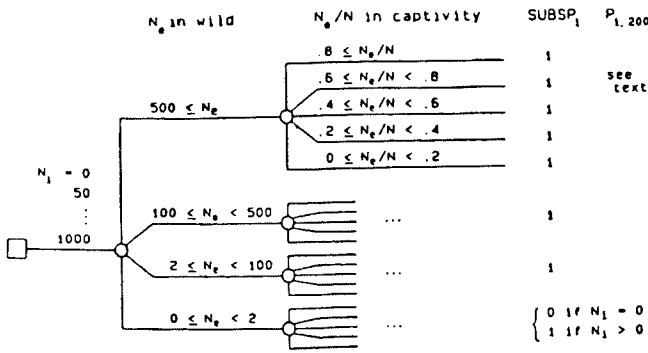


Figure 2. Decision tree for selection of subspecies captive population sizes ( $N_c$ ) under uncertainty about subspecies effective population size in the wild ( $N_e$ ) and about the ratio of effective to census population size in captivity ( $N_e/N$ ).  $SUBSP_i$  = number of subspecies surviving;  $P_{1,200}$  = panmictic index, the proportional gene diversity of subspecies  $i$  after 200 years of captive management.

tion size for each subspecies. The random nodes (circles) represent uncertainty about effective population sizes in the wild and in captivity. Values to the right of the terminating branches of the tree show the impact of each combination of captive and wild effective population size on subspecies survival and genetic variability.

Since these effective population sizes are uncertain, the best we can do to anticipate their impacts on subspecies survival and genetic variation is to estimate the probability of each scenario and use these probabilities to weight the possible outcomes. We elicited probabilities from a group of experts on tiger biology and management using procedures similar to those described by Behn and Vaupel (1982). These probabilities reflect the experts' knowledge of current conditions affecting tigers in the wild and in captivity and their best judgments about natural and cultural factors that will influence tiger populations over the next 200 years. The Bengal tiger (*tigris*) has greater numbers in the wild, better habitat protection, and better representation in western and Indian zoos than the other subspecies. The status of the Indochinese tiger (*corbettii*) is very uncertain due partly to political instability; only about twenty are in captivity, none in western zoos. The Sumatran tiger (*sumatrae*) is in great jeopardy; several hundred remain in habitat increasingly threatened by resource exploitation and human population growth. Moderate numbers are scattered among western zoos. The Siberian tiger (*altaica*) lingers in forest reserves in north-eastern Russia and China, where conflict with human activities outside the reserves is increasing. Breeding of this subspecies in western zoos has been very successful, with the captive population several times as large as the wild. The experts' "optimistic," "realistic," and "pessimistic" interpretations of these events are re-

flected in the probabilities in Table 1; the "pessimistic" consensus was that all subspecies would be extinct in the wild within 200 years.

We elicited probabilities for the  $N_e/N$  ratio in captive populations from a group of experts on captive breeding (Table 2). Recent estimates of the  $N_e/N$  ratio in captive tiger populations range from 0.2 to 0.4 (Flesness & Cronquist-Jones 1987; Ballou & Seidensticker 1987). We are uncertain how difficult it will be to raise  $N_e/N$  above this level through more careful captive management.

Both effective population size in the wild and the ratio of effective to census size in captivity will fluctuate over the next 200 years. The long-term effective size of a fluctuating population may be approximated by the harmonic mean of the population sizes over time, so the sizes listed in Tables 1 and 2 may be viewed as harmonic means of the fluctuating populations.

### Calculating Subspecies Survival and Genetic Variability

For a given subspecies, each combination of captive population size, effective population size in the wild, and ratio of effective to census size in captivity represents a scenario for which we can calculate subspecies survival and retention of genetic variability at the subspecies level (see Appendix). Expected values for subspecies survival and genetic variability were obtained by weighting each scenario by its probability. Not surprisingly, larger captive population sizes improve both survival and retention of variability. If there were no constraints on total captive population size, the best strategy would be to have 1000 (or more) of each sub-

Table 1. Probability that the harmonic mean of subspecies effective population sizes ( $N_e$ ) in the wild over the next 200 years falls within certain ranges. Probabilities derived from consensus of expert opinion using methods of Behn and Vaupel (1982). T = *tigris*; A = *altaica*; S = *sumatrae*; C = *corbettii*.

$N_e$ in Wild	Probability			
	Subspecies			
	T	A	S	C
Optimistic				
$N_e > 500$	0.1	0.0	0.0	0.0
$100 < N_e < 500$	0.4	0.0	0.0	0.2
$2 \leq N_e < 100$	0.4	0.5	0.3	0.5
$0 \leq N_e < 2$	0.1	0.5	0.7	0.3
Realistic				
$N_e > 500$	0.0	0.0	0.0	0.0
$100 < N_e < 500$	0.05	0.0	0.0	0.0
$2 \leq N_e < 100$	0.1	0.0	0.05	0.05
$0 \leq N_e < 2$	0.85	1.0	0.95	0.95
Pessimistic				
All subspecies extinct in wild.				

Table 2. Probability that the ratio of effective to census population size ( $N_e/N$ ) in captivity falls within a certain range.

Captive $N_e/N$	Probability
$N_e/N > .8$	.05
$.6 < N_e/N \leq .8$	.15
$.4 < N_e/N \leq .6$	.5
$.2 < N_e/N \leq .4^*$	.2
$0 \leq N_e/N \leq .2$	.1

\* = current level (Ballou & Seidensticker 1987; Flesness & Cronquist-Jones 1987). Probabilities derived from consensus of expert opinion. Assumed to be identical for all subspecies.

species, ensuring survival of all subspecies and retention of more than 96% of the genetic variation in each. Unfortunately, zoo space is limited, and the 1000 spaces must be divided among the four subspecies.

To evaluate what combinations of captive population sizes totaling 1000 best meet the conservation objectives, we combined the expected values for subspecies survival and gene diversity over the four subspecies for several captive management strategies to obtain the number of surviving subspecies (SUBSPP); the average gene diversity retained within subspecies ( $P_w$ ); and the gene diversity retained by the species as a whole ( $P_T$ ) (Tables 3 and 4; see Appendix for calculations).

The values of the subspecies-level criteria ( $P_w$  and SUBSPP) are independent of genetic structure, but retention of variation at the species level under different allocations of captive space ( $P_T$ ) depends on the distribution of variation within and between tiger subspecies. We can see the possible impact of genetic structure by first looking at two extremes: (1) no alleles shared by the four subspecies, and (2) all subspecies genetically identical. The first case, where the variation in each subspecies is unique, is adequately covered by criterion  $P_w$ , which assigns equal weight to the variability expressed in each subspecies, regardless of how variable each subspecies is or how many unique alleles each carries. In the second case, where all subspecies are genetically identical, allocation of space among subspecies is irrelevant from a genetic perspective and the nongenetic considerations are adequately covered by

criterion SUBSPP, which assigns equal value to the survival of each subspecies. Neither of the two extremes is at all likely, although the low  $F_{ST}$  value from electrophoretic studies suggests that the genetic structure of tigers is closer to the second extreme than to the first.

We can use these electrophoretic results to make a best guess at retention of genetic variability by the species as a whole ( $P_T$ ), based on subspecies population sizes (in the wild and in captivity) and on the initial levels of heterozygosity within each subspecies. Subspecies with larger effective population sizes and with higher initial levels of heterozygosity (e.g., *tigris* with  $H_0 = 0.041$ ) have a greater impact on retention of variation in the species as a whole because they have more variation to lose than do subspecies with lower initial levels of heterozygosity (e.g., *altaica* or *sumatrae* with  $H_0 = 0.015$  and  $0.014$ , respectively).

### Evaluating Allocation Strategies

We used expected values of the three criteria (number of surviving subspecies, SUBSPP; average gene diversity within subspecies,  $P_w$ ; and species gene diversity,  $P_T$ ) to rank different strategies for allocating the 1000 captive spaces among the four tiger subspecies (Table 3). Allocation strategies with the largest representation of *tigris* in the captive population are best for maximizing genetic variation in the species as a whole ( $P_T$ ), but they are poor for maximizing variability and survival of individual subspecies ( $P_w$  and SUBSPP) (S1, S2 vs. S3, Table 3). If fewer than four subspecies can be accommodated in the captive program, including the most variable subspecies, *tigris* and *corbetti*, it is most important for maximizing  $P_T$  (S1 vs. S4, S5 vs. S6, Table 3). Since these subspecies are the ones most likely to survive in the wild (Table 1), this recommendation contradicts the conventional wisdom that captive programs should emphasize species or subspecies least likely to survive in the wild. This contradiction arises because none of the tiger subspecies are likely to survive in large numbers in the wild; the primary hope for retaining diversity lies in the captive populations. Maintaining the most variable

Table 3. Combined expected values of the three decision criteria for "realistic" probabilities of subspecies survival in the wild.  $P_T$  = gene diversity retained by the whole species after 200 years;  $P_w$  = average gene diversity retained by individual subspecies after 200 years; SUBSPP = number of subspecies surviving after 200 years.  $N_i$  = captive population size of subspecies *i*.

Strategy	$N_i$				Expected Values		
	T	A	S	C	$P_T$	$P_w$	SUBSPP
S1	1000	0	0	0	1.08	0.26	1.1
S2	850	50	50	50	1.06	0.59	4.0
S3	250	250	250	250	0.75	0.84	4.0
S4	0	0	1000	0	0.42	0.28	1.2
S5	500	0	0	500	0.95	0.47	2.05
S6	0	500	500	0	0.46	0.50	2.2
S7	550	150	150	150	0.93	0.80	4.0
S8	700	100	100	100	1.00	0.73	4.0

Table 4. Combined expected values of the three decision criteria for "optimistic" probabilities of subspecies survival in the wild. Headings as in Table 3.

Strategy	$N_i$				Expected Values		
	$T$	$A$	$S$	$C$	$P_T$	$P_W$	SUBSPP
S5	500	0	0	500	0.97	0.62	2.8
S9	333	333	0	333	0.88	0.74	3.3
S6	0	500	500	0	0.67	0.79	3.6
S4	0	0	1000	0	0.66	0.66	3.1

subspecies in captivity preserves greater diversity for the species as a whole than allocating space to the less diverse subspecies.

In contrast, strategies that include all four subspecies in equal numbers (S3, Table 3) maximize survival and variation for individual subspecies ( $P_W$  and SUBSPP), but do not maximize variation for the species as a whole ( $P_T$ ). If it is necessary to omit one or more subspecies from the captive program, it is best for  $P_W$  and SUBSPP to omit those with the best chances for survival in the wild, i.e., *tigris* (S6 vs. S5, S4 vs. S1, Table 3). This contradicts the strategy for maximizing  $P_T$ , where it is best to omit those subspecies with lowest variability (which are also those least likely to survive in the wild).

In compromising between maximizing retention of variability at the species level and at the subspecies level, we placed a high priority on survival of all four subspecies and restricted our attention to strategies which include all four in the captive program. Deviating from approximately equal numbers of the four subspecies in the direction of including more *tigris* increases  $P_T$  substantially, with only modest drops in  $P_W$  (S7, S8, S2, Table 3). Perhaps the best compromise is strategy S7, which allocates a little more than half the captive space to *tigris*, with the remainder divided equally among the other three subspecies. This strategy retains about 93% of the genetic variation currently represented in the species, an average of about 80% of the variation in each subspecies, and assures the survival of all four subspecies, at least in captivity.

## Discussion

Since our results are based on limited and uncertain information on tiger genetics and population dynamics, it seems prudent to ask under what circumstances our recommendations could prove misleading. The first source of error we will consider is uncertainty about the fate of wild tiger populations over the next 200 years, as represented by the range of probabilities in Table 1. The results reported in Table 3 are based on the "realistic" probability estimates for effective population size in the wild. In general, results from the "optimistic" probabilities give higher values for all three criteria (Table 4), and results from the pessimistic scenario, where all sub-

species become extinct in the wild, give slightly lower values. The patterns of response and recommendations for allocation do not change. One interesting exception to this generalization is that, under the "optimistic" probabilities, some strategies allocating space to larger captive populations of fewer subspecies are better for both subspecies survival and subspecies gene diversity than strategies which include more subspecies at smaller population sizes. For example, 1000 *sumatrae* (S4, Table 4) gives higher  $P_W$  and SUBSPP than does 500 *tigris* plus 500 *corbetti* (S5, Table 4); and 500 each of *altaica* and *sumatrae* (S6, Table 4) gives higher  $P_W$  and SUBSPP than 333 each of *tigris*, *altaica*, and *corbetti* (S9, Table 4). In these cases, limiting captive programs to the subspecies least likely to survive in the wild (*altaica* and *sumatrae*) is a better strategy than also including *tigris* and *corbetti*. It is the combination of subspecies survival probabilities and subspecies gene diversities that produces these patterns.

Another possible source of error is our probability distribution for  $N_c/N$  under careful captive management. To explore the impact of different  $N_c/N$  ratios on the three evaluation criteria, we calculated the three measures under fixed values of  $N_c/N$  ranging from 0.2 to 0.5. Within this range, there were few differences in qualitative conclusions about which strategies are best for  $P_T$  versus  $P_W$  and what the best compromises might be.

The last sources of error we will discuss stem from limitations of the genetic data used to estimate the current distribution of variability among subspecies. With only 26 tigers sampled, it is quite likely that failure to identify variation unique to particular subspecies is an artifact and that variation between subspecies is higher than estimated. If so, allocations of captive space should be shifted toward those strategies that maximize subspecies survival and retention of subspecies variation, i.e., allocations that maximize our first two criteria.

Sample sizes of some subspecies may be small enough (e.g., *sumatrae*, with  $n = 3$ ) that some of the apparent differences in variability among subspecies may be due to sampling error. We estimated the likelihood that the more limited variability in the samples from *altaica* and *sumatrae* could have occurred by chance alone when sampling from the same pool of variation exhibited by

*tigris*. This probability is less than 0.001 for *altaica* and about 0.08 for *sumatrae* (G-tests of significant differences in allelic frequencies), indicating that lower variability in *altaica* and *sumatrae* relative to *tigris* cannot be attributed to small sample size.

It is possible that the electrophoretic data do not reflect the distribution among subspecies of genetic traits important to fitness. If the level of variation important to fitness were disproportionately underestimated for subspecies showing lower levels of electrophoretic variation, allocations of captive space should again shift toward those suggested by the subspecies survival and subspecies variability criteria.

The only circumstance in which the electrophoretic data might be truly misleading would be if the less variable subspecies electrophoretically were actually the most variable for traits important to fitness. Such a reversal seems unlikely because the patterns of electrophoretic variation are consistent with those expected from the biogeography and population histories of the different subspecies. The most variable subspecies (*tigris*) is centrally located within the historic range (Fig. 1) and has maintained larger wild populations than the other subspecies. The subspecies with lowest levels of electrophoretic variation (*altaica* and *sumatrae*) are at the extremes of the current distribution. *Sumatrae* is the last island subspecies (the Bali and Javan subspecies having disappeared in recent years) and presumably has been isolated for some time. *Altaica* went through a bottleneck, perhaps as low as 20–30 animals, about 50 years ago. Although our genetic data are admittedly limited, there is little reason to believe that recommendations based on our results would misdirect tiger conservation plans.

### Implications for the Tiger Species Survival Plan

An early version of the analysis presented here showed that excluding *tigris* and *corbetti* from the tiger SSP could undermine retention of genetic variability for tigers as a species and prompted a plan to allocate approximately equal space to each of the four subspecies (U.S. Seal, personal communication). The current analysis suggests that it may be better to tip the balance in favor of *tigris*, despite its relatively well-protected status. Over the next 200 years, even *tigris* is not assured of large enough populations to avert genetic or demographic disaster in the wild. The other three subspecies may well have unique genetic adaptations that should be conserved, but from the standpoint of maximizing genetic diversity for the species as a whole, including *tigris* should be a priority. Opportunities to construct a captive *tigris* population that represents current levels of variation in this subspecies will not last forever; wait-

ing until *tigris* is as imperiled as some of the other subspecies can only jeopardize survival of the species as a whole. Because of biological and institutional inertia in reallocating captive space among taxa, there will be plenty of opportunity to reevaluate the allocation of space (perhaps as a consequence of more complete genetic data), provided that all four taxa are included in the SSP now, and provided that they are managed to maximize retention of variability in whatever subspecies population sizes are initially chosen.

### Implications for Management of Other Species

#### Factors Influencing Tiger Management Strategies

The optimal strategy for allocating captive space among tiger subspecies depends on the goals of tiger conservation and on the details of tiger genetics, taxonomy, and population ecology. Among the factors determining the optimal strategy are: (1) the structure of genetic variation among tiger subspecies populations; (2) the relative probabilities of survival of different subspecies in the wild; (3) the absolute probabilities of subspecies survival in the wild; (4) the size of the captive population relative to that of the wild population; and, (5) interactions between genetic variation within subspecies and probability of survival in the wild. We will not explore the implications of all combinations of these factors here, but we will discuss how our results for tigers can and cannot be applied to conservation of other taxa.

For tigers, there appears to be a tradeoff between maximizing retention of genetic variation for the species as a whole and maximizing retention of genetic variation by individual subspecies. This tradeoff arises because (1) the most variable subspecies, *tigris*, contains all the variation found in the less variable subspecies (at least according to available data); and (2) the most variable subspecies is the most abundant and best protected in the wild and, therefore, least likely to become extinct. The circumstance where all the measured variability for a species is expressed in a single subspecies, and where that subspecies is most abundant and least likely to become extinct, may be common for large, mobile species that once were widely distributed but have been fragmented recently by habitat destruction and exploitation. The apparent conflict between species welfare and subspecies welfare that arises in tiger management may occur for other endangered taxa as well.

For tigers, resources for both captive and wild conservation are relatively abundant. Tigers are popular exhibit animals, and they breed easily in captivity. The amount of zoo space for tigers, although limited, is sufficient to maintain all four subspecies with negligible

risk of extinction of each captive population. Wild tigers have enormous public appeal, evidenced by the millions of dollars contributed to Project Tiger to design and protect reserves in India and Southeast Asia. Because of these resources, the plight of tigers is not nearly so critical as that of many other large mammals. Even the compromise strategies would maintain as much as 80% of the variation for each subspecies and more than 90% of total species variation over 200 years.

#### Impact of Resource Limitations

For many other taxa, resources are more limited relative to the size of the conservation task. For example, there are four genera of rhino worldwide, all threatened or endangered. The African black rhino alone has seven designated subspecies, several of which are probably already extinct. There are about 800 zoo spaces for rhino of all genera worldwide (Cumming 1987). Some rhino species are difficult to breed in captivity, perhaps because they require large social groups (Lindemann 1982). In situations such as these, finding a satisfactory compromise between the welfare of the species as a whole and the welfare of individual subspecies is more difficult. Managers must set clear priorities among evaluation criteria in order to decide which to emphasize. It may be necessary to omit some subspecies from the captive program, or to merge subspecies populations. In these cases, information about the genetic relationships among subspecies is critical.

#### Limitations of Genetic Information

Even the meager data on tiger genetics is more than is available for many endangered species. The very circumstances that make a species endangered — small, fragmented populations in the wild; absence of stable captive populations — make it difficult to obtain the genetic data needed for conservation decisions. Given the limitations on number of animals and number of loci that can be sampled, it may not be possible to demonstrate that a subspecies lacks unique genetic variation. We cannot examine every locus, nor even all loci that promote local adaptation. Indeed, the relationship between the types of variation measured by existing genetic techniques and fitness is so poorly understood that the application of genetic management to conservation is more a matter of principle than of well-tested practice.

Given these pessimistic views on the utility of available genetic information for conservation planning, one direction for future research is to analyze the allocation of resources among subspecies in the face of uncertainty about their genetic relationships. We intend to repeat our allocation analysis for several alternative genetic structures (e.g., some subspecies less variable, but with unique variation; no measurable genetic differences

among subspecies; all subspecies with some unique variation). We also intend to vary other factors that influence the optimal allocation of resources to see which strategies, if any, are robust to changes in genetic and demographic circumstances. Such robust strategies can be used in situations where genetic information is unavailable. In addition, knowing the circumstances in which these robust strategies perform poorly will focus research on those cases where genetic information is most needed to resolve planning dilemmas.

Although this analysis has dealt with the allocation of resources for captive management among endangered subspecies, the issues raised here, and the methods used to address them, are equally applicable to conservation of higher taxa and to management of endangered populations in the wild. Allocating limited resources, coping with uncertainty in the biological and sociopolitical environment, resolving tradeoffs among conflicting objectives, and planning in the absence of complete information are common to most conservation problems.

## Appendix

### Electrophoretic Data for Tigers

Stephen J. O'Brien and colleagues electrophoretically analyzed blood proteins at 50 loci from a small sample of captive tigers (Newman et al. 1985; O'Brien et al. 1987; S. O'Brien, unpublished data). Five loci varied within or among subspecies. Sample sizes and expected heterozygosity for each subspecies ( $H_i$ , expressed as an average across all sampled loci) are as follows: *tigris* ( $n = 9$ ), 0.041; *altaica* ( $n = 14$ ), 0.015; and *sumatrae* ( $n = 3$ ), 0.014. Assuming that the numbers of each subspecies are as shown in Figure 1, and that allele frequencies in *corbetti* equal the averages of the three subspecies that have been studied, the total expected heterozygosity ( $H_T$ ), the weighted mean within-subspecies expected heterozygosity ( $H_W$ ), and the between-subspecies expected heterozygosity ( $H_B = H_T - H_W$ ) are 0.036, 0.033, and 0.0026, respectively.

The most variable subspecies, *tigris*, contains all the allelic variation found in the species at the sampled loci. The two less variable subspecies studied, *altaica* and *sumatrae*, contain subsets of the variation found in *tigris*. Given the current geographic separation among subspecies, each may have unique genetic variants at some unstudied loci. Electrophoresis of proteins from 50 loci (out of perhaps 100,000 protein-coding and regulatory loci in the mammalian genome) provides a good statistical sample for estimating average genetic divergence, but very limited assessment of the genetic variants in each population.

Because no samples were obtained for *corbetti*, we assigned this subspecies the average of the allele frequencies in the other subspecies sampled, then calcu-



lated its heterozygosity based on these average allele frequencies ( $H_i = 0.028$ ). *P. t. corbetti* occupies a geographic range in between *tigris*, *sumatrae*, and *altaica* (Fig. 1). It is thought to be fairly widely distributed in the wild, numbering fewer than *tigris* but more than *altaica* or *sumatrae* (Seal et al. 1987). It seems plausible, therefore, that *corbetti* is intermediate in heterozygosity and allele frequencies between *tigris* and the two less variable subspecies.

#### Calculation of Evaluation Criteria for Individual Subspecies

We imposed a minimum size of 50 for subspecies populations in captivity so that the risk of extinction of the captive subpopulations due to demographic stochasticity would be negligible. A subspecies survives if it is represented in the captive population or if the effective size of the wild population is at least two. The panmictic index at 200 years (32 generations) for each subspecies ( $P_{1,200}$ ) is calculated according to the formula:

$$P_{200} = (1 - 1/2N_e)^{32} \quad (\text{Eq. 1})$$

(Crow & Kimura 1970), where  $N_e$  is the effective population size in the wild plus the product of captive population size and  $N_e/N$  in captivity. (We used the values 0, 50, 250, and 1000 to represent the ranges of effective population sizes in the wild in Table 1; and the values 0.1, 0.3, 0.5, 0.7, and 0.9 to represent the ranges of  $N_e/N$  in Table 2.) We used the probability distributions listed in Tables 1 and 2 to calculate statistical expectations for the subspecies panmictic index ( $P_{1,200}$ ) and subspecies survival (SUBSP<sub>i</sub>) by multiplying the values at each terminating branch of the decision tree by the probability of that branch. (See Behn & Vaupel 1982 and Maguire 1986 for decision tree calculations.)

#### Combining Criteria over the Four Subspecies

To form an overall expected value for number of subspecies surviving, we summed the four  $E(\text{SUBSP}_i)$  values. Each of these can range from 0 to 1, so the possible range for the combined expected value (designated SUBSPP in Tables 3 and 4) is 0 to 4. To form a combined expected value for gene diversity retained by all subspecies (panmictic index:  $P_w$ ), we averaged  $P_{1,200}$  over the four subspecies.  $P_w$  can range from 0 to 1. This measure of within-subspecies gene diversity assigns equal weight to each of the four subspecies regardless of their abundances or initial levels of heterozygosity.

Gene diversity within each subspecies declines at the rate described by Equation 1 above. With  $s$  extant subspecies (equal to or less than four, depending on the choice of captive population sizes), a fraction  $(s - 1)/s$  of the within-subspecies gene diversity that is lost each generation is converted to between-subspecies gene diversity as the subspecies diverge genetically ( $H_{B,t} =$

$H_{B,0} + [s - 1](H_{w,0} - H_{w,t})/s$ ). The total gene diversity ( $H_T = H_w + H_B$ ) decays according to the equation  $H_{T,t} = H_{w,t} + H_{B,t} = H_{T,0} - (H_{w,0} - H_{w,t})/s$ . This calculation ignores the partial separation of the captive from the wild population of each subspecies, which is appropriate if there is occasional migration between the captive and wild populations (Lacy 1987). The loss of diversity will be more rapid if no such interchange takes place. We calculated  $H_{T,t}$  as the expected heterozygosity at time  $t$  for the species as a whole, as if the subspecies populations were mixed and immediately attained Castle-Hardy-Weinberg equilibrium at that point.

After calculating  $H_{T,200}$  for each combination of wild and captive population sizes, we obtained an expected value for  $H_{T,200}$  from the joint probabilities of effective population size in the wild (Table 1) and  $N_e/N$  ratio in captivity (Table 2). Finally, we expressed the expected value for  $H_{T,200}$  as a proportion of  $H_{T,0}$  to obtain  $P_T$ , the gene diversity retained by the species as a whole, as reported in Tables 3 and 4.

Because the captive tiger population is a substantial fraction of the total world population (about 20% currently, and likely to increase as wild populations decline), the relative representation in the captive population of tiger subspecies having different levels of heterozygosity can have a marked impact on  $H_T$  for the species. Allocation strategies that increase or decrease the relative representation of the more variable subspecies from current levels produce an apparent increase or decrease in  $H_T$ , independent of the loss of variation due to drift and inbreeding that will occur over the 200-year period of concern. That is why  $P_T$  values for allocations with large proportions of *tigris*, the most variable subspecies, may exceed 1 (Table 3).

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#### Literature Cited

- Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57-76 in M. E. Soulé, editor. Conservation biology. Sinauer Associates, Sunderland, Massachusetts.
- Ballou, J. D., and J. Seidensticker. 1987. The genetic and demographic characteristics of the 1983 captive population of Sumatran tigers (*Panthera tigris sumatrae*). Pages 329-347 in

- R. L. Tilson and U. S. Seal, editors. *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*. Noyes Publications, Park Ridge, New Jersey.
- Behn, R. D., and J. W. Vaupel. 1982. *Quick analysis for busy decision makers*. Basic Books, New York.
- Chambers, S. M., and J. W. Bayless. 1983. Systematics, conservation and the measurement of genetic diversity. Pages 349–363 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Crow, J. F., and M. Kimura. 1970. *An introduction to population genetics theory*. Harper and Row, New York.
- Cumming, D. 1987. Small population management of black rhinos. Pages 12–13 in R. duToit and T. Foose, editors. *Proceedings of the 1986 Cincinnati African Rhino Workshop*. Pachyderm No. 9, December 1987.
- Flesness, N. R., and K. G. Cronquist-Jones. 1987. Possible selection in captive *Panthera tigris altaica*. Pages 363–370 in R. L. Tilson and U. S. Seal, editors. *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*. Noyes Publications, Park Ridge, New Jersey.
- Fuerst, P. A., and T. Maruyama. 1986. Considerations on the conservation of alleles and of genic heterozygosity in small managed populations. *Zoo Biology* 5:171–179.
- Hedrick, P. W., P. F. Brussard, F. W. Allendorf, J. A. Beardmore, and S. Orzack. 1986. Protein variation, fitness, and captive propagation. *Zoo Biology* 5:91–100.
- Herrington, S. J. 1987. Subspecies and the conservation of *Panthera tigris*: preserving genetic heterogeneity. Pages 51–62 in R. L. Tilson and U. S. Seal, editors. *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*. Noyes Publications, Park Ridge, New Jersey.
- Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology* 1:143–158.
- Lindemann, H. 1982. *African rhinoceroses in captivity*. Ph.D. dissertation. University of Copenhagen, Copenhagen, Denmark.
- Maguire, L. A. 1986. Using decision analysis to manage endangered species populations. *Journal of Environmental Management* 22:345–360.
- Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. *Theoretical Population Biology* 13:121–177.
- Newman, A., M. Bush, D. E. Wildt, D. Van Dam, M. Th. Frankenhuis, L. Simmons, L. Phillips, and S. J. O'Brien. 1985. Biochemical genetic variation in eight endangered or threatened felid species. *Journal of Mammalogy* 66:256–267.
- O'Brien, S. J., G. E. Collier, R. E. Bienveniste et al. 1987. Setting the molecular clock in Felidae: the great cats, *Panthera*. Pages 10–27 in R. L. Tilson and U. S. Seal, editors. *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*. Noyes Publications, Park Ridge, New Jersey.
- Panwar, H. S. 1987. Project Tiger: the reserves, the tigers and their future. Pages 110–117 in R. L. Tilson and U. S. Seal, editors. *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*. Noyes Publications, Park Ridge, New Jersey.
- Ralls, K., and J. Ballou. 1983. Extinction: lessons from zoos. Pages 163–184 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and conservation: a reference for managing wild animal and plant populations*. Benjamin/Cummings, Menlo Park, California.
- Seal, U. S. 1986. Goals of captive propagation programmes for the conservation of endangered species. *International Zoo Yearbook* 24/25:174–179.
- Seal, U. S., P. Jackson, and R. L. Tilson. 1987. A global tiger conservation plan. Pages 487–498 in R. L. Tilson and U. S. Seal, editors. *Tigers of the world: the biology, biopolitics, management and conservation of an endangered species*. Noyes Publications, Park Ridge, New Jersey.
- Soulé, M. E., M. Gilpin, W. Conway, and T. Foose. 1986. The millenium ark: how long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101–113.
- Wilson, E. O., and W. L. Brown, Jr. 1953. The subspecies concept and its taxonomic application. *Systematic Zoology* 2:97–111.