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Siberian Tiger Species Survival Plan: A Strategy for Survival

U.S. SEAL*, T. FOOSE**

ABSTRACT — The wild population of Siberian tigers (Panthera tigris altaica) is estimated at about 300 in six separate populations. Since an effective population size of at least 500 is necessary for long-term survival and evolution, and since the wild populations are not going to be able to expand in their natural habitat, it is evident that a captive breeding program is necessary for sustained preservation of this form. There are 1000 living Siberian tigers in zoos; only three outside of Russia are wild-born. About 250 are in North American zoos. Although about 68 wild-caught animals have been brought into zoos, six animals account for 69% of the founder representation of the living population. The population is inbred with mean F = 0.113, and 70% of the population has a positive inbreeding coefficient. Inbreeding in tigers results in a decrease in life span in animals living longer than one year. The genetically effective population size (N_e) is about 0.35 of the census size (N)when it could be 2N. This is a result of unequal family sizes of both male and female parents. About 50 North American zoos are participating in a tiger Species Survival Plan (SSP) formulated by the American Association of Zoological Parks and Aquariums. An 11-person propagation committee was elected by the institutional representatives to work with the Species Coordinator in developing and implementing the plan. The breeding strategy includes agreements to maintain an effective population of 250 animals, to maintain a demographically stable population and to provide for maximum retention of available genetic diversity by maximizing the N_e in relation to N and minimizing inbreeding. These objectives will be accomplished by introducing new founder stock; equalizing representation of founders; equalizing family sizes, with each animal contributing to the next generation; avoiding inbreeding; avoiding phenotypic selection; producing 10 to 15 litters per year, and removing from the SSP population all animals reaching the age of 13 years if they have made their genetic contribution. A detailed plan specifying by zoo, for each animal, recommended animals to be bred and the year for the matings has been through three revisions and is being used by participants. The plan also identifies animals that are not to be bred for the SSP and the dates all animals are to be considered surplus to the SSP.

Overview: Management for Species Survival

The wild population of Siberian tigers (*Panthera tigris altaica*) is estimated at about 300 individuals in 6 populations (Matjuskin et al. ?1979). Since an effective population size of at least 500 is necessary for long-term survival of a vertebrate species (Frankel and Soule, 1981), it is evident that the wild populations are not viable evolutionary units as currently managed and that a captive breeding program will be necessary for sustained preservation or conservation of this subspecies.

Survival of tigers and other large felid species will increasingly depend upon captive populations and programs. Wild populations are under severe pressures. Habitats are being destroyed and animals are being exterminated. Conservation measures such as the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES) treaty may provide temporary relief, but even where felids survive in the wild, many of the populations are becoming so diminished and fragmented that they are not viable genetically or demographically. Gene pools are being converted into gene puddles (Frankel and Soule 1981; Foose 1983b). Therefore, long-term survival of the large felid species will depend upon management of the animals in captive collections as populations rather than as fragmented units and will involve interactive management with the wild populations where necessary. The goal of a captive management program designed for preservation of a species is "retention of the maximum amount of genetic diversity available in the founder stock" (Foose 1983b). Management programs must be aimed at maintaining an effective population size that is sufficient to allow increased diversity via mutations at a rate at least equal to the loss of diversity by genetic drift and inbreeding. This objective also implies a criterion for termination of a captive program based upon the secure existence of wild populations large enough to allow continuing evolution by natural selection of the species, i.e. conservation (Frankel and Soule 1981).

Two biological problems must be confronted if we are to develop captive breeding programs for the preservation of endangered species. One is an assessment of priorities for the selection of taxa and for allocation of our resources to the taxa in greatest need of sanctuary in zoo-based captive breeding programs — our "arks." The second problem is the management of the collections as biological populations.

In order to fulfill these preservation and conservation objectives, the American Association of Zoological Parks and Aquariums (AAZPA) has committed itself to a Species Survival Plan (SSP). Selection of taxa requires evaluation of the space or habitat available in zoos and aquariums for a taxon and estimation of the minimum size of the captive population necessary for long term servival. Population geneticists have recommended a genetically effective number of 250 to 500 as the absolute minimum for preservation without steady loss of genetic variability by drift and inbreeding (Figure 1).

What does this mean for the number of taxa of felids that can be maintained in our institutions? A first approximation is

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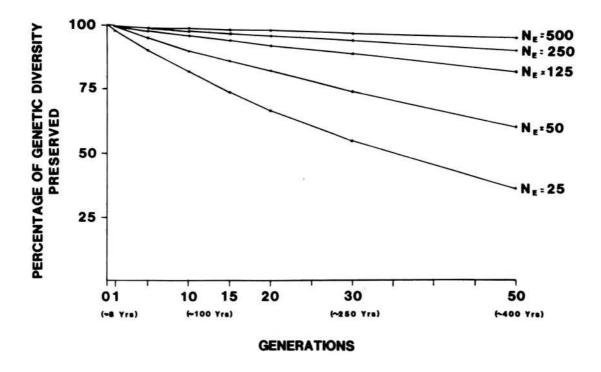


Figure 1. Decline of genetic diversity for various effective population sizes (N_e) if the total number of animals maintained is 250. The generation time of 8 years has been computed from demographic data on Siberian tiger, but is probably applicable to most of the larger felids. Genetic diversity can be measured in terms of either heterozygosity or, somewhat more approximately, heterogeneity (polymorphism).

available from International Species Inventory System (ISIS) data on living mammals in participating zoos. Of about 31,000 specimens of live mammals registered in ISIS, 40% are ungulates, 24% are primates, and 18% are carnivores. About half of the 5640 specimens of carnivores are felids; 2000 of these are large cats (Figure 2).

The strategic and biological management of species requires that there be a minimum basic data set on the populations and on each specimen including individual identification, sex, parentage, birth date, death date, and tracking of animals among institutions. Three sources of data are currently available.

1) The tabulations in the International Zoo Yearbook provide data on populations and births each year for endangered species but lack age, pedigree and other demographic information.

2) International Studbooks are available for 58 species, 5 of which are felids. Many of these books are updated too infrequently for active management of a population. The Studbook for Siberian tigers is an exemplary exception. It is published yearly and is remarkably thorough. It has served as the source of the data for our genetic and demographic analyses of this species.

3) ISIS, housed at the Minnesota Zoo, has been established to facilitate collection of such data for the immense number of species in zoos and to provide timely and accessible compilations of the data necessary for these analyses.

Space or zoo habitat availability for felids may be estimated from these data. Table 1 indicates that the capacity of North American zoos is not sufficient to maintain adequate numbers of the 82 extant or even the 45 endangered species and subspecies of felids. There appears to be space for about 1000 lions and tigers; 725 leopards, jaguars, and pumas; and 175 cheetahs. The low numbers of large felids that can be housed

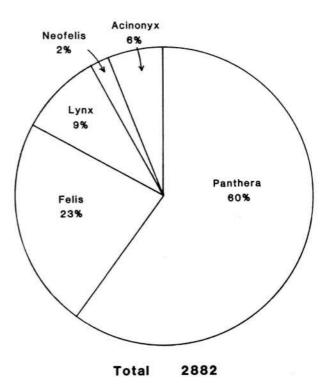


Figure 2. The distribution by genus of specimens of the Felidae in institutions participating in ISIS.

in zoos (1800 to 2000) means that only 7 or 8 taxa (species or subspecies) can be managed for survival if a population size of 250 is be maintained.

We can estimate the number of taxa that could be accommodated at effective population sizes of 100, 250, and 500. For example, there is estimated to be space and resources for about 450-500 tigers. If populations of 250 of each type designated are maintained then only 2 subspecies could be sustained. Since captive habitat is limited, choices will have to be made.

Discussions on criteria for taxon selection are vigorous. Selection of species for the SSP program of the AAZPA is guided by a comprehensive set of criteria that reflect guidelines of the World Conservation Strategy produced by the International Union for the Conservation of Nature and Natural Resources and its component Commissions including the Species Survival Commission (IUCN/SSC). The process considers status in the wild, representation of biological diversity, and feasibility of captive propagation.

A difficult and unresolved topic is recognition and selection of subspecies or forms. The North American captive tiger population now include 250 Siberian, 225 Bengal, 29 Sumatran, and 9 Corbetti specimens. The space problem for tigers is further compounded by the expanding numbers of white tigers which are novelties with great public appeal and thus serve to increase attendance at zoos.

Initial selections for the SSP have concentrated on species that can serve as models for the entire program, represent a diversity of vertebrates, and present a variety of management and biological problems. Thirty-four taxa have been designated for SSP programs. The list includes four large felids: Snow Leopard, Cheetah, Asian Lion, and Siberian Tiger.

Each of the 34 SSP programs is organized around a Species Coordinator assisted by a Propagation Group elected by and from the participating institutions. The AAZPA has also created a position of Conservation Coordinator (Dr. Tom Foose), located in the ISIS offices at the Minnesota Zoo, to facilitate development and operation of these programs.

A memorandum of participation serves to document the commitment of an institution to participate in the program and to breed its animals in accordance with the recommendations of the Species Coordinator and the Propagation Group. The substance of an SSP program is the Population Master Plan. All SSP programs are predicated on multigeneration masterplans for genetic and demographic management derived from data from ISIS, studbooks, and the participants.

The taxa must be managed intensively as biological populations if they are to be propagated and preserved in captivity. Reproduction alone is not enough for either preservation of genetic diversity or demographic stability as is recognized in the SSP. For example, tigers reproduce well in captivity—at one litter every two years for each female, and current mortality rates, the population could expand to 6000 animals in 20 years (Figure 3). However, simply curtailing reproduction

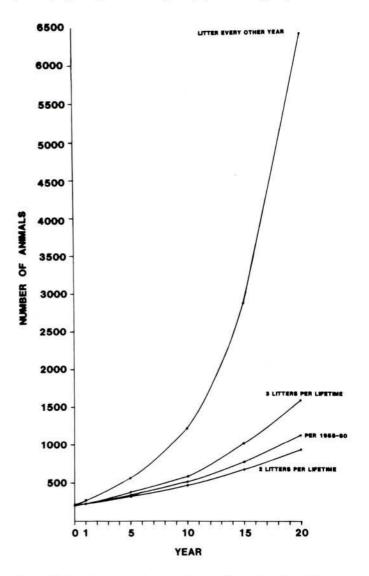


Figure 3. Population projections for the North American Siberian tiger population with several different reproductive strategies and maintaining the current mortality schedule. Note that even limiting reproduction to 2 litters per lifetime still yields growth to 3 times the current population in 20 years.

Species	Living	Subspecies in	Institutions	Population	Subspeciesb		
	Subspecies	Red Data Book	(In ISIS) ^a	(ISIS)	100	250	500
Panthera leo	11	1	97	381	4	1	1
Panthera tigris	8	8	110	450	4	2	1
Lions and tigers	19	9	120	831	8	3	2
Panthera onca	8	8	. 65	178	2	1	0
Panthera pardus	15	15	72	246	2	1	0
Panthera uncia	1 1	1	35	128	1	0	0
Felis concolor	29	2	69	173	2	1	0
"Intermediate cats"	53	26	С	725	7	3	1
Neofelis nebulosa	4	4	20	63	1	0	0
Acinonyx jubatus	6	6	32	166	1	0	0
"Other" large felids	10	10	С	229	2	1	0
TOTALS	82	45		1785	18	7	3

Table 1. Capacity of ISIS-participating captive facilities for large felids.

^a Number of institutions listed in ISIS with this species.

b Number of forms that could be managed as SSP populations for three population sizes.

^c Not calculated.

periodically is not an adequate strategy for either maintaining a stable population or preventing inbreeding.

A Case Study: The Siberian Tiger

The effective management of the Siberian tiger in captivity began with the publication of the first Tiger International Studbook in 1976. The captive population of this subspecies has increased from a few wild-caught animals in 1957 to about 1000 tigers living in zoos and other institutions throughout the world at the close of 1981. About 250 of these animals were living in North American zoos. The data for the following analysis were taken from the seven volumes of the studbook, ISIS, and correspondence with participating institutions.

The studbook registered 977 living animals, 29 of which were living wild-caught animals, as of 31 December 1981. Three of the wild-caught animals were in East Germany and the remainder were in 10 zoos in Russia. There are currently no wild-caught animals in the North American population.

A total of 68 wild-caught animals have entered the world captive population and thus could potentially have served as founders. All appear to have originated from the Russian wild population. Twelve died with no surviving offspring. Nine of the 29 living wild-caught animals have not produced offspring and only three of these animals have offspring outside the Soviet Union.

Thus, the current living captive population of Siberian tigers could have been derived from about 44 animals. If each animal were represented equally its proportion in the population would be 2.5%. However, six animals (studbook numbers 14, 15, 5, 7, 1, and 2) account for 69.4% of the founder representation in the living world captive population (Figure 4). Another 18.9% is derived from six other animals and the remaining 32 animals have contributed only 11.7%.

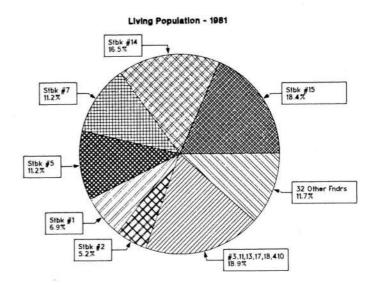


Figure 4. The proportional representation of 44 founders in the world living captive population of Siberian tigers. Note that 6 founders have 69% of the representation.

This represents a major loss of available genetic diversity.

The distribution of founder representation in North America reflects the same excessive representation of 5 of these six founders and includes studbook numbers 17 and 18 as additional major contributors (Figure 5). North American zoos have recently acquired three new animals from the Moscow Zoo, three from China, and three from Leipzig that represent new founder stock for our population.

Inbreeding in the captive tiger population began in 1965 with sibling matings of offspring from the founder stock. The mean inbreeding coefficient(F) has fluctuated around 0.120

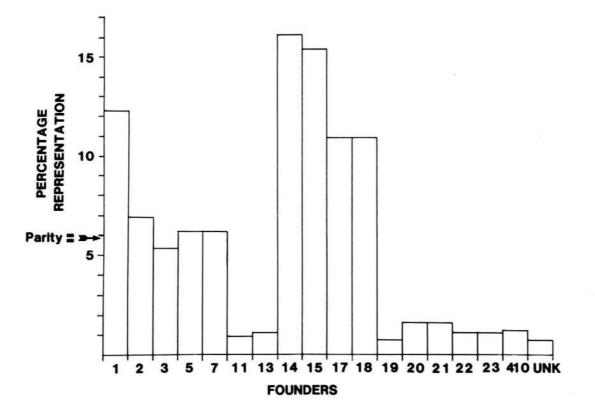


Figure 5. The proportional representation of founders for the North American population of Siberian tiger (*Panthera tigris altaica*).

Founder numbers were assigned by the keeper of the International Studbook for Tigers, Dr. S. Seifert.

since 1968 (Figure 6). About 70% of animals born each year have a positive inbreeding coefficient. This could be reduced to near zero with careful management of the available stock and the introduction of available new founder stock. Inbreeding values (F) that equal or exceed 0.25 in Siberian tigers result in a reduction in life span of animals surviving beyond one year (Seal, unpublished).

One measure of the efficiency of genetic management of a captive population is the effective population size or N_e . This can be understood as a measure of the proportion of genetic representation or genetic diversity present in a population which is transmitted from one generation to the next (Table 2). It is a function of (1) the number of animals which produce offspring which then reproduce, (2) the sex ratio of the breeding population, and (3) the surviving family size of the breeding males and females.

Fluctuations in population size from one generation to the next result in loss of genetic variability. The family size of male and female tigers in the world population and in the North American population has been very variable, and 114

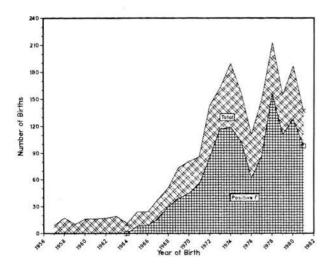


Figure 6. Inbreeding began in 1968. The mean inbreeding coefficient (F) in animals born each year has been about 0.120. About 70% of animals born have an F greater than 0. The mean F in animals with F>0 has been about 0.212 for the world population.

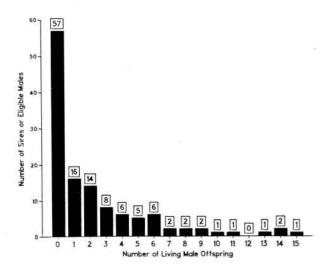


Figure 7. Variation in number of male offspring from male parents. Only males 8 years old or greater were considered for tabulation in the zero offspring category. Table 2. Equations for estimation of effective population size.

Sex ratio effect:	$N_e = \frac{(4 * M * F)}{}$
	N
Family size variance:	N _e = (4N - 2) =
	$\frac{1}{(V_k + 2)}$ $\frac{1}{2 + s^2}$
Effects on heterozygosity:	$H = (1 - 1/2N_{e})^{t}$

animals older than 8 years in the world population have not reproduced at all (Figure 7). This results in an enormous waste of captive resources relative to captive preservation of the species. Calculation of N_e for the world population yields an estimate of 350 for a census population of 1000 with a ratio N_e/N = 0.35. A similar ratio was obtained for the North American population. Thus the efficiency of genetic management has been about 20% in the world and North American populations since it is theoretically possible to achieve a ratio of nearly two.

Demographic management is also essential for captive populations. Evaluation of the demographic status of a population requires knowledge of age and sex structure of the population, the age at death (survivorships), and the age of the dams at the birth of their young (fecundity). In a stable population, the highest proportion of animals is in the younger age classes regardless of the number of animals in the population with a steady decline in the size of older age classes.

The age structure of the world population shows a history of oscillations which will continue if deliberate cooperative management is not established. The North American population, examined at five-year intervals, has varied widely in the number of young born and surviving each year. The current age structure has a number of gaps and reflects a definite favoring of female survival (Figure 8).

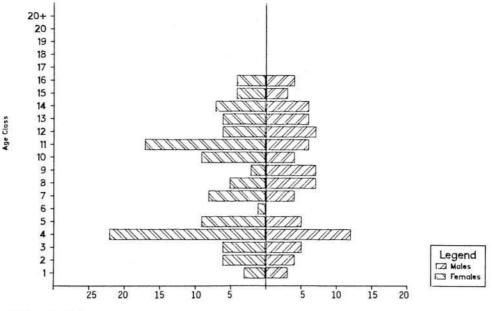
Models for a Stable Population

The demographic parameters calculated from the entire captive history in North America and from data for a recent five-year period were used to construct models for a stable population. The number of litters to be produced were calculated on the basis of a mean of 2.4 young per liter.

The modeling was done using spreadsheet programs such as Visicalc, Supercalc, and Multiplan on microcomputers. These simulations (Figure 9, option 6) indicated that a stable population, with each animal contributing equally to the next generation, would require that (1) each female produce two litters in her lifetime, at about age 4-5 and 8-9 years; (2) all animals older than 12 be removed from the population, and (3) that about 30% of animals of prereproductive age would need to be removed. Many other options were explored but none were more efficient and assured satisfaction of both genetic and demographic requirements for long-term survival.

The choices are not easy but must be confronted if we are to be serious about our commitment to long-term survival or preservation of the Siberian tiger.

In summary, the goal of the North American AAZPA SSP captive propagation plan for Siberian tigers is (1) retention of the maximum amount of genetic diversity available in the founder stock and (2) maintenance of an effective population size of 250. Corollaries are (1) to minimize inbreeding; and (2) to generate and maintain a demographically stable population.



ISIS Data - Age Structure

Figure 8. Age structure of Siberian tigers in North American zoos (according to ISIS and the Studbook) on 1 January 1983.

AAZPA Tiger Management Program

A policy has been developed and endorsed by the AAZPA and a detailed document for the tiger SSP has been developed and approved by the AAZPA. Each of the following specific guidelines for management of the captive population of Siberian tigers has implications for zoo professionals, governing authorities, and interested public. Similar plans are being prepared for about 40 species and several are in operation now. Decisions are required on the fate of healthy animals that become surplus in a species survival plan. It is very important for all participating institutions to develop, through thorough discussions among staff, a policy and guidelines for disposal of surplus animals. Specific SSP genetic and demographic management guidelines for the Siberian tiger are to:

- 1) incorporate new founder stock by:
 - (a) acquiring offspring from unrepresented founders,
 - (b) not breeding new founders with each other,
 - (c) producing litters from new founders with 5 different mates;
- 2) equalize founder representation by:
 - (a) trying to achieve parity within three generations,
 - (b) reducing contributions of over-represented founders,
 - (c) expanding the contribution of under-represented founders;
- equalize family sizes by having each male and female contribute equally to the next generation with an exception made for introduction of new stock or expansion of poorly represented stock;

	OPTION 1	OPTION 2	OPTION 3	OPTION 4	OPTION 5	OPTION 6	OPTION 7	OPTION 8	OPTION S
IF REPRODUCTION	EQUIVALENT TO	ADJUSTED TO COMPENSATE				TWO LITTERS	TWO LITTERS	THREE LITTERS	LITTER OF
IS	1955-80 LITTER SIZE	FOR MORTALITY	2.43 CUBS	3 CUBB	3 CUBS	2.43 CUBB EACH	2.43 CUBB EACH	2.43 CUBS EACH	2.43 CUBS
THEN	2.43 CUBS	DISTRIBUTED OVER AGES	AT ANY AGE	AT AGE 4	AT AGE S	AT AGES 5 & 10	AT AGES 4 &7	AT AGES 4, 9, 12	YEARS
THE REMOVAL OF 0-1 YEAR OLDS REQUIRED FOR STABILITY IS -OR-	46%	0%	THIS LEVEL OF REPRODUCTION APPEARS WEUFFICKENT	PROBABLY 0%	THIS LEVEL OF REPRODUCTION APPEARS INSUFFICIENT	30%	35%	53%	72%
REMOVAL FROM Each age class Required for Stability is	7%	0%	TO SUSTAN POPULATION WITH PRESENT MORTALITY	PROBABLY 0%	TO SUBTAM POPULATION WITH PRESENT MORTALITY	4.85%	7.75%	9.5%	15.5%
	7.75 YEARS	7 YEARS	WEL VARY	4 YEARS	5 YEARS	7 YEARS	7 YEARS	7.5 YEARS	7.5 YEARS
									TABLE 5

Figure 9. Nine options for demographically managing Siberian tigers to stabilize the population at a carrying capacity of 250. Each option represents a different combination of restricting reproduction and removing animals. Generation time is a function of the age-specific survivorships and fertilities and hence varies as management is modified from option to option.

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- avoid selection for genotypes or phenotypes: if an animal survives to reproductive age do not select for or against size, configuration, zoo adaptable behavior, stripe patterns, clinical disorders, or phenotypic defects;
- 5) manage for a demographically stable population by:
 - (a) allowing each animal to produce only two litters, at about ages 4-5 and 8-9;
 - (b) removing all animals from the population that are older than 12 years and have made their genetic contribution (about 12 animals per year when the population is stabilized);
 - (c) removing up to 30% of animals in the pre-reproductive age classes each year (this may be about 6-8 one-yearolds when the population is stable);
 - (a) removing animals from the current population which are castrate, have already made their genetic contribution, are in the older age classes, or are from over represented lineages (this includes about 40 living animals).

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