action or directing further study. in the first example, different probabilities of extinction of *bicornis, minor,* and *michaeli* were used to show how the decision strategy might change. In the second example, sensitivity of the decision to the probabilities of outbreeding depression, of survival in the wild, and of successful establishment of separate captive populations can help identify the circumstances under which semicaptive management would be better than zoos.

A structured analysis shows where additional information about chance events could reduce uncertainty and lead to a better decision. Genetic analyses of rhino subspecies can help reduce uncertainty about outbreeding depression in mixed populations, guiding the sampling of geographic regions for founders of captive and semicaptive populations and the merging of these populations in the future.

Tradeoffs among conflicting criteria, particularly between financial and biological criteria, are typical of endangered species management decisions. The two examples presented here raise the difficult question of how the value of obtaining founder animals from the northern-western subspecies of black rhino should be weighed against the difficulty and expense of doing so.

in addition to the two questions addressed by these preliminary examples, many other rhino management decisions might benefit from formal analysis:

(i) Under what circumstances is wild, intensive *In situ,* or *ex situ* management best? Among the criteria to be used for this decision are: biological impacts, including disruption of behavioural adaptations or coadapted gene pools; political impacts on local and national support for conservation; socio-economic impacts on local economies; and likelihood of sub-species survival.

(ii) How many founders are required to justify maintaining a separate subspecies population? At what point should some subspecies populations be merged for semicaptive or captive management? Among the issues here are the genetic and demographic risks of few founders weighed against the irreversibility of merger.

(iii) What are the optimal strategies for translocating animals among semicaptive and/or captive populations? Which sexes and ages should be moved, what size groups, how frequently? The concerns here are the relative genetic and demographic contributions of different sexes and ages, social disruption caused by moving animals, risks of mortality during and after translocation, financial cost, and hazards of inbreeding in isolated populations. Some of these issues are addressed in Maguire (1986) and in previous analyses of translocations to augment grizzly bear populations (Maguire, unpublished report to U.S. Forest Service).

(iv) What are the risks and benefits of ongoing exchanges of animals, or genetic material, among captive, semicaptive and wild populations? Social disruption, impact of removals, transmission of disease, risks of injury or death to individual animals, disruption of local adaptation, and loss of genetic variation from drift and inbreeding are among the considerations here.

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SMALL POPULATION MANAGEMENT OF BLACK RHINOS
Session Chairman DAVID CUMMING

STATUS OF BLACK RHINOS IN THE WILD

The black rhino has declined more rapidly over the past 20 years than any other large mammal. In 1970 there were about 65 000 black rhinos in Africa; the total is now under 4 000, a decline of 94%. The population sizes in the various African countries within this decade are roughly as shown in Table 3. The remnants of a number of the populations are scattered as individuals or in very small groups over vast areas. For instance, the estimated 200 rhinos remaining in the Selous Game Reserve of Tanzania are dispersed over 55 000 km^2.

The recent decline of the species is due almost entirely to commercial poaching for rhino horn. The decline in South Africa, due to natural factors in the Umfolozi-Hluhluwe complex, appears to be the one exception (the 1984 figure was probably an overestimate). In the early 1980's about half of the horn put onto the world market went to North Yemen where it is used for making dagger handles, while the remaining half went to eastern Asia for the production of traditional medicines. Most of these rhino horn mixtures are produced because they are believed to lower fevers, not

because of alleged aphrodisiac properties. North Yemen has recently strengthened some controls on the import and use of rhino horn, so there may be changes in the relative importance of the markets.

Prices for African rhino horn have risen from about $30 per kg wholesale in 1970 to about $900 per kg today. Asian rhino horn is believed to have more potent medicinal properties and therefore commands much higher prices in eastern Asia. To halt and reverse the precipitous decline in the numbers of black rhinos will require concerted action by many individuals and organisations. International, national and local conservation efforts will be most effective and make the best use of scarce resources if they are part of a planned campaign. To achieve this coordination of effort, a broad framework of policies on rhino conservation (i.e. a continental rhino conservation strategy) must be agreed upon by the principal agencies involved, and plans of action ——with clear priorities ——must also be elaborated in line with—these policies, and kept updated as the black rhino situation changes. The African Elephant and Rhino Specialist Group (AERSG) is currently developing a continental black rhino conserva-

Table 3. Status of black rhinos in Africa.

	1980	1984	1987	% of total 1987 rhino population
Tanzania	3 795	3130	270	7%
C.A.R.	3 000	170	10?	0.2%
Zambia	2 750	1650	110	3%
Kenya	1 500	550	520	14%
Zimbabwe	1 400	1 680	1 760	46%
South Africa	630	640	580	15%
Namibia	300	400	470	12%
Sudan	300	100	3	—
Somalia	300	90	?	—
Angola	300	90	?	—
Mocambique	250	130	?	—
Cameroon	110	110	25?	0.7%
Malawi	40	20	25	0.7%
Rwanda	30	15	15	0.4%
Botswana	30	10	10	0.2%
Ethiopia	20	10	?	—
Chad	25	5	5?	—
Uganda	5	—	—	—
TOTAL	**14 785**	**8 800**	**3 800**	

tion strategy, and has been producing annually-revised action plans for the conservation of rhinos and elephants.

In discussing the draft strategy, an emphasis that emerged from the workshop was the need for interactive management of wild and captive populations in order to maintain genetic variability. However, it was agreed that *ex situ* breeding programmes should avoid mixing rhinos from different regions of Africa in order not to destroy probable adaptations to particular environmental factors in these ecologically divergent regions. The numbers of remaining rhinos in the four regional groups that were identified for separate genetic management are shown in Table 4.

Table 4. Estimated numbers of black rhinos in regional units.

Regional conservation unit	Number
Southwestern	500
Southern/Central	2 600
Eastern	600
Northern/Western	50

STATUS OF BLACK RHINOS IN CAPTIVITY

Tables 5 and 6 summarize the current status of black and other rhinos in captivity at the time of the workshop. Figures differ slightly from those used by Lynn Maguire and Robert Lacy in their analyses in these proceedings—owing to different sources of information—but not to a significant extent. There appears to be captive habitat in zoos for about 700-800 rhinos, using current collections as a crude estimate. Black rhinos are currently allocated about 20% of these spaces, while white rhinos occupy a disproportionate 60% (owing largely to their ready availability from South Africa). The black rhino population in North America, now under management of the AAZPA Species Survival Plan (SSP), has been increasing slowly over the last five years at a rate of about 2% per annum (Table 7). Birth rates have been quite encouraging (in contrast to the white rhinos, which have not reproduced well as a probable consequence of this species' inclination to breed better in group situations than when kept

Table 5. Current populations of rhino in captivity. Sources are AAZPA Species Survival Plans (SSP), the international Species Inventory System (ISIS), International Zoo Yearbook (IZY), and the International Studbooks for African Rhinos (Zoo Berlin) and Indian Rhinos (Basel Zoo).

Species	North America	World	
		IZY	Studbook
Black	30/38 =68	68/80 = 148	82/98 =180
White			
Southern	70/93 = 163	177/215 = 392	313/357 = 670
Northern	1/0 = 1	6/5 = 1	6/5 = 1
Indian	16/12 = 28	44/35 = 79	44/35 = 79
Sumatran	0	3/6 = 9	3/6 = 9
Javan	0	0	0
TOTAL	117/143 = 260	298/341 = 639	448/501 = 949

Table 6. Estimated captive capacity or habitat (space and resources) for rhinos in the world's zoos.

Species	North America	World
Black	125	200-250
White	100 (+25?)	200-250
Indian	75	150
Sumatran	75	150
Javan	?	?
TOTAL	375-400	700-800

Table 7. Performance of North American zoos with black rhinos, 1982-1986.

Year	Births	Deaths	Dispersed	Imported
1982	1/3	2/2		1/1
1983	2/2	0/1		2/0*
1984				
1985	2/5	3/2	0/1	
1986	4/3	3/3		
TOTAL	9/13	8/8	0/1	3/1

*Captive born in Japan

as pairs). Death rates in black rhinos have been high, largely because of the haemolytic anaemia syndrome discussed later in these proceedings. intensive research to resolve this problem is in progress and some hopeful insights have already been obtained, especially in terms of possible vitamin E deficiencies.

LONG-TERM MANAGEMENT OF SMALL RHINO POPULATIONS

Thomas Foose (American Association of Zoological Parks and Aquariums).

Overview of concerns

As discussed by Lynn Maguire in the preceding session, and elaborated by Robert Lacy in the following presentation, the trend towards very small and fragmented populations in the wild (i.e. towards the situation of rhinos to captivity) makes these populations vulnerable to extinction for genetic and demographic reasons. Small populations lose genetic diversity rapidly at the population level (Fig. 3) as well as at the individual level. At the population level, genetic diversity Is

Figure 3. The decline of genetic diversity (measured as average heterozygosity in the total population) over 50 generations for various effective population sizes (Ne), possible for a total population (N) of 250.
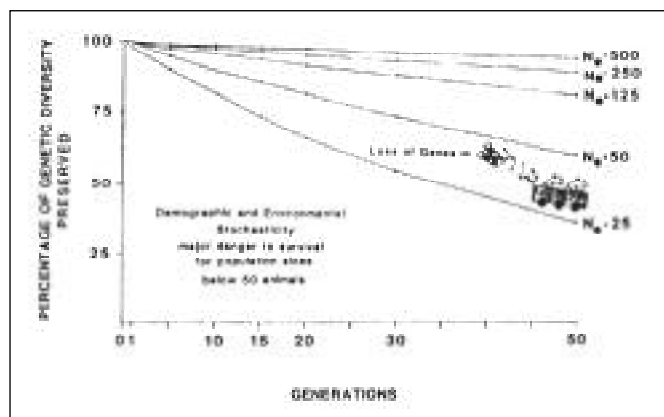
vital to permit adaptation to continually changing environments. At the individual level, genetic diversity is required to maintain the "vigour" of the animals; loss of diversity in individuals is known as inbreeding and a consequent decline in survival and fecundity rates is inbreeding depression.

Conservation biologists have suggested that genetically effective population sizes (Ne's) of 50 or more are necessary for the shorter term (5-10 generations) mainly to counteract inbreeding depression, while Ne's of 100-500 or even more may be necessary over the longer term to maintain adaptability. The vulnerability of small populations to demographic risks (disease epidemics, natural disasters, uneven sex ratios, etc.) imposes a further minimum limit to desirable population size: conservation biology—models suggest that populations must be no smaller than 25-50 total individuals to survive unpredictable (stochastic) demographic risks.

To preserve a species against these genetic and demographic risks, it is therefore necessary to establish some *minimum viable population size* (MVP). The actual MVP that is recommended will depend on the defined objectives for the species at risk as well as the biological characteristics of that species (Soule *et al.,* 1986). The major relevant concerns are as follows.

1.) The probability of survival of the population. No finite population size will completely insure a species against stochastic extinction, but It is sometimes possible to specify population sizes that will insure some probability of survival (e.g. 50%; 90%). For some given period of time, the higher the stipulated probability of survival, the larger the MVP required. 2.) The level of genetic diversity to be preserved. Obviously, the top objective would be to retain all the genetic diversity. However, with the restricted populations possible (In the wild or captivity), something less than all may have to be accepted for some period of time. Preserving rarer alleles (i.e. specific varieties of genes) will require larger MVP's than merely maintaining average heterozygosity (some variation of any, non-specific kinds). Preserving 95% of average heterozygosity will require an MVP twice as large as'90% will. Population geneticists are not certain how much genetic diversity is enough but levels of at least 90% of average heterozygosity have been strongly suggested.

3.) How long this level of genetic diversity must be preserved. The optimal answer is indefinitely, i.e. the species could then continue to evolve as environments change. But again, there may have to be compromises. Hopefully, intensive programmes will be needed only through the present ""demo-

graphic winter"' (the period extending for the next 200 to 500 years, during which human population growth and development will continue and intensify disruption of natural systems). However, the winter may vary on a species-by-species and area-by-area basis.

Biological characteristics that influence MVP sizes include the following:

1.) The generation time of the species. Genetic diversity is lost generation by generation, not year by year. Thus some given period of time, e.g. 200 years, represents more generations, hence more opportunity to lose diversity, for a species like a galago than it does for a species like a rhino.

2.) The Ne/N ratio of the population. Loss of diversity does not depend simply on total population size, but rather on the genetically effective size (which reflects how the animals are actually reproducing to transmit genes to the next generation). Very generally, the genetically effective size of a population depends on:

— the number of animals actually reproducing;
— the sex ratio of the reproducing animals;
— the relative lifetime number of offspring (i.e. family size of animals in the population).

Since Ne is normally less (often much less) than the census number (N), MVP's must be larger than the population sizes prescribed by genetic calculations since these prescriptions are always in terms of Ne.

3.) The number of founders that establish a population. Founders are animals out of a wild population that are used to establish a captive or a new wild population (or augment a recovering wild population). Conversely, they could be animals from captivity that are used to re-establish a species in the wild. in general, the larger the number of founders, the smaller the MVP needed for some genetic objectives. However, there is a point of diminishing returns so that usually 20-30 founders may be adequate.

4.) The reproductive rate or recovery potential of the population. Much genetic diversity can be lost either as the population grows from its foundation size to carrying capacity or during recovery from periodic reductions. in general, the higher the reproductive rate and hence growth or recovery to carrying capacity, the less genetic diversity is lost.

5.) The degree of subdivision or fragmentation in the population. If a species is fragmented into a number of subdivisions which are Isolated from one another, animals may not be able to move around for breeding and hence exchange of genetic material. Such situations can cause loss of genetic diversity. On the other hand some subdivision may assist retention of some kinds of genetic diversity. The important point is that conservationists must analyze the genetic processes in the species under consideration and develop an appropriate management plan that may include artificial movement or manipulation of animals, to synthesize many separate smaller populations into a so-called metapopulation capable of greater long-term viability.

Clearly, there is no single MVP figure that will apply to all species or to all situations for any given species. Rather, MVP's will vary depending on the objectives of the program and the circumstances of the species. Detailed explanation and expansion of the MVP concept are provided by Gilpin and Soule (1986), Shaffer (1987) and Soule (1987). The process of determining the size of a population that is required to achieve some level of genetic and demographic security has come to be known as *population viability analysis (PVA).*

PVA attempts for black rhinos

Table 8 represents some initial attempts at prescribing MVP's for both wild and captive black rhinos. These analyses were performed using microcomputer software developed by Jon Ballou of the National Zoological Park in Washington, DC, and are extremely tentative. To refine the PVA models and their data inputs, there needs to be more collaboration between conservation biologists and field managers of black rhinos. However, since there is an urgent need for management guidelines, a number of preliminary recommendations based on these rough analyses have been generated for consideration.

An Ne = 500 is proposed for each regional conservation unit of black rhinos. This represents a number sufficiently high to ensure maintenance of genetic diversity (e.g. 90% average heterozygosity for 50 rhino generations) and demographic security.

An Ne/N ratio of 0.25 to 0.5 is proposed as a further operational guideline in formulating conservation strategies for black rhinos. With management, especially in captivity, it may be possible to improve this ratio. Simple arithmetic indicates that to achieve an Ne = 500 with a worst case situation of Ne/N = 0.25, an MVP of 2 000 would be required for each conservation unit of rhinos.

Since black rhino populations will be fragmented and resources for conservation limited, it also seems advisable to suggest a size for individual populations of black rhinos within each conservation unit. The number roughly indicated by analyses so far is 100-200. This guideline does not dictate that populations smaller than this size are worthless but that they should probably receive lower priority for conservation efforts than larger ones. Realistic cost-benefit analyses need to be performed on each of the rhino populations of limited viability to determine if intensive and interactive management in feasible in both logistic and economic terms, it should be emphasized that the figure suggested here applies not to actual current population, but to potential size of the population in the given area if rhinos can be adequately protected to reach carrying capacity.

Finally, it should be realized that individual populations of 100-200 are not likely to be genetically and demographically viable by themselves over periods of time in the order of centuries. There will need to be interchange between separate populations to create the so-called "metapopulations" for each conservation unit. Where natural migration is not possible between separate populations, management will have to artificially move animals for genetic and demographic reasons as suggested by appropriate PVA analyses.

Because of the limited space and resources available in ex situ facilities, MVP's may have to be, and probably can be, even more precisely defined for captive than for wild populations. An objective for captive propagation of preserving 90% of average heterozygosity for 200 years is a common recommendation of conservation biologists considering principles of population genetics (i.e. inbreeding) and demography as well as the likely period of time that human pressures will be most intense on wildlife. To achieve objectives of preserving a significant fraction (90%) of the wild gene pool for 200 or so years, a number of combinations of ultimate carrying capacity, initial founder numbers, and population growth rates will produce the desired results (as demonstrated in Table 8).

As a result of these preliminary analyses, the zoo community is proposing to develop captive populations of 150 each

Table 8. Minimum viable populations required to preserve 90% average heterozygosity for various periods, in several demographic situations.

A. GENERATION TIME = 15 YEARS.
POPULATION GROWTH RATE = 1.03/YEAR
Ne/N Ratio = 0.5

		YEARS						
		75	150	225	300	450	600	750
EFFECTIVE	10	–	–	–	–	–	–	–
NUMBER	20	62	131	236	367	603	891	1134
OF	25	50	121	189	273	459	641	832
FOUNDERS	30	50	103	170	241	393	551	712
	50	50	100	156	203	319	439	561
	75	50	100	150	193	297	404	513
	100	50	100	150	193	289	392	495

B. GENERATION TIME = 15 YEARS. POPULATION GROWTH RATE = 1.06/YEAR
Ne/N Ratio = 0.5

		YEARS						
		75	150	225	300	450	600	750
EFFECTIVE	10	115	292	534	786	1310	1842	2384
NUMBER	20	50	115	187	261	414	568	727
OF	25	50	106	170	235	369	505	642
FOUNDERS	30	50	102	160	221	345	471	598
	50	50	100	147	200	308	417	527
	75	50	100	150	193	293	397	501
	100	50	100	150	193	289	389	489

C. GENERATION TIME = 15 YEARS. POPULATION GROWTH RATE = 1.06/YEAR
Ne/N Ratio = 0.25

		YEARS						
		75	150	225	300	450	600	750
	10	230	583	1069	1573	2621	3685	4769
EFFECTIVE	20	101	231	374	522	829	1136	1451
NUMBER	25	100	212	339	470	737	1010	1284
OF	30	100	204	320	442	689	942	1195
FOUNDERS	50	100	200	295	400	615	835	1054
	75	100	200	295	386	589	794	1001
	100	100	200	295	386	579	778	997

for at least two of the conservation units of black rhinos; the North American AAZPA SSP will attempt captive populations of 75 for each of these two units. The constraints imposed by the biological characteristics of the species will prescribe a critical minimum for the number of founders (i.e. animals out of the wild) that will be needed to establish the captive population. For black rhinos, 20-25 effective founders for each conservation unit maintained seems desirable.

FURTHER GENETIC AND DEMOGRAPHIC ANALYSES OF SMALL RHINO POPULATIONS
Summary of presentation by Robert Lacy
(Chicago Zoological Society)

This work is quite preliminary, providing initial insights and possible directions for future analysis, not definite conclusions or recommendations about rhino populations. The

analyses were conducted using best-guess data available from a variety of sources; the data, the models used, and the analyses of the results can and should be improved.

Analysis of founder members for the captive populations

Captive populations often derive from so few wild-caught "founders" that they poorly represent the genetic (and morphological, ecological, physiological, and behavioural) diversity of the wild populations. To examine the founder stock from which the captive populations of African rhinos descend, I analyzed the international studbooks for black and white rhinos (updated computer versions provided just prior to the October 1986 workshop). Numbers of living wild-caught animals, numbers of founders, and numbers of""effective founders" were calculated.

Founders were defined as wild-caught animals (currently alive or not) that have living descendants in captivity. Thus, if a wild-caught animal left no living descendants, it is not a founder of the captive population. Even if a wild-caught animal is still alive, but has not left any progeny, it is still not a founder but rather is a"*potent/al* founder, of potential genetic value but so far just an occupant of valuable space for breeders.

Effective founder number is a measure that I devised to account for unequal representation of founders in the gene pool of the present population, it is analogous to the concept of ""effective number of alleles'" at a genetic locus, and related to the concept of ""effective population size". Algebraically, the effective number of founders is

$$1/(P_1^2 + P_2^2 + ... + P_n^2),$$

In which P_i is the proportion of the captive (and non-wild-caught) gene pool that has descended from founder I. The P_is are the founder representations calculated from pedigree data and often discussed in studbook management. If the founder representations are all equal, then the effective number of founders will equal the actual number of founders. If founders have contributed unequally, the effective number will be less. For example, if three founders have contributed 50%, 25% and 25% to the living captive population, the effective number of founders would be 2.67. If one founder contributes 50% of the gene pool, and a very large number of founders each contributes a small fraction of the other 50 %, then the effective number of founders approaches 4. The effective number of founders can be thought of as the number of ideal (equally contributing) founders that would be required to obtain a population with the genetic diversity represented in the actual population. Bottlenecks in the pedigree can alter this somewhat, because they make it more likely that the entire genetic contribution of a founder derives from only half its genes. in the case of rhinos, however, bottlenecks exist only in the lineages of poorly represented founders, and therefore affect the effective number of founders almost not at all.

The results of the analyses of studbook data are as follows.

BLACK RHINOS

World captive population:

87 males (38 wild-caught, 20 captive born)

103 females (55 wild, 48 captive born)

82 identifiable founders (12% of captive animals are of unknown parentage and source, thus more founders may exist)

49.6 effective founders.

North American population:

32 males (12 wild, 20 captive born)

41 females (19 wild, 22 captive born)

(17% are of unknown history)

35 identifiable founders

24.6 effective founders

WHITE RHINOS

World captive population:

309 males (195 wild, 114 captive born)

348 females (259 wild, 89 captive born)

(28% are of unknown parentage)

121 identifiable founders

17.6 effective founders

(Male No. 52 contributed 11% of current gene pool) North American population:

86 males (53 wild, 33 captive born)

113 females (74 wild, 39 captive born)

(21 % are of unknown history)

47 identifiable founders

16.1   effective founders

(Male No. 52 contributed 16% of gene pool)

The captive populations have enough effective founders to be sufficiently representative of the gene diversity in the wild. However, most founders have contributed very little, a few founders have left many descendants, and about a third of the black rhinos and about half of the while rhinos in captivity are wild-caught animals that have never bred. Thus, the captive population should be in reasonable shape genetically, but a large number of wild-caught animals have been wasted with respect to genetic and demographic goals of captive breeding.

Analysis of demographic stability of small populations of rhinos

Even if a population is growing, on average, random fluctuations in births and deaths can lead to chance extinction of a small population. Once a population has grown to large size, such chance extinction is unlikely. I used a population stimulation program written by James Grier of North Dakota State University to examine the likelihood of success (non-extinction) of rhino populations started from small numbers of founders. The intent was to provide some rough guidelines for the re-establishment of populations in reserves. The simulation model very optimistically assumes that births and deaths are random processes that occur with some constant probability in each year. Thus, fates of individuals are independent; good years and bad years are due to accidental concordance between reproduction and mortality within the population; no environmental fluctuations exist that would cause population-wide trends in reproduction and mortality. Because environmental fluctuations do exist in the wild and do affect populations as a whole, the results below should be thought of as upper limits on the likelihood of a small population persisting.

The demographic parameters input into the model were obtained from field data on East African black rhino populations, gleaned from AERSG reports, reports of Peter Jenkins to Kenyan authorities, and other published and unpublished sources. Rhinos were assumed to be capable of breeding at

age 7, with each adult female producing offspring in 28% of the years (3.57 year average interbirth interval).

Juvenile (first year) mortality in the wild has been reported be about 16%, with 5 to 10% annual mortality of adults. I explored the models with 13%, 15%, 16%, or 20% juvenile mortality, and 5%, 60/a, or 6.808% adult mortality. This last value of adult mortality would lead to a stable, non-growing population when juvenile mortality was 160/a. Higher values of adult mortality were not modelled (even though higher values have been recorded in the field), because they would lead to precipitous declines in the population and thus extinction of the population would be virtually certain. Either 10 or.20 animals were used to begin each simulated population, and populations were followed for 85 or 170 years (5 or 10 generations). Table 9 gives the expected reproductive rates (Ro, population growth per generation, determined from life table analysis, not from the simulation program), the percent of the simulated populations (out of 100 in each case) that did not go extinct in the time span considered, and the average population size at the end of the simulation of those populations that survived. Not all combinations of parameters were tested.

Over the time span considered, random fluctuations in births and deaths would lead to the extinction of relatively few populations of rhinos that have long-term average growth rates greater than one. However, the field estimates of birth and death rates, if accurate, mean that rhino populations have very low net reproductive rates (not a surprise), and that even slight increases in deaths or decreases in births will lead to long-term decline rather than population growth. Note that the claimed rates of population growth in some game reserves (e.g. those in South Africa) do not seem compatible with the reported birth and death rates that were used in this model.

To a considerable extent, the high rate of population survival in this model results from the short time span considered and the lack of any limit to population growth. Because rhinos are so long-lived, even a declining population has a reasonable chance of surviving 85 to 170 years. Because no upper limit was put on population growth, some simulation populations grew to more than 100 individuals and thus became fairly immune to random processes.

Table 9. Results of simulation study of extinction in small populations of rhinos.

Juvenile mortality %	Adult mortality %	Number founders	R_0	85 years % surviving	N	170 years % surviving	N
13	5	10	1.35				
		20	1.35				
	6	10	1.12	90	34	82	168
		20	1.12	100	74	96	251
	7	10	0.94	68	16	48	50
		20	0.94	92	32	86	60
15	5	10	1.32	93	93		
		20	1.32	100	152		
	6	10	1.10	85	36	74	154
		20	1.10	98	61	96	259
16	5	10	1.30	95	86	94	711
		20	1.30	100	136		
	6	10	1.08	89	43	70	146
		20	1.08	98	62	95	215
	6.808	10	1.00	37	14	18	56
		20	1.00	72	19	52	41
		40	1.00	94	33	76	62
		80	1.00	100	64	98	97
20	5	10	1.24				
	6	10	1.03	87	34	67	100
	6	20	1.03	97	55	96	149

Adult mortality affects the growth rate and persistence of the populations more than does juvenile mortality; even slight increases in adult mortality have very large effects, while small increases in juvenile mortality have little effect.

Loss of genetic variability in black rhino reserves in Kenya

Soon, few black rhinos will exist outside of carefully managed and guarded parks and reserves. One consequence will be that formerly contiguous populations will be isolated and, unless animals are moved between reserves, inbreeding and loss of gene diversity within the populations could lead to their demise. (Because of the slow growth of rhino populations, even moderate inbreeding depression could cause populations to decline). I used a simulation program to examine the loss of genetic diversity from semi-isolated populations of black rhinos remaining on reserves in Kenya. The simulation program models the random transmission of genes through generations, given input parameters for population sizes, migration rates, population growth rates, limiting population sizes, and (though not shown here) mutation, and selection. Although the model assumes random mating within each population, population censuses can be (and were) adjusted to produce estimated genetically "effective population sizes", Ne (the size of a randomly mating population that would lose genetic variability at the same rate as does the real population).

Eight Kenyan populations that have a reasonable probability of receiving sufficient protection from poaching were considered. Estimated population sizes and carrying capacities were obtained from reports by Peter Jenkins and others. it was assumed that only those rhinos within areas proposed to be fenced would be protected from poaching. The ratio of effective population size to census population size was perhaps optimistically assumed to be 1:2.

Simulations were run assuming that each population started growing from its 1985 numbers, with growth rates of 25%, 50%, 1290/a, 2160/a, or 270% per generation (1.3%, 2.4%, 50/a, 70/a,"or 8% per year). The first two growth rates match some of the more optimistic, but not unrealistic, growth rates obtained from demographic analyses. The latter three match estimates reported at the Cincinnati meeting for variability after populations reached carrying capacity, simulations were also run assuming that each population was begun at its carrying capacity. in all cases, random demographic fluctuations were incorporated into the population sizes, 170 years modelling the fluctuations that would be expected if births and deaths were independent (Poisson) processes.

Table 10. Population estimates used In analysis of gene diversity.

Park	1985 census	Ne	Carrying Capacity Total	Fenced	Ne
Aberdare	80	30	600	100	50
Amboseli	15	7.5	150	50	25
Laikipia	60	30	50	50	25
Masai Mara	12	6	180	50	25
Meru	5	2.5	300	20	10
Nairobi	28	14	50	50	25
Nakuru	2(10)	5	80	80	40
Sollo	71	35.5	50	50	25

Notes: Although Nakuru had only 2 rhinos in 1985, It was assumed that more would be brought in, bringing the number used to start that population to perhaps 10. Based on reports of habitat degradation, it was assumed that the Solio population was currently above its long-term carrying capacity.

The genetic fates of the populations were monitored by the percent of the initial heterozygosity that would be expected to remain in each population, and by the overall gene diversity (the sum of within-population variability and between-population genetic variability) encompassed by the eight populations. The overall gene diversity can be thought of as the heterozygosity that would be present if all eight populations freely interbred. Populations were followed through 20 simulated generations (about 340 years).

The fate of gene diversity over the twenty simulated generations is shown on the four accompanying figures, for either

Figures 4-7. Results of simulation Study of decline of heterozygosity in small populations of Kenya rhinos. These graphs correspond to data in Table 11. Data points connected by lines represent average (of 25 runs) of the total gene diversity across all 8 populations of each generation. Data points not connected by lines are the average within-population heterozygosities. The graphs differ in the growth rate of the population per generation (25% or 50%) and whether the populations commence at 1985 levels (growing populations) or at the ultimate carrying capacity estimated for the reserve (stable populations).

25% or 50% population growth per generation, and either growth from 1985 levels to carrying capacities ("growing populations") or populations begun at carrying capacities ("stable populations"). In each case 25 simulations were run with no movement of animals between populations, the movement of one animal per generation per population, the movement of two animals per generation, and the movement of so many animals that the populations were essentially panmictic. Data points connected by lines display average (across 25 runs) of the total gene diversity present across all 8 populations at each generation; data points not connected by lines are the average within-population heterozygosities.

Table 11 Summarizes the simulation results for the cases shown in the figures, and also simulated populations with higher rates of population increase (average of 25 simulations in each case).

Over just 20 generations, more than 95% of the gene diversity would be expected to remain somewhere ln the 8 rhino populations, assuming of course that all grow at the rates modelled and then hover around the assumed carrying capacities. Total gene diversity is preserved somewhat better If the 8 populations are kept fully isolated (""no migration" case), because different genetic variants can become "'fixed"
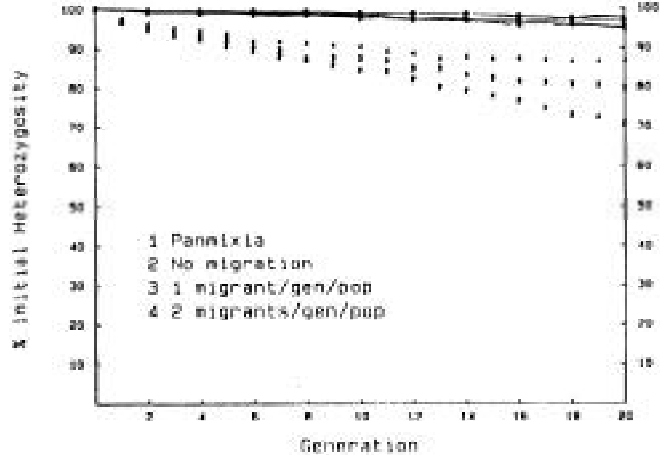
Kenya Black Rhinos: Growing Populations
INITIAL SUBPOP SIZES: 30 7 30 6 3 14 5 35
CARRYING CAPACITIES: 50 25 25 25 10 25 40 25
GROWTH RATE = 0.250
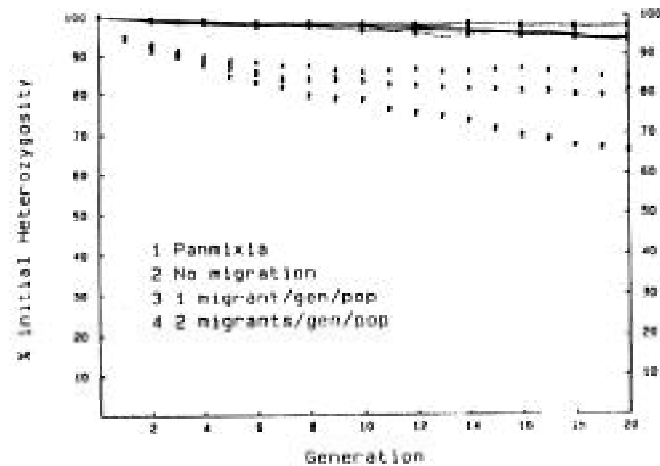
Kenya Black Rhinos: Growing Populations
INITIAL SUBPOP SIZES: 30 7 30 6 3 14 5 35
CARRYING CAPACITIES: 50 25 25 25 10 25 40 25
GROWTH RATE = 0.500
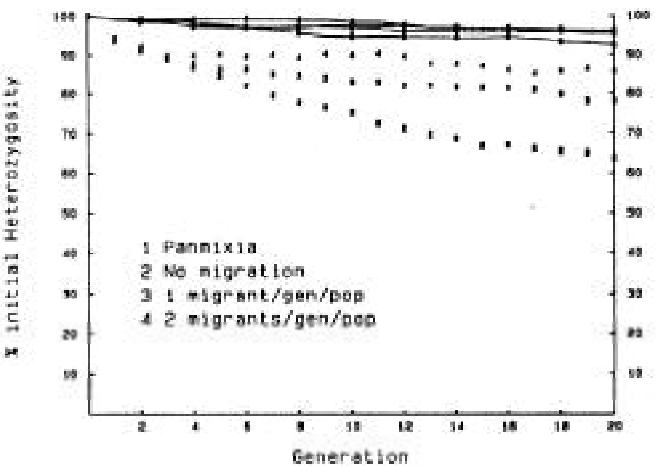
Kenya Black Rhinos: Stable Population
INITIAL SUBPOP SIZES: 50 25 25 25 10 25 40 25
CARRYING CAPACITIES: 50 25 25 25 10 25 40 25
GROWTH RATE = 0.250

Kenya Black Rhinos: Stable Population
INITIAL SUBPOP SIZES: 50 25 25 25 10 25 40 25
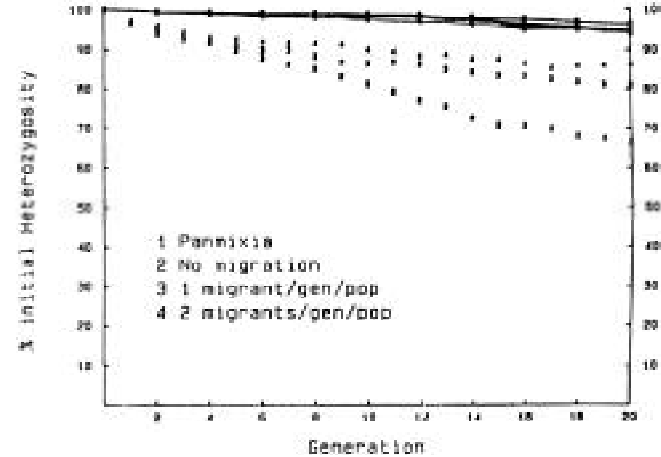CARRYING CAPACITIES: 50 25 25 25 10 25 40 25
GROWTH RATE = 0.500

Table 11. Heterozygosity remaining at generation 200 as % of initial heterozygosity.

Annual growth	Generation growth	No migration	1 migrant	2 migrants	Panmixia
1.3%	25%	97	95	93	94
		66	81	84	94
2.4%	50%	96	92	95	96
	64	78	86	96	
5.0%	129%	93	95	95	97
	63	81	87	97	
7.0%	216%	95	94	95	96
	69	80	87	96	
8.0%	270%	97	98	92	96
	64	80	84	96	

Top values of each pair are average total gene diversity, bottom values are average within-population heterozygosities. Differences of less than 5% are probably not significant.

In each population, but the difference (in gene diversity preserved) between isolated populations, populations exchanging some migrants, and even a panmictic population is trivial for the rhinos.

Although total gene diversity is well maintained under all of the assumed population structures, heterozygosity is lost from within populations (i.e. some "inbreeding" occurs within each population). In the worst case (no migration), up to 35% of the heterozygosity would be lost, on average, from each isolated population. The average results from a much greater loss in the smaller populations (the Meru population would be expected to lose 64% of its heterozygosity In 20 generations, even if it were begun at its carrying capacity of 20) countered"by lesser losses in the larger populations (Aberdare would lose about 180/s of its heterozygosity in 20 generations). As very rough rules-of-thumb, the effect ("'inbreeding depression") of a loss of less than 5% heterozygosity in any one generation is generally hard to detect, and animal breeders notice little or no effect of the loss of 1 % heterozygosity per generation continued over many generations. Thus, the small rhino reserves are probably too small to sustain populations for many generations, In the absence of occasional inter-reserve movements of animals, free from genetic problems. Relatively low rates of migration, 1 or 2 migrants per generation per population, would probably be sufficient to prevent genetic problems. (This assumes migrants are as successful as are residents at breeding).

Neither starting the populations at carrying capacity (rather than 1985 levels) nor varying the population growth rate had much effect on the genetic results. This is because only rapidly growing populations were considered.. At even the lowest population growth, 25% per generation, most of the populations would reach carrying capacities in just a few generations.   The genetic fates of these populations are much more determined by their limited sizes than by the number of founders.

General comments

Rhinos, both in the wild and in captivity, are probably not in Immediate danger of genetic problems arising from loss of diversity. Given the long generation time, all except the very smallest captive and wild stocks would experience minimal inbreeding in the next century or so. (For example, a population of 64 could be propagated for 6 generations with no matings between even distantly related animals). This optimistic genetic picture assumes, however, that protected rhino populations are currently at minima (i.e. they are at the worst phase of the population bottlenecks) and that they grow at reasonable rates over the next century.

Demographically, both wild and captive populations may be in serious trouble. The captive record is not good: as many as half of the animals have never reproduced, and birth rates approximately equal death rates. The large, and seemingly stable, captive population results in large part from the many wild-caught animals, not from a good record of captive breeding. As discussed in Cincinnati, there is reason to hope that this picture is changing, but the zoo community cannot yet claim to be able to sustain continuously growing stocks of black and white rhinos.

The small rhino reserves that are likely to receive adequate protection from poaching may not be large enough to prevent extinction due to random fluctuations in births and deaths, even under the most optimistic scenarios of environmental. and demographic constancy. The primary cause for hope for the African rhinos lies in the very long generation times and low-adult mortality (in the absence of poaching): traits that make population decline a very slow process, but also make rapid recovery difficult (witness the condor).

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DEVELOPING STRATEGIES FOR NORTHERN WHITE RHINOS
Session Chairman DAVID JONES

NORTHERN WHITE RHINOS IN GARAMBA NATIONAL PARK

Summary of presentation by Kes Hillman-Smith
Background

Garamba National Park in northern Zaire is now the last known place where the northern sub-species of white rhinoceros *(Ceratotherium simum cottoni)* exists in the wild with any chance of survival. At the turn of the century, the sub-species occurred from southern Chad, through South Sudan as far east as the Nile, and through the northern edge of Zaire to West Nile Province in Uganda (Hillman—Smith *et al.*, 1986).

When the Park was established In 1938 there were probably not more than 100 white rhinos there (Curry-Lindahl, 1972). Black rhinos *(Diceros bicornis)* have never occurred in this part of Zaire. The rhino numbers increased, until by 1963 there