

1991 VORTEX SIMULATIONS OF JAVAN RHINO POPULATIONS IN UJUNG KULON

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INTRODUCTION

PVA analyses use computer models which incorporate demographic and genetic characteristics of the population(s) and conditions in the environment to simulate probable fates (especially extinction) of the population(s) under these circumstances.

Since the 1989 Workshop and Report on population viability assessment of the Javan Rhino in Indonesia, the computer simulation models have evolved and improved. A density dependence model, as described in the VORTEX documentation, is now incorporated into the VORTEX software. This permits the model to decrease reproduction as the population approaches carrying capacity or to increase reproduction as the population is reduced below carrying capacity. Hence, the model now permits the population to "recover" more realistically from declines below carrying capacity. The state of the art is described in the VORTEX section of this Briefing Book.

Using the improved models, a number of the population viability analyses are repeated here as a basis for further analysis at this 1991 Workshop. The results are presented in the next 6 tables (Tables 1-6) which attempt to develop the scenario of small population problems and risks in what hopefully is a logical sequence.

Each case investigated is represented by a row in the tables. A case is defined by the conditions represented by the columns of the table. Blocks of rows defined by the double lines above and below represent cases subjected to similar sets of conditions.

The simulations for each case are repeated through 1000 runs, i.e. 1000 populations are subjected to the conditions of this case.

All populations are simulated for 200 years with results reported at the end of both 100 and 200 years.

The sequence of cases are:

- (1) Basic scenarios are established by assigning demographic parameters for each case. "POPULATION PARAMETERS" column". Important demographic variables include: the carrying capacity K ; the pattern of survivorship L_x . (Table 7); the pattern of fertility or reproduction M_x .

After basic scenarios are constructed, a number of the problems that can afflict small populations are added.

- (2) First, the effects of catastrophes are explored (CATASTROPHE columns).
- (3) Then, the effects of inbreeding are investigated. "INBRD" column
- (4) Lastly, the effects of removing rhino from the population are examined (REMOVALS" column).

All simulations are investigated at 3 levels of carrying capacity (K): 100, 70, 50.

The results of the population simulations are reported in terms of:

- P(E):** Probability of extinction, i.e. the number of populations out of 1000 that became extinct in the simulations.
- T_E:** The mean time to extinction for those populations that did not survive. The result is reported as the mean \pm the standard deviation to provide a view of the range of extinction times.
- POP.:** The mean final size for those populations that survive, again presented as a mean \pm the standard deviation.
- H_E:** The expected fraction remaining in the surviving populations of the original heterozygosity (genetic diversity).

BASIC SCENARIOS - (Table 1)

Basic population parameters are derived from 3 sources:

- (1) Demographic data on *Rhinoceros unicornis* in the wild in Nepal (Dinerstein & Price 1991, included in this Briefing Book)
- (2) Demographic analysis of the captive population of *Rhinoceros unicornis* in captivity in North America. (SSP 1988, included in this Briefing Book)
- (3) Limited data demography of *Rhinoceros sondaicus* in Ujung Kulon (Amman 1982, included in this Briefing Book)

Survivorship and mortality schedules are selected to produce an age structure approximating these three reference populations.

In formulating the basic parameters, there is an attempt to replicate the population structure and dynamics reported in these populations, e.g. the 7% annual growth rate (λ) observed in both the Nepal and Ujung Kulon populations during periods of maximal increase or the 4-5% growth rate more recently prevailing in the Nepal population. These two rates of growth are achieved by varying the average level of reproduction.

Level 1 (7% growth rate): On the average, 33% of the females in the population produce a calf in a given year. This pattern is equivalent in the demographic models to each female producing a calf every 3 years.

Level 2 (5% growth rate): On the average, 25% of the females in the population produce a calf in a given year. This pattern is equivalent in the demographic models to each female in the population producing a calf every 4 years.

Incorporating density dependence permits the model population to emulate these rates of growth when density is lower and still achieve zero population growth near carrying capacity. The pattern of density dependent change in reproduction used are presented in Table 8. These patterns also cause the interbirth intervals to increase near carrying capacity consistent with what has been suggested for the Javan rhino in Ujung Kulon.

The newer models also produce more reasonable estimates of generation time (G) than was the case in 1989, i.e. the G's are similar to what is calculated for *Rhinoceros unicornis* populations in Nepal and in North American zoos.

Results:

At both levels of reproduction, the populations maintain their sizes near carrying capacity and their heterozygosity at high levels over the 200 year period.

EFFECTS OF CATASTROPHES (Table 2)

Catastrophes can increase mortality and fertility below the level that occurs because of normal events in the population. Two types and severities of catastrophes suggested by the recent history of the Ujung Kulon population are investigated:

- Type I: A "disease" catastrophe (suggested by the 1982 death event) occurring on the average once every 10 years (.1 frequency (FRQ) of occurrence). It is assumed here that the effect of the catastrophe will be to increase mortality (although VORTEX also permits decrease in fertility). Two levels of severity (SRVT) in mortality are imposed.
- Severity 1: .1 (10%) increase in mortality which is equivalent to a survivorship of .9 (90%) of what it is without the catastrophe. This level of mortality is suggested by the 5 carcasses actually discovered in the 1982 death event when the total population was estimated at about 50.
- Severity 2: .2 (20%) increase in mortality which is equivalent to a survivorship of .8 (80%) of what it is without the catastrophe. This level is suggested by the speculations that not all carcasses were discovered in 1982 (Van Sirien report).
- Type II: A "poaching" catastrophe. Poaching can be modelled as either a stochastic or a deterministic event. It is here modelled as a stochastic event, as a continuing catastrophe. The frequency is .5 (50%) which is equivalent to an event occurring every other year. The severity is .02 (2%) removal of the existing population which in a population of about 50-60 animals represents a loss of 1 individual. This level is consistent with estimates at the last Workshop.

The catastrophes are investigated with respect to both levels of reproduction (.33 and .25).

Results: Four sets of cases:

At the higher level of reproduction (.33) and the lesser severity of the "disease" Catastrophe I (.9), all populations maintain their sizes near carrying capacity. By year 200, genetic diversity is at high levels for populations with $K = 100$; lower for $K = 70$; and for $K = 50$, almost 25% of the original genetic diversity is lost. (As is true in all "50 K" cases in this Table.)

At the higher level of reproduction (.33) and the greater severity of Catastrophe I (.8), mean final population sizes are slightly lower and standard deviations around mean (instability) are higher. Moreover, the cases with carrying capacity of 50 are already manifesting some extinctions.

At the lower level of reproduction (.25) and the lesser severity of Catastrophe I (.9), mean final populations are again lower than in the basic scenarios and the populations with carrying capacity of 50 exhibit problems.

At the lower level of reproduction (.25) and the greater severity of Catastrophe I (.8), populations at all 3 carrying capacity levels have lower final population sizes and are experiencing extinctions. The smaller the carrying capacity, the greater the extinctions. Expected heterozygosity is appreciably reduced by year 200 in the populations with carrying capacities 70 and 50.

EFFECTS OF INBREEDING (Tables 3 & 4)

Inbreeding can reduce ("depress") the survival and fertility (fitness) of a small population. Inbreeding is incorporated using a heterosis model where level is measured by the number of lethal equivalents per diploid genome. The lethal equivalents are assumed to reduce fitness by increasing juvenile mortality. There is a simplistic and approximate way of appreciating what lethal equivalents are. A 10% loss of heterozygosity is equivalent to a 10% decline in fitness (as measured by increased juvenile mortality) which represents 1 lethal equivalent; 20% loss of heterozygosity = 20% decline in fitness = 2 lethal equivalents. For a fuller explanation the reader is referred to the VORTEX program as well as Ralls et. al (1988), both of which are provided in this Briefing Book.

Two levels of inbreeding are investigated:

- Level 1: 3.5 lethal equivalents per diploid genome which is a value between the mean and the median for a wide range of mammals investigated by Ralls et al. (copy of paper provided in Section of this Briefing Book)
- Level 2: 7 recessive lethals which represents a high value of the range reported by Ralls et al., e.g. approximates the value discovered for Eld's deer.

Inbreeding is investigated at two levels of severity of the "disease" Catastrophe I.

- Severity 1: The 10% increase in mortality (i.e. the .9 survivorship value). Table 3 - INBREEDING I.
- Severity 2: The 20% increase in mortality (i.e. the .8 survivorship value). Table 4 - INBREEDING II.

The "poaching" Catastrophe II is applied in all cases.

Results: Eight sets of cases.

INBREEDING I: (Lesser severity of Catastrophe I) 4 sets of cases.

At higher levels of reproduction (.33) and lower levels of inbreeding (3.5), there is some further reduction in final population sizes and genetic diversity over the "Effects of Catastrophe" cases.

At lower levels of reproduction (.25) and lower levels of inbreeding (3.5), the final populations and genetic diversity are reduced even more and for populations with carrying capacity 50, extinctions are occurring and appreciable decline in mean size occurs from Year 100 to Year 200. This latter trend is evident even for populations with carrying capacity 70.

At higher levels of reproduction (.33) but higher levels of inbreeding (7), declines of final population and expected heterozygosity are greater than at lower levels of inbreeding. Populations at all levels of carrying capacity have population sizes appreciably lower at Year 200 than at Year 100.

At lower levels of reproduction (.25) and higher levels of inbreeding (7), problems are evident for populations at all 3 levels of carrying capacity, but for $K = 70$ and especially $K = 50$, the populations clearly seem to be in an "extinction vortex".

INBREEDING II: (Greater severity of Catastrophe I) 4 sets of cases.

Populations at all levels of reproduction and degree of inbreeding are exhibiting extinction problems. Problems are least in the first set of cases (reproduction .33 and inbreeding 3.5) in Table 4. The problems increase for the 3rd set of cases (reproduction .33 and inbreeding 7) in Table 4. The problems are greatest and very severe in the two sets of cases with lower reproductive potential (.25) at either level of inbreeding but with the worse with inbreeding at 7. Populations at all levels of carrying capacity are clearly in "extinction vortices".

In general there seems to be a synergism between catastrophes and inbreeding that produce such "extinction vortices". This synergism is plausible. When catastrophes reduce the populations to low size, they experience genetic bottlenecks which increases inbreeding and can further reduce fitness and decrease the size of the population even more.

EFFECTS OF REMOVALS (Tables 5 & 6)

For purposes of this preliminary analyses, 12 adult rhino (4 males and 8 females) are removed from Ujung Kulon to establish a second population.

Animals are removed using the previous worst case scenario for catastrophes, i.e. EFFECTS OF INBREEDING II. A worst case scenario is initially investigated on the premise that the most secure approach for conservation is a strategy that will minimize regrets.

Two removal schedules are explored:

- (1) removing all the animals at once in a single year (Removal I);
- (2) removing 3 animals per year (1 male and 2 females) over 4 years (Removal II)

Results:

Results indicate that there is no significant effect on the population of removing this number of adult animals. Moreover, there is no significant difference between removing all the animals in one year or over 4 years. These results are consistent with the analyses conducted to produce the 1989 Javan Rhino PVA report. Obviously, other scenarios in terms of both numbers of animals removed and period over the removals occur can be explored.

CONCLUDING COMMENTS

One conclusion that emerges from these analyses appears to be the particular vulnerability of rhino populations with carrying capacity of 50 (and lower). Risks of extinction are appreciable to significant in many of the "50 K" cases. Moreover, loss of genetic diversity (heterozygosity) is significant (< 85%) by 200 years in all "50 K" cases investigated.

Many other analyses could and should be conducted. For example, it is possible also to simulate competition, e.g. from Banteng, in the models. Very importantly, it is possible to simulate a metapopulation situation, i.e. what are the expected outcomes if there are 2 populations (Ujung Kulon and a second population, wild or captive). These simulations can be performed at the Workshop.

VORTEX -- simulation of genetic and demographic stochasticity

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1 population(s) simulated for 200 years, 1000 runs

HETEROSIS model of inbreeding depression

with 3.50 lethal equivalents per diploid genome

First age of reproduction for females: 6 for males: 6

Age of senescence (death): 35

Sex ratio at birth (proportion males): 0.5000

Population 1:

Reproduction is assumed to be density dependent, according to:

Percent breeding = 24.79020980

+ 0.03799530 N

+ 0.00244760 NN

+ -0.00016320 NNN

+ 0.00000000 NNNN

EV in reproduction (SD around the first term in the above Eq.) = 6.25

Of those females producing litters, in an average year ...

100.00 percent of adult females produce litters of size 1

11.00 (EV = 5.50 SD) percent mortality of females between ages 0 and 1

0.50 (EV = 0.25 SD) percent mortality of females between ages 1 and 2

0.50 (EV = 0.25 SD) percent mortality of females between ages 2 and 3

0.50 (EV = 0.25 SD) percent mortality of females between ages 3 and 4

0.50 (EV = 0.25 SD) percent mortality of females between ages 4 and 5

0.50 (EV = 0.25 SD) percent mortality of females between ages 5 and 6

2.50 (EV = 1.25 SD) percent annual mortality of adult females (6 <= age <= 35)

27.00 (EV = 13.39 SD) percent mortality of males between ages 0 and 1

1.00 (EV = 0.50 SD) percent mortality of males between ages 1 and 2

1.00 (EV = 0.50 SD) percent mortality of males between ages 2 and 3

1.00 (EV = 0.50 SD) percent mortality of males between ages 3 and 4

1.00 (EV = 0.50 SD) percent mortality of males between ages 4 and 5

1.00 (EV = 0.50 SD) percent mortality of males between ages 5 and 6

2.50 (EV = 1.25 SD) percent annual mortality of adult males (6 <= age <= 35)

EVs may have been adjusted to closest values possible for binomial distribution.

EV in mortality will be correlated among age-sex classes

but independent from EV in reproduction.

Frequency of type 1 catastrophes: 10.000 percent
 with 1.000 multiplicative effect on reproduction
 and 0.800 multiplicative effect on survival

Frequency of type 2 catastrophes: 100.000 percent
 with 1.000 multiplicative effect on reproduction
 and 0.980 multiplicative effect on survival

Polygynous mating; 60.00 percent of adult males in the breeding pool.

Initial size of Population 1:
 (set to reflect stable age distribution)

Age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Total		
1	2	2	1	2	1	1	1	1	1	1	1	1	1	1	0	1	0	1
0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	24 Males		
3	2	2	2	1	2	2	1	2	1	1	1	1	1	1	1	0	1	1
0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	1	32 Females		

Carrying capacity = 50 (EV = 2.50 SD)

Animals harvested from population 1, year 1 to year 4 at 1 year intervals:

2 female adults (6 <= age <= 35)

1 male adults (6 <= age <= 35)

Deterministic population growth rate (based on females, with assumptions of
 no limitation of mates and no inbreeding depression):

$$r = 0.009 \quad \lambda = 1.009 \quad R_0 = 1.142$$

Generation time for: females = 15.61 males = 15.61

Stable age distribution:	Age class	females	males
	0	0.043	0.043
	1	0.036	0.030
	2	0.034	0.028
	3	0.032	0.026
	4	0.031	0.025
	5	0.029	0.023
	6	0.028	0.022
	7	0.026	0.021
	8	0.024	0.019
	9	0.022	0.018
	10	0.021	0.016
	11	0.019	0.015
	12	0.018	0.014
	13	0.016	0.013
	14	0.015	0.012
	15	0.014	0.011
	16	0.013	0.011
	17	0.012	0.010
	18	0.011	0.009
	19	0.011	0.008
	20	0.010	0.008
	21	0.009	0.007
	22	0.008	0.007
	23	0.008	0.006
	24	0.007	0.006
	25	0.007	0.005
	26	0.006	0.005
	27	0.006	0.005
	28	0.005	0.004
	29	0.005	0.004
	30	0.005	0.004
	31	0.004	0.003
	32	0.004	0.003
	33	0.004	0.003
	34	0.003	0.003
	35	0.003	0.003

Ratio of adult (≥ 6) males to adult (≥ 6) females: 0.800

Population1

Year 25

N[Extinct] = 0, P[E] = 0.000
N[Surviving] = 1000, P[S] = 1.000
Population size = 32.25 (0.31 SE, 9.67 SD)
Expected heterozygosity = 0.945 (0.001 SE, 0.020 SD)
Observed heterozygosity = 0.991 (0.001 SE, 0.018 SD)
Number of extant alleles = 27.60 (0.23 SE, 7.22 SD)

Year 50

N[Extinct] = 27, P[E] = 0.027
N[Surviving] = 973, P[S] = 0.973
Population size = 27.33 (0.37 SE, 11.51 SD)
Expected heterozygosity = 0.890 (0.002 SE, 0.049 SD)
Observed heterozygosity = 0.954 (0.002 SE, 0.052 SD)
Number of extant alleles = 15.24 (0.15 SE, 4.79 SD)

Year 75

N[Extinct] = 86, P[E] = 0.086
N[Surviving] = 914, P[S] = 0.914
Population size = 22.62 (0.37 SE, 11.21 SD)
Expected heterozygosity = 0.829 (0.003 SE, 0.084 SD)
Observed heterozygosity = 0.901 (0.003 SE, 0.096 SD)
Number of extant alleles = 10.06 (0.11 SE, 3.45 SD)

Year 100

N[Extinct] = 204, P[E] = 0.204
N[Surviving] = 796, P[S] = 0.796
Population size = 18.98 (0.39 SE, 10.90 SD)
Expected heterozygosity = 0.773 (0.004 SE, 0.107 SD)
Observed heterozygosity = 0.856 (0.005 SE, 0.129 SD)
Number of extant alleles = 7.46 (0.10 SE, 2.71 SD)

Year 125

N[Extinct] = 357, P[E] = 0.357
N[Surviving] = 643, P[S] = 0.643
Population size = 15.44 (0.40 SE, 10.25 SD)
Expected heterozygosity = 0.711 (0.005 SE, 0.130 SD)
Observed heterozygosity = 0.811 (0.007 SE, 0.166 SD)
Number of extant alleles = 5.78 (0.09 SE, 2.27 SD)

Year 150

N[Extinct] = 553, P[E] = 0.553
N[Surviving] = 447, P[S] = 0.447
Population size = 14.42 (0.44 SE, 9.36 SD)
Expected heterozygosity = 0.661 (0.007 SE, 0.153 SD)
Observed heterozygosity = 0.745 (0.009 SE, 0.192 SD)
Number of extant alleles = 4.90 (0.09 SE, 1.88 SD)

Year 175

N[Extinct] = 709, P[E] = 0.709
N[Surviving] = 291, P[S] = 0.291
Population size = 11.43 (0.46 SE, 7.86 SD)
Expected heterozygosity = 0.617 (0.010 SE, 0.168 SD)
Observed heterozygosity = 0.719 (0.013 SE, 0.214 SD)
Number of extant alleles = 4.17 (0.10 SE, 1.62 SD)

Year 200

N[Extinct] = 845, P[E] = 0.845
N[Surviving] = 155, P[S] = 0.155
Population size = 9.81 (0.59 SE, 7.37 SD)
Expected heterozygosity = 0.586 (0.014 SE, 0.174 SD)
Observed heterozygosity = 0.710 (0.019 SE, 0.233 SD)
Number of extant alleles = 3.75 (0.12 SE, 1.45 SD)

In 1000 simulations of 200 years of Population1:
845 went extinct and 155 survived.

This gives a probability of extinction of 0.8450 (0.0114 SE),
or a probability of success of 0.1550 (0.0114 SE).

845 simulations went extinct at least once.

Median time to first extinction was 143 years.

Of those going extinct,

mean time to first extinction was 130.73 years (1.39 SE, 40.28 SD).

No recolonizations.

Mean final population for successful cases was 9.81 (0.59 SE, 7.37 SD)

Age	1	2	3	4	5	Adults	Total
	0.17	0.18	0.17	0.23	0.23	3.52	4.50 Males
	0.22	0.25	0.28	0.23	0.21	4.12	5.30 Females

During years of harvest and/or supplementation
mean lambda was 0.9152 (0.0012 SE, 0.0753 SD)

Without harvest/supplementation, prior to carrying capacity truncation,
mean lambda was 0.9879 (0.0003 SE, 0.1107 SD)

Note: 0 of 4000 harvests of males and 0 of 8000 harvests of females
could not be completed because of insufficient animals.

Final expected heterozygosity was	0.5864 (0.0140 SE, 0.1740 SD)
Final observed heterozygosity was	0.7098 (0.0187 SE, 0.2331 SD)
Final number of alleles was	3.75 (0.12 SE, 1.45 SD)

KEY TO ABBREVIATIONS IN PVA SIMULATION TABLES

YRS = Years Over Which Simulation Extends

K = Carrying Capacity

λ = Annual Growth Rate

M_x = Average Fraction of Females Reproducing/Year

G = Generation Time

CATASTROPHES

I = Type I Catastrophe

II = Type II Catastrophe

FRQ = Frequency of Occurrence (Fraction of 100 yrs)

SVRT = Severity (In Terms of Fraction of Original Survival)

INBD = Level of Inbreeding (Lethal Equivalents/Genome)

REMOVALS

TOT# = Total Number Removed

YRS = Number of Years Over Which Removals Occur

P_E = Extinction Probability

T_E = Average Time to Extinction

POP. = Mean Size of Surviving Populations

H_E = Expected Heterozygosity in Surviving Populations