

# Sumatran Rhinoceros Crisis Summit: FINAL Interim Wild Population Modelling

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## Summary

- Simulation models explored a range of plausible starting points for remaining Sumatran rhino populations, from the most pessimistic predictions of species biology and population numbers, to the most optimistic.
- Annual growth rates in the baseline models ranged from -1.0% to 3.5% per year. This is low compared to the 4 – 15% per year reported for other rhino species. Given the small numbers estimated at occupied sites this leaves no margin for error in the protection of remaining individuals. Even at the highest growth rates modelled, simulated populations remained vulnerably small for the first few decades.
- Female inter-birth interval was found to be the single most important predictor of population performance.
- Over 50 years, for the population sizes modelled (N=50 to 5 individuals), and in the absence of poaching or extreme environmental perturbation, extinction risks ranged from 0 to 34% for the most optimistic scenarios, to 0.4 to 88% for the most pessimistic.
- Due to risks related to genetic impoverishment and demographic stochasticity, simulated populations numbering 10 individuals or fewer struggled to recover solely through protection, whereas those numbering 30 or more showed convincing recovery in all cases. The future of populations numbering between 10 and 30 was more variable and may hinge on population-specific characteristics such as age-structure, sex-ratio, and individual reproductive competence.
- The following measurable characteristics of a wild population would align it with simulation models that grow positively and consistently over time and show a less than 5% probability of extinction over fifty years:
  - the population numbers 20 individuals or more with a roughly 50:50 sex-ratio AND
  - over a four-year period, each breeding age female produces at least one-calf AND
  - around 6 to 7 out of 10 female calves survive to age of first breeding (6 years).
- Populations of more than 20, if otherwise healthy and completely protected, should be able to tolerate a harvest of 1-2 females at year 5.

## CAUTION

*Note that the findings described below are based on models built using data and expert opinion provided in advance of and during the Sumatran Rhinoceros Crisis Summit. Though this represented the best information available at the time, there are significant gaps and uncertainties. Findings should be treated as an INTERIM GUIDE to the likely range of outcomes for rhino populations under the scenarios explored, pending re-analysis once more data are available.*

## Introduction

Little is known about the biology of Sumatran rhinos, about the numbers and reproductive capacity of remaining populations and about the carrying capacity, safety and quality of currently occupied sites. To prevent further decline of the species management decisions need to be made urgently and in the context of this uncertainty. Simulation models, though not expected to be an accurate depiction of wild rhino populations, can inform decisions by: identifying key aspects of life history; clarifying the relative impact of different threats; comparing the likely performance of alternative management interventions.

To construct population simulation models, estimates of parameters were made based on limited data from previous population viability analyses (Soemarna et al., 1994; Ellis et al, 2011) and expert opinion provided prior to and during the Sumatran Rhino Crisis Summit.

## Baseline Models

Given the uncertainty involved in establishing a reasonable representation of species' biology in this case, three baseline models were built to span a plausible range of life history profiles (details are provided in Appendix 1):

- **Baseline:** “best-guess” performance with respect to reproduction (4 year inter-birth interval) and survival, plus susceptibility to inbreeding.
- **Pessimistic:** higher juvenile mortality, lower female reproductive output (emulating fertility issues leading to an average inter-birth interval of 5 years) and increased susceptibility to inbreeding.
- **Optimistic:** higher female reproductive output (3 year inter-birth interval) and longer reproductive life, plus no susceptibility to inbreeding.

**It should be noted that though the models include a range of life-history types (from optimistic to pessimistic) and include the impact of year to year variations in reproductive success, mortality and sex-ratio, they are all optimistic with respect to several other factors as they assume:**

- 100% protection from poaching and habitat encroachment
- No significant disease outbreak
- No extreme environmental perturbation
- No density-related disadvantages (i.e. animals are able to locate each other and are not over-crowded).

**THE INCLUSION IN THE MODELS OF ANY OR ALL OF THESE WILL DEPRESS RESULTS.**

## Projections

FIGURE 1A. OPTIMISTIC BASELINE (500 SIMULATIONS, 100 YEARS)

From a starting population of  $N=50$ , average growth over time is 3.5% per year. Most populations grow convincingly to carrying capacity over 25-45 years, with zero extinction probability. Long-term projections converge on a positive outcome.

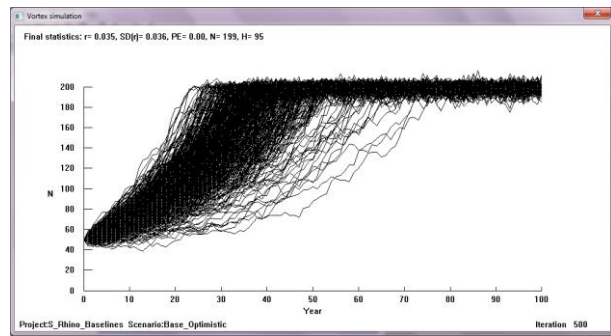


FIGURE 1B . BEST GUESS BASELINE (500 SIMULATIONS, 100 YEARS)

From a starting population of  $N=50$  growth averages approximately 1% per year across iterations. Many populations experience sustained negative growth and the long-term future is highly uncertain.

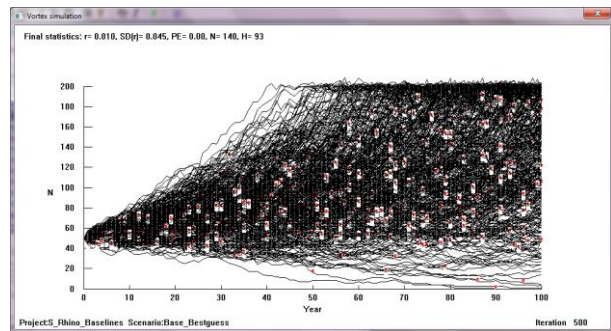


FIGURE 1C. PESSIMISTIC BASELINE (500 SIMULATIONS, 100 YEARS)

From a starting population of  $N=50$ , most populations experience a steady decline averaging 1.0% per year, with 11% extinct at 100 years. Long-term projections are variable with few showing a positive trend.

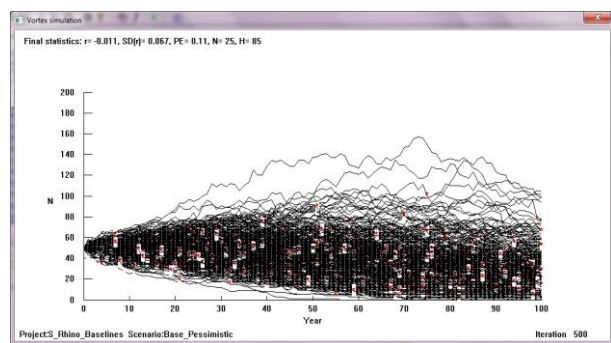


FIGURE 2. AVERAGE POPULATION SIZE OVER TIME FOR OPTIMISTIC, BEST GUESS AND PESSIMISTIC SCENARIOS.

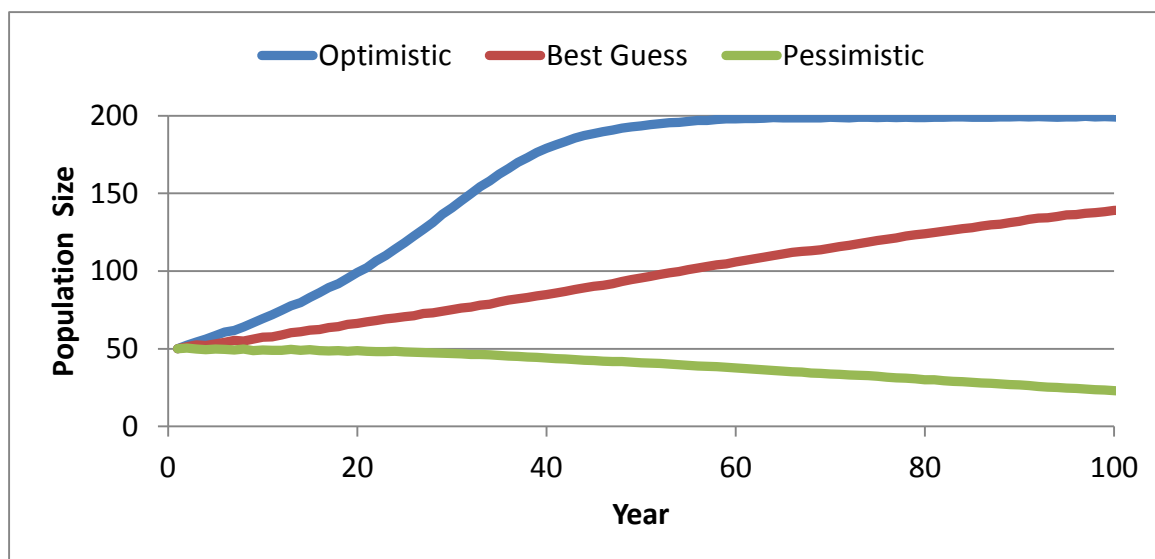


Figure 2. shows average trajectories for the three baseline scenarios. Both Optimistic and Best Guess scenarios show positive growth over the period whilst the Pessimistic scenario shows sustained negative growth. Figures 1a – c illustrate the level of uncertainty around these results. Whilst all of the Optimistic simulations moved in the same direction and converged on a consistent size at or around carrying capacity, the long-term projections for the Best Guess scenario diverged widely over the long-term, with many simulations showing a sustained decline over time. The Pessimistic simulations were also variable but most showed a negative trend. The consistently positive results seen in the Optimistic scenario can be largely attributed to the decreased inter-birth interval (from 5 and 4 years to 3 years) and the extended reproductive life of females (from 28 and 29 years to 34 years).

## Growth

The range of baseline models places annual growth rates between -1.0 and 3.5% per year. This is markedly lower than the range presented at the meeting for other rhino species, of 4-15% per year<sup>1</sup>. For much larger populations and under relatively stable conditions, a low but positive growth rate would not necessarily be of concern. However, at the low numbers estimated for remaining occupied sites (between 5 and 50 individuals) these rates leave no margin for error in the protection of all remaining individuals as even very low rates of loss to poaching or habitat encroachment can push a population into decline. Further, this slow rate of growth means that even at the highest growth rates modelled, simulated populations remain vulnerably small for the first few decades.

It is possible that the species has the capacity for higher growth rates. In discussions relating to optimal habitat, participants suggested that remaining populations may be in relatively marginal environments, having retreated there as a result of habitat encroachment and poaching pressure. Assuming this to be the case, the unusually low growth rates indicated by the models may be the result of sub-optimal nutrition (Emslie, pers. comm.), such that females are taking longer to recover

<sup>1</sup> Growth of 4% per year inferred for Indian rhinos from estimated 50-year increase from 366 – 2329. 5-15% per year depending on circumstances referred to in presentations by R. Emslie and associates.

breeding condition after pregnancy, thereby increasing inter-birth interval – a key influence on population performance (see below). In Africa there are studies underway to compare growth rates across a nutrient gradient for black rhinos and the results may be of value to Sumatran rhino management (Emslie, pers. comm.).

Other discussions pointed to low population densities and the resulting difficulties for individuals in finding mates. For females this can mean difficulty in achieving pregnancies sufficiently early and sufficiently often, to avoid deterioration in reproductive physiology, leading to long-term fertility issues.

If low growth is a result of either of these two factors then it may be possible to improve performance either by:

- Assessing and consolidating reproductively competent individuals into larger, higher density populations. Thresholds for considering this option are discussed below.
- Actively providing a richer diet through short-term supplementary feeding and longer-term habitat management.

These options were discussed by Summit working groups but were not explored any further in the models.

## **Sensitivity testing**

A range of tests were carried out to identify those aspects of the Sumatran rhino biology that have the biggest impact on population performance. Tests involved selecting one parameter at a time (e.g. age at first breeding, inter-birth interval, sex-ratio etc) and varying it across a plausible range of values, measuring any resulting changes in key performance indicators. The results are summarised in Table 1., which categorises parameters according to their impact on annual percentage growth. Only the “Best Guess” baseline model was used in this analysis.

Female inter-birth interval is the single largest predictor of population performance for the scenarios considered. Also of importance are other factors that operate on female reproductive output (female age at first and last breeding, starting age-structure, changes in mortality rates); on the proportion of females in the population (sex-ratio bias); and inbreeding depression, which in the model acts on juvenile survivorship. Parameters showing only a small impact on population projections were: those relating to male contributions to population performance (percentage of males in the breeding pool, length of reproductive life); the amount of year to year variation in average mortality and reproductive rates; and density-dependent factors. The range considered for the latter may have been too conservative and would benefit from further review.

TABLE 1. IMPACT ON POPULATION GROWTH OF CHANGES TO INDIVIDUAL MODEL PARAMETERS

<b>Change in Annual Percentage Growth (resulting from varying each individual parameter in turn across a hypothesised plausible range)</b>		
<b>BIG CHANGE (&gt;1%)</b>	<b>MEDIUM CHANGE (0.5-1.0%)</b>	<b>SMALL CHANGE (0-0.5%)</b>
<b>Female inter-birth interval</b> 3, 4, 5, 6 years	<b>Female age at first/last breeding (years)</b> <ul style="list-style-type: none"> <li>• First – 6, 8</li> <li>• Last – 32, 36, 40</li> </ul>	<b>Density dependence</b> (Low density inter-birth interval=4 years; High density inter-birth interval=6 years; Effect occurs approaching near and almost at, capacity (B=4, 8, 16))
	<b>Male bias in birth sex-ratio</b> <ul style="list-style-type: none"> <li>• 50:50</li> <li>• 55:45</li> </ul>	<b>Coupling good years for birth with good years for survival</b> YES/NO
	<b>Starting age-structure (N=60)</b> <ul style="list-style-type: none"> <li>• Young - all 0-20yrs</li> <li>• Medium - all 10-20yrs</li> <li>• Ageing - all 20-40yrs</li> </ul>	<b>Variance in breeding and survival rates</b> <ul style="list-style-type: none"> <li>• 20, 30, 40% of mean values</li> </ul>
	<b>Age-specific mortality</b> <ul style="list-style-type: none"> <li>• High juvenile – 25% year 1, 5% after</li> <li>• Baseline – 15% year 1, 5% after</li> <li>• High Adult – 20% years 30-40</li> </ul>	<b>Male age at first/last breeding (years)</b> First – 10, 12, 14
	<b>Inbreeding</b> 3.14, 6.00, 9.00LEs	<b>Percent of males in breeding pool</b> <ul style="list-style-type: none"> <li>• 60, 80, 100%</li> </ul>

## Triggers for consolidation

Small size and isolation increase risk of extinction. At present, remaining Sumatran rhino populations are fragmented, small and, as far as Summit participants could judge, diminishing. Whilst an urgent escalation of security and protection were agreed priorities, this may not be sufficient to allow populations to recover once they have declined to very low numbers. A threshold for this of about five individuals was suggested for black rhinos (Emslie, pers. comm.). However, this may be too low a threshold for Sumatran rhinos and models were used to explore this further.

At the outset of the workshop, remaining numbers of Sumatran rhinos were estimated at between 200 and 300 individuals, spread across 3 strongholds (Way Kambas, Bukit Barisan and Gunung Leuser), with a small population possibly remaining at Danum and additional animals “stragglers” residing at low densities at a number of other locations.

TABLE 2: PRE-SUMMIT POPULATION SIZE ESTIMATES FOR OCCUPIED SITES (ELLIS, PERS. COMM.)

Site	Population size estimates
Way Kambas	30-35
Bukit Barisan	30-50
Gunung Leuser	40-50
Danum	5-15

During the workshop, data were presented which both supported the likelihood of much smaller numbers, possibly less than 100 in total, and highlighted the lack of evidence for any firm estimates (Yoganand, pers. comm.).

Due to this lack of certainty, no attempt has been made to model specific sites. Instead, population scenarios have been run at a range of starting population sizes selected to cover the range of estimates put forward for the sites discussed (5, 10, 15, 20, 30, 50). Simulations were run for 50 years.

FIGURE 3A. PROBABILITY OF EXTINCTION OVER TIME FOR OPTIMISTIC SCENARIOS BEGINNING AT DIFFERENT POPULATION SIZES (N) WITH PERCENTAGE OF SIMULATED POPULATIONS EXTINCT AT 50 YEARS INDICATED.

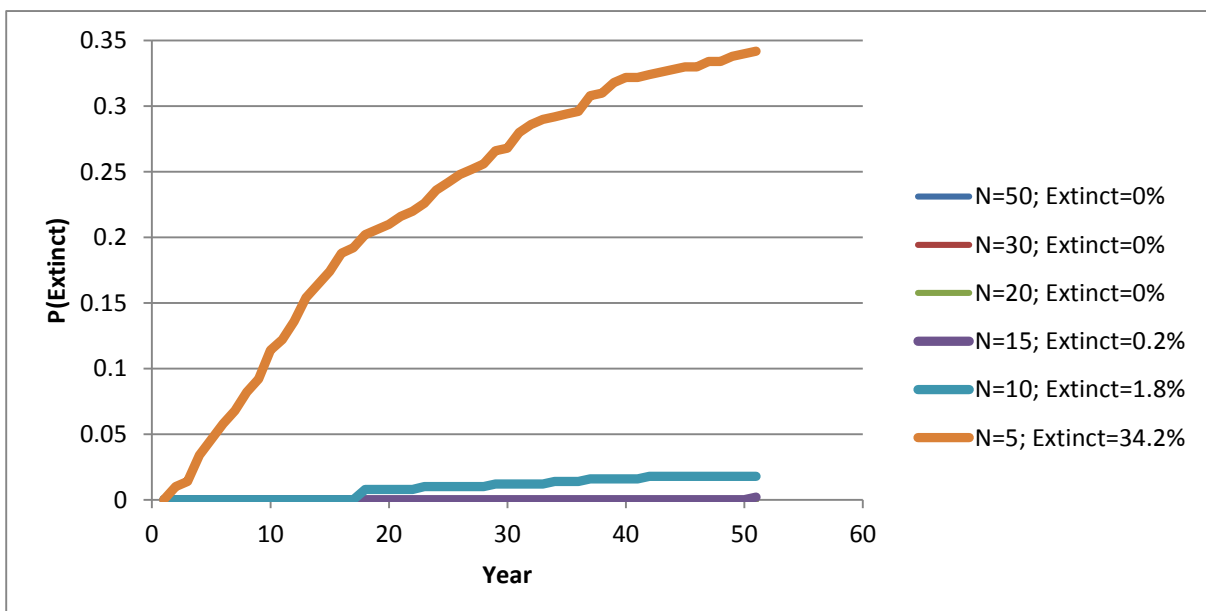


FIGURE 3B. PROBABILITY OF EXTINCTION OVER TIME FOR BEST GUESS SCENARIOS BEGINNING AT DIFFERENT POPULATION SIZES (N) WITH PERCENTAGE OF SIMULATED POPULATIONS EXTINGUISHED AT 50 YEARS INDICATED.

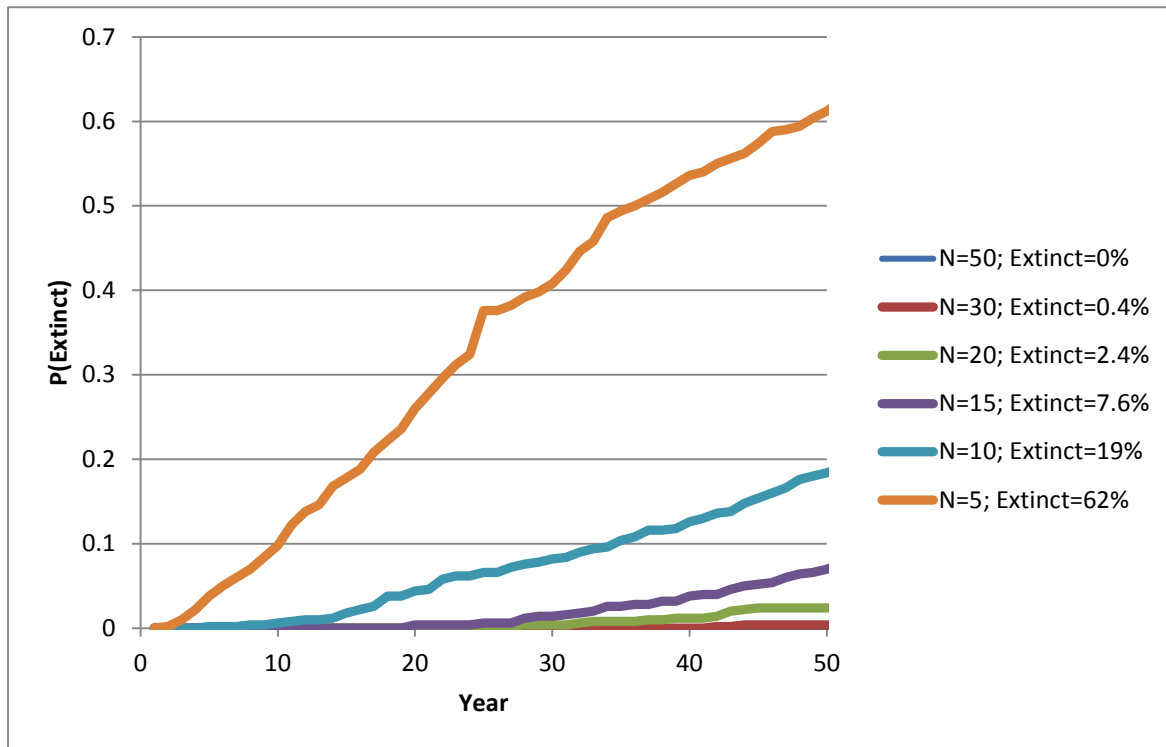
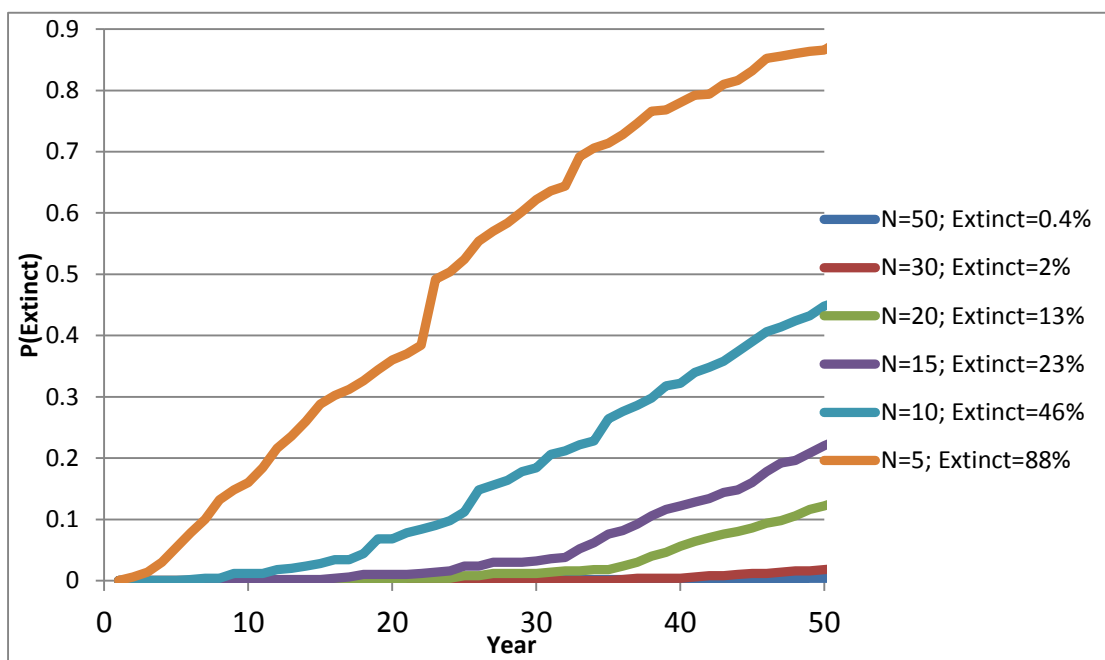


FIGURE 3C. PROBABILITY OF EXTINCTION OVER TIME FOR PESSIMISTIC SCENARIOS BEGINNING AT DIFFERENT POPULATION SIZES (N) WITH PERCENTAGE OF SIMULATED POPULATIONS EXTINGUISHED AT 50 YEARS INDICATED.





## Results

Starting population sizes of 30-50 show a low risk of extinction ( $\leq 2\%$ ) across all three scenarios whilst starting populations of 5 show a universally high risk (34-88%) across all three.

Populations beginning with 10 individuals show a high risk of extinction (19-46%) for the Best Guess and Pessimistic models. For populations beginning with 15 and 20 individuals, extinction risk exceeds 10% only in the Pessimistic models.

This analysis provides some insight into the extent to which extinction risk may vary depending both on the starting population size and on where the species or population sits with respect to its biological characteristics – that is, whether it sits closer to the optimistic or to the pessimistic end of the estimated range of possibilities. Gaining more information about this will be important to assessing the most effective course of action for each population's management.

In summary, populations numbering 10 individuals or fewer may not be capable of recovering solely through protection and might be considered candidates for consolidation or for some other more intensive form of management intervention.

Those numbering 30 or more showed convincing recovery under full protection (though issues of reproductive opportunity related to density were not accommodated in the model and need to be considered).

Recovery of populations numbering between 10 and 30 is likely to depend on where that population sits with regard to factors such as starting age-structure, sex-ratio, and the reproductive performance of individuals. Information on these may be particularly important in determining appropriate management for populations in this size range.

Once again, these analyses assume an optimistic environment for the rhino, which sees no poaching or sustained impact of habitat disturbance or encroachment. Where either of these is likely to be operating, the prognoses for populations will be worse.

## Characteristics of a viable population

More intensive monitoring was discussed at the workshop. Models were used to provide an interim guide to the likely observable characteristics of a healthy population.

The following measurable characteristics of a wild population would align it with simulation models that grow positively and consistently over time and show a less than 5% probability of extinction over fifty years:

- the population numbers 20 individuals or more with a roughly 50:50 sex-ratio AND
- over a four-year period, each breeding age female produces at least one-calf AND
- around 6 to 7 out of 10 female calves survive to age of first breeding (6 years).

Note that these are an interim guide only and should be updated as more species and site-specific information becomes available.

## Harvesting potential

Workshop deliberations included discussions of harvesting from wild populations for captivity, or to bolster smaller populations at other wild sites. Models were used to consider the impact of harvesting small numbers of individuals at year 5, on populations of different sizes. The results are summarised in Table 3.

TABLE 3. IMPACT OF HARVEST AT 5 YEARS ON POPULATIONS OF DIFFERENT INITIAL SIZES.

Initial Size	No Harvest	Females harvested at Year 5	
		1	2
10	PE = 0.160	PE = 0.260	PE = 0.376
	N <sub>10</sub> = 17	N <sub>10</sub> = 16	N <sub>10</sub> = 14
15	PE = 0.094	PE = 0.106	PE = 0.156
	N <sub>10</sub> = 23	N <sub>10</sub> = 21	N <sub>10</sub> = 22
20	PE = 0.024	PE = 0.040	PE = 0.038
	N <sub>10</sub> = 36	N <sub>10</sub> = 35	N <sub>10</sub> = 32
25	PE = 0.008	PE = 0.008	PE = 0.018
	N <sub>10</sub> = 44	N <sub>10</sub> = 40	N <sub>10</sub> = 39
30	PE = 0.006	PE = 0.006	PE = 0.006
	N <sub>10</sub> = 56	N <sub>10</sub> = 52	N <sub>10</sub> = 47
40	PE = 0.000	PE = 0.002	PE = 0.000
	N <sub>10</sub> = 78	N <sub>10</sub> = 73	N <sub>10</sub> = 69
50	PE = 0.000	PE = 0.000	PE = 0.000
	N <sub>10</sub> = 194	N <sub>10</sub> = 195	N <sub>10</sub> = 193

What the models indicate is that under benign conditions (no poaching or sustained environmental challenges and reasonable reproductive rates) harvesting 1 or 2 animals as early as year 5 has no obvious impact on the performance of populations beginning with 30 or more individuals. For those beginning with 20-25 individuals, probability of extinction is increased, but remains low (4% or less at 50 years). For populations beginning with 10 to 15 individuals, extinction risk is already high (9% and 16% respectively, over 50 years) and is increased to 10% and 26% as a result of harvesting 1, or 15% and 37% as a result of harvesting 2 individuals, at year 5.

This suggests that, as an interim guide, any conservation-directed harvest over the next 5 years would ideally be attempted from populations known to number at least 30 individuals, or from populations known to number at least 20 AND known to be in otherwise good shape.

## Risk of doing nothing

Some of the management interventions discussed during the workshop may carry a risk to individual animals, some may be particularly expensive and all carry risk of failure. Knowledge of these factors can cause risk-averse agencies to delay or avoid action. However, given the level of uncertainty around remaining population numbers at each site, and the additional uncertainty around what

levels of mortality and reproduction can be expected both from the species as a whole and from remaining populations, there are significant risks to taking no action. These risks are illustrated here in the Pessimistic and Best Guess scenarios.

## Appendix 1: Summary of baseline model parameters

Differences are highlighted.

Vortex Parameter	Baseline 1 - Optimistic	Baseline 2 - Best Guess	Baseline 3 - Pessimistic
# of populations	1	1	1
Period	100 years	100 years	100 years
Inbreeding depression included?	No	Yes - 3.14LEs	Yes - 6.00LEs
Concordance of environmental variation (EV) across reproduction and survival	no	no	no
EV correlation among populations	0	0	0
Breeding system	polygamous	polygamous	polygamous
Age of first reproduction (♂ / ♀)	8 / 6	8 / 6	10 / 7
Maximum age of reproduction	40	35	35
Annual % adult females breeding (inter-birth interval)	33 (3 years)	25 (4 years)	20 (5 years)
% males in breeding pool	100	100	100
Litter size	1	1	1
Proportion of males at birth	0.5	0.5	0.55
EV in breeding (measured as standard deviation about the mean % of breeding females)	20% of mean	20% of mean	20% of mean
EV annual mortality (measured as standard deviation about the mean age-specific mortality)	20% of mean	20% of mean	20% of mean
0-1 years	15	15	20
1-35 or 40 years	5	5	5
Initial population size	50	50	50
Carrying capacity	200	200	200
Breeding pair selection	random	random	random
Genetic management	none	none	none

<b>Vortex Parameter</b>	<b>Baseline 1 - Optimistic</b>	<b>Baseline 2 - Best Guess</b>	<b>Baseline 3 - Pessimistic</b>
Catastrophe	0	1 (1% chance ; reprod=0.95 ; survival=0.90)	1 (1% chance ; reprod=0.95 ; survival=0.90)
Supplementation	no	no	no

## Appendix 2: Vortex Model Parameters

### The *Vortex* Simulation Model

Computer modelling is a valuable and versatile tool for quantitatively assessing risk of decline and extinction of wildlife populations, both free ranging and managed. Complex and interacting factors that influence population persistence and health can be explored, including natural and anthropogenic causes. Models can also be used to evaluate the effects of alternative management strategies to identify the most effective conservation actions for a population or species and to identify research needs. Such an evaluation of population persistence under current and varying conditions is commonly referred to as a population viability analysis (PVA).

The software used in these analyses is the simulation program *Vortex* (v9.99b) (Lacy et al., 2009). *Vortex* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events, on small wild or captive populations. *Vortex* models population dynamics as discrete, sequential events that occur according to defined probabilities. The program begins by either creating individuals to form the starting population, or by importing individuals from a studbook database. It then steps through life cycle events (e.g., births, deaths, dispersal, catastrophic events), for each individual and typically on an annual basis. Events such as breeding success, litter size, sex at birth, and survival are determined based upon designated probabilities that incorporate both demographic stochasticity and annual environmental variation. Consequently, each run (iteration) of the model gives a different result. By running the model hundreds of times, it is possible to examine the probable outcome and range of possibilities. For a more detailed explanation of *Vortex* and its use in population viability analysis, see Lacy (1993, 2000) and Miller and Lacy (2005).

### Model Input Parameters

The International Sumatran Rhinoceros Studbook provides little data to inform model parameters because only a small number of Sumatran rhinos have been held in captivity ( $n = 49$ ). Thus, parameters have been based on Sumatran rhino information provided by the IRF, previous PVA work on wild Sumatran rhinos, and analyses of other rhino studbooks (Appendix Table 1).

### Number of Populations

Only one wild population was modelled in any scenario. It would be possible to model a number of populations linked by animal movements but this was not required in this case.

### Number of Years and Iterations

All scenarios were simulated 500 times. The reported results were averaged across all iterations. Each model projection extended to 50 years with demographic and genetic results summarised at the end of each year.

### Inbreeding depression

VORTEX allows the detrimental effects of inbreeding to be modelled through a reduction in first year survival. No data are currently available that would allow an assessment of the susceptibility of Sumatran rhino populations to inbreeding, however a survey of 40 other mammal taxa in captivity found that inbreeding depressed juvenile survival by a median effect of 3.14 “lethal equivalents” (Ralls et al. 1988) and this is the default value in VORTEX. Until recently, Sumatran rhinos lived in

large continuous tracts of forest. Given the species' historic population size and range, there is no reason to suspect that Sumatran rhinos have evolved an unusual tolerance of inbreeding. The "Best Guess" baseline assumes the default of 3.14 lethal equivalents, whilst the "Pessimistic" baseline incorporates greater susceptibility, at 6.0 lethal equivalents. The rationale for this increased value is that captive populations are likely to be cushioned to some extent from the effects of inbreeding. In wild populations, which are under greater stress, the impact of inbreeding may be more severe (O'Grady et al., 2006). Inbreeding depression is not included in the optimistic model.

50% of the total genetic load is derived from lethal alleles (the default values provided by VORTEX).

### **Breeding System**

The breeding system was specified as polygamous, with each male being able to breed with multiple females in a single year.

### **Age of first reproduction**

VORTEX precisely defines reproduction as the time at which offspring are born, not simply the age of sexual maturity. Sumatran rhinos have been recorded to breed for the first time at 6 years (females) and 8 years (males). These are the values used in the "Optimistic" and "Best Guess" baselines. Values of 7 (for females) and 10 (for males) are used in the "Pessimistic" baseline.

### **Maximum age of reproduction**

VORTEX assumes that animals can reproduce throughout their entire adult lives and does not model reproductive senescence. Individuals are culled from the model once they surpass the specified maximum age. The maximum age of reproduction for both sexes was set at 35 years in the "Best Guess" and "Pessimistic" models and at 40 in the "Optimistic" one.

### **Offspring production**

Females produce only one calf per parturition, with a birth sex ratio of 50% each sex, except for in the "Pessimistic" model, in which males make up 55% of the offspring at birth, on average. This latter figure was taken from the captive sex-ratio at birth in the International captive population of Indian rhinos.

### **Percent females breeding**

The shortest inter-birth interval for a female Sumatran rhino that produces surviving offspring is approximately 3 years. Thus, in the "Optimistic" baseline model, ~33% of adult females can breed each year. Remaining wild populations may not be reproducing at this rate. They may be inhabiting relatively marginal habitat, in which it may take females longer to recover breeding condition after calving, or some females may suffer from lowered fertility as a result of low density populations in which animals struggle to find mates early enough and often enough. Inter-birth intervals of 4 and 5 years (25 and 20% of females breeding annually) were set for the "Best Guess" and "Pessimistic" baseline models respectively.

### **Percent males in breeding pool**

All adult males were available for breeding each year. In other words, it was assumed that there were no social or behavioural constraints that would restrict a male from breeding.

### **Mortality rates**

There are few data on the mortality rates observed in captive Sumatran rhinos. Based on average first-year and adult mortality rates for other captive rhino species, 15% and 5%, respectively, were used in the “Optimistic” and “Best Guess” baselines, with first year mortality increased to 20% in the “Pessimistic” model.

### **Carrying capacity**

A carrying capacity of 200 animals for each population was imposed on the models. No information is available on the carrying capacities of remaining wild sites.

### **Genetic management and breeding pair selection**

No genetic management was included in the wild models.

### **Transfer rates**

No transfers between wild populations were modelled.

### **Catastrophes**

One catastrophe is included. It occurs, on average, once in 100 years and results in a 5% drop in reproduction and a 10% drop in survival.

## **Citations**

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