APPENDIX 3

FURTHER POPULATION MODELLING OF NORTHERN WHITE RHINOCEROS POPULATIONS UNDER VARIOUS MANAGEMENT SCENARIOS

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BACKGROUND

Purpose of Modelling

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model which incorporates the processes which cause fluctuations in the population, as well as those which control the long-term trends in population size (Shaffer 1981). Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in "Population Viability Analysis" (PVA) (Lacy 1996). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species such as the white rhinoceros, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can be modelled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modelling can be used. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which factors analyzed are most important to the population dynamics. PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models probably underestimate the threats facing the population. Finally, the models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modelled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed.

For the analyses presented here, the VORTEX computer software (Lacy 1993a) for population viability analysis was used. VORTEX is probably the most widely used software of its kind, with researchers, students, wildlife managers, and governmental agency personnel utilizing it to examine and make predictions about the dynamics of 100s of species in at least 68 countries. VORTEX has been used to guide conservation planning and management of all five species of rhinoceros. VORTEX models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. VORTEX also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations. Further information on VORTEX is available in Lacy (1993a) and Lacy et al. (1995).

Questions to be Explored

In preparation for the meeting at White Oak, Tom Foose and Holly Dublin, with assistance from Kes Smith, Fraser Smith, and others, examined a number of options for metapopulation management of the Northern White Rhino by simulation modelling with the VORTEX program. Those analyses provided valuable background material for the discussions at the meeting. During the discussions, participants suggested a few modifications of the parameters used in the modelling, requested that a wider range of some parameters be explored, and suggested some additional management options that could be tested via the simulation modelling. Recognizing that the data on a small population will necessarily be an imprecise guide to future performance, testing some values more extreme than those indicated as most likely from the available data can be a useful way to explore the effects if biological parameters change from those experienced by the population in the recent past.

Below are the questions raised by workshop participants which will be addressed by this modelling. As more data on the biology and circumstance of the Northern White Rhino become available, and as conservation options under consideration change, the stability of the population and the most likely impacts of management changes can be studied further with modelling.

(1) How well does the simulation model predict the growth of the Garamba population that occurred from 1984 (N = 15) to the present (N = 31)?

(2) What is the viability of the population at Garamba if it receives no support from the captive population? What is the probability of extinction, if poaching continues to be prevented? What is the expected rate of growth of the population?

(3) How do our predictions of population stability and vulnerability change if the mean age of first breeding for female Northern White Rhinos is later (9 or 11 years) than had been assumed previously (7 years)?

(4) How sensitive are the predictions to variation in the rates of infant mortality, adult mortality, and breeding?

(5) How is the probability of extinction and population growth affected by episodes of moderate or severe poaching, or by continuous (annual) low levels of poaching?

(6) How many animals would be needed for translocation if a second free-ranging population were to be established?

(7) What would be the impact on the growth and stability of the Garamba population if some animals were removed in order to establish a second population?

(8) How are the predictions of impacts on the Garamba population changed if some animals die as a result of a translocation, so that more rhinos must be removed from Garamba in order to provide the founders for a second population?

(9) What would be the impact on the growth and stability of the Garamba population if two males were removed for transfer to an independent captive population?

INPUT PARAMETERS

Estimates of many of the key biological parameters are possible because of the intensive monitoring of the population at Garamba since 1985. Except as described below, the reasons for choosing the values for the modelling are explained in the Options document prepared as background for the White Oak workshop.

General characteristics of the taxon (used for all scenarios)

Impact of any inbreeding: Set at 3.14 "lethal equivalents." This is the mean value observed in a survey of the effects of inbreeding on juvenile mortality in 40 captive mammalian populations (Ralls et al. 1988). No data on the impacts of inbreeding on populations of rhinoceros are available, but other Perissodactyla show inbreeding effects similar to the mammalian mean. No attempt has been made to model the impact that inbreeding might have on reproduction, disease resistance, or any component of fitness other than calf survival. Thus, the effects of inbreeding in the model probably underestimate (to an unknown extent) the impacts that would occur if the population becomes inbred.

Density dependence: Except for a "ceiling" maximum set on the number of rhinos that could be maintained within each population, no attempt was made to model any possible effects of increased population density on breeding or mortality rates. If there is density dependence, then the population might grow more slowly as it approaches the carrying capacity of the habitat.

Environmental variation in birth and death rates: Few data are available on the variation across years in the probabilities of reproduction and mortality in the Northern White Rhinos in Garamba Park. Since 1985, the five breeding females have together averaged 2.0 offspring per year (40% breeding per year), with a variation across years of SD = 26.8%. Some of this variation is the "demographic stochasticity" expected when five females breed at random. Subtracting this expected random variation from the observed variation leaves a residual annual variation in the breeding rate of SD = 15% due to fluctuations in the environment. (See Lacy [1993a] and Lacy et al. [1995] for more details on the methodology for estimating environmental variation in birth and death rates.) Therefore, the percent of females breeding in the simulations was set at 40% $\pm$ 15%, 30% $\pm$ 11.3%, or 20% $\pm$ 7.5%.

Estimates of annual variation in mortality are even less certain, because very few rhinos have died since 1985. In the past 11 years, the annual mortality has averaged about 2.2% $\pm$ 3.5% SD. After subtracting the variation in mortality expected due to random demographic stochasticity, the residual environmental variation in mortality is about SD = 2.3%. Therefore, for each age class, the annual variation in mortality was set equal to the mean mortality rate (e.g., 10% $\pm$ 10% SD for first year mortality, 1% $\pm$ 1% SD for juvenile and subadult mortality, and 3% $\pm$ 3% SD for adult mortality).

Parameters varied across scenarios

Age of first reproduction (i.e., parturition) of females: Set at 7, 9, or 11 years. The mean age of first calving and of subadults which have not yet bred at Garamba is about 8 years. If the females which have not yet had calves do so within the next year, the mean age of first calving would be a little greater than the mean observed in some other populations of rhinos (with larger data sets). Later mean ages of first breeding were examined also in order to test the impact if some females delay breeding for several years beyond the normal age of first calving.

Age of first reproduction (i.e., birth of first calf) by males: Set at 10, 12, or 15 years.

Breeding rate: Set at 20%, 30%, or 40% of adult females breeding each year, corresponding to inter-calf intervals of 5 years, 3.3 years, and 2.5 years.

Calf (first year) mortality: Set at 10% or 20%. The lower of these values approximates the calf mortality rate observed at Garamba since 1983 (24 calves surviving of 26 or 27 born).

Natural adult mortality: Set at 3% or 5%.

Poaching: The levels of poaching tested were those described in the Options document. Moderate episodic poaching was modelled with an episode of poaching every 10 years on average (probability each year of 10%) in which 25% or the rhinos are lost. Severe episodic poaching was modelled with an episode of poaching every 15 years in which 50% of the rhinos are lost. A low level of continuous poaching was modelled by assuming that every year about one rhino is lost (3.3% of the population killed). A higher level of continuous poaching was modelled by assuming that every year two rhinos are killed (6.7% of the population).

Carrying Capacity: More than 1,000 rhinos were thought to inhabit the Garamba National Park in 1961. The carrying capacity of the Garamba Park was set at 500 in the modelling, to allow for growth to large numbers. (Even more rhino might be accommodated in the park, as in the past, but modelling even larger populations is time-consuming, and a population of 500 would be considered healthy.) In the meeting, a potential second population was considered to be a small back-up population for Garamba, so the carrying capacity for a second free-ranging population was set at either 20 or 50 in the modelling.

Numbers and sex/age composition of the Garamba population: Set at 31 (15 males, 16 females), as observed in the Garamba population as of October 1995. (Note: this number reflects three recent births that occurred since the modelling for the Options document was completed.) Set at 15 (7 males, 8 females) for a simulation of the Garamba population as it existed at the beginning of 1985. The age and sex distribution was set to match the known or presumed ages of the animals at Garamba.

Numbers removed from Garamba for establishment of another population: Scenarios examined included the removal of 2 males, 2 males and 2 females, 3 males and 3 females, 4 males and 4 females, 5 males and 5 females, or 6 males and 6 females. The highest number would provide 10 founders for a second population, even if there were 20% mortality during translocation. The animals moved were selected primarily from the subadult age classes, in order to minimize impact on the existing breeders at Garamba. At attempt was also made to distribute the animals to be translocated across a range of ages, rather than selecting all animals from just a few age cohorts. Results of the simulations would not be affected by which animals are selected from each age class, nor would results change noticeably if the animals of slightly different (but similar) ages are selected for removal.

2.0 removed: Males aged 12 and > 20 years
2.2 removed: Males aged 12 and > 20; females aged 7 and 10
3.3 removed: Males aged 11, 12, and > 20; females aged 4, 7, and 10
4.4 removed: Males aged 7, 11, 12, and > 20; females aged 4, 7, 9, and 10
5.5 removed: Males aged 6, 7, 11, 12, and > 20; females aged 4, 5, 7, 9, and 10
6.6 removed: Males aged 6, 7, 10, 11, 12, and > 20; females aged 4, 5, 7, 9, 10, and 10

Demographic parameters for a second population: Because it is assumed that a second population, if established, would be in a habitat similar to that in Garamba, the demographic rates tested were the same as those examined for the Garamba population. It was also assumed that a small second population would be in an area that could be well protected from poaching. To accomplish this level of security, it is assumed that the population would be contained within a small area, with carrying capacity of just 20 or 50.

Numbers and age/sex composition of a second population: A possible future second population was examined in scenarios with 4, 6, 8, or 10 founders, with the age/sex compositions of these cases the same as in the analyses of removals from Garamba.

Modelling particulars: Duration, number of iterations, output results

The populations were modelled for 100 years, with population performance reported at 25, 50, and 100 years. Although conservation management will likely be concerned with the shorter of these time frames, it can be useful to project population dynamics also for the longer time period. The impacts of population processes may not be apparent until many years after the onset of the effect, especially in long-lived species such as the white rhinoceros. Also, when the probability of extinction predicted for 50 years is low (say, 1% or 2%), it is important to determine whether the population is becoming unstable (so that the probability of extinction at 100 years is much higher) or, alternatively, whether the population was at risk when small, but is relatively safe from extinction if it survives the early years of unstable growth (so that the probability of extinction at 100 years remains low). Thus, projecting population dynamics for long periods of time is important not because we expect the predictions for 100 years to be accurate, but rather because the long-term projections can make it easier to identify whether the population was stable or unstable in the earlier years of the simulation.

Each scenario was simulated 500 times in order to produce consistent estimates of the mean result and the variability in results. This provides an accuracy of the simulation results of about $\pm$ 1 for the percent of simulated populations extant at any time and for the gene diversity retained within the populations, and an accuracy within a few individuals for the predictions of population size. (The "accuracy" of the simulation model is the repeatability of the mean result if the analysis were done again. It is not the expected concordance with the real population, which may diverge from the mean trajectory predicted by the model because of random error, because of inaccurately known or changing population parameters, and because of impacts not included in the model.)

RESULTS

Results for each scenario reported below include:
Det. r -- The deterministic population growth rate, a projection of the mean rate of growth of the population expected from the average birth and death rates. When $r = 0$, a population with no growth is expected; $r < 0$ indicates population decline; $r > 0$ indicates long-term population growth. The value of r is approximately the rate of growth or decline per year. [More precisely, the predicted annual percent change is $100 \times (e^r - 1)$.]

Stoch. r -- The mean rate of stochastic population growth or decline demonstrated by the simulated populations, averaged across years and iterations, for all those simulated populations that are not extinct. Usually, this stochastic r will be less than the deterministic r predicted from birth and death rates because random effects such as temporary deficiencies of one sex or the other for breeding and inbreeding in small populations will depress long-term population growth. The stochastic r from the simulations will be close to the deterministic r if the population growth is steady and robust. The stochastic r will be notably less than the deterministic r if the population is subjected to large fluctuations due to poaching catastrophes or the instability inherent in small populations.

PE -- the probability of population extinction, determined by the proportion of 500 populations of that scenario which have gone extinct in the simulations.

N -- mean population size, averaged across those simulated populations which are not extinct.

SD(N) -- variation across simulated populations (expressed as the standard deviation) in the size of the population at each time interval. SDs greater than about half the size of mean N often indicate highly unstable population sizes, with some simulated populations very near extinction. When SD is large relative to N, and especially when SD increases over the years of the simulation, then the population is vulnerable to large random fluctuations. SD will be small and often declining relative to N when the population is either growing steadily toward the carrying capacity or declining rapidly (and deterministically) toward extinction. Sd will also decline considerably when the population size approaches and is limited by the carrying capacity.

H -- the gene diversity or expected heterozygosity of the extant populations, expressed as a percent of the initial gene diversity of the population. Fitness of individuals usually declines proportionately with gene diversity (Lacy 1993b), with a 10% decline in gene diversity typically causing about 15% decline in survival of mammals (Ralls et al. 1988). Adaptive response to natural selection is also expected to be proportional to gene diversity. Long-term conservation programs often set a goal of retaining about 90% of initial gene diversity (Soulé et al. 1986). Reduction to 75% of gene diversity would be equivalent to one generation of full-sibling or parent-offspring inbreeding.

MODEL PREDICTIONS

Growth of the Garamba population from 1985 through 1995 -- To confirm that the model and parameter values used to examine the dynamics of the Garamba population of Northern White Rhino were appropriate, the size and age structure of the Garamba population at the beginning of 1985 was entered into the model and the population growth through 1995 was simulated. Mortality rates (10% for infants, 1% annual for subadults, and 3% annual for adults) and breeding rates (an average of 40% of adult females breeding each year) as observed in Garamba were used. Because there is uncertainty regarding at what year females begin breeding, the population was modelled with females breeding at year 7, 9, or 11. The growth of the real population was similar to the growth of the simulated populations (see Figure 1), although the range of possible population trajectories with the observed parameters was broad. The mean rate of population growth in the model was r = 0.066, 0.062, and 0.056 for the three ages of breeding. The actual population grew at a rate of r = 0.066. The fluctuations in the modelled populations resulted in variation in the growth rate of SD(r) = 0.078, 0.076, and 0.071. A similar variation in growth rate of SD(r) = 0.072 was observed in the real population. The match between the population growth in the simulations and the real population is a confirmation that the mean birth and death rates used in the model are close to the rates experienced at Garamba. The similarity of the fluctuations in population growth indicates that the model represents well the degree of uncertainty and vulnerability faced by the population at Garamba since 1985.

Predicted future growth and stability of the Garamba population -- The model results indicate that the population of northern white rhinoceros at Garamba National Park is presently sufficiently large so that, with the observed rates of breeding and survival, it is likely to continue to grow at a rapid rate, it is not highly vulnerable to extinction, and it should retain much of the existing genetic diversity (see Table 1, first scenario). The population is projected to reach 500 animals within 41 years. This prediction is cause for optimism, and is possible only because of the protection offered the rhinos at Garamba since 1984. There is reason to hope that the northern white rhino, like the southern white rhino and the greater one-horned Indian rhino, can be recovered to large numbers after having come perilously close to extinction.

As all parties concerned with the future of the rhino recognize, however, a number of threats still face the remnant population, and the notable success of the past decade could still be lost. Renewed poaching or epidemic disease could decimate again the one remaining natural population, and our uncertainty regarding some aspects of the biology of the taxon should cause us to view the results of the population modelling with caution.

Effects of delayed reproduction -- At the workshop at White Oak, concern was expressed by some participants that it is possible that only one or a few of the young adult females in the Garamba population (those born since the population was at its low point in 1984) have begun to breed. Although one or several females bred at about age 7, several females 7 to 10 years of age have not yet produced calves. It might be typical for northern white rhinos (and perhaps southern white rhinos as well) to begin breeding anywhere from 7 to 11 years of age, or it might be that some of the young females at Garamba are for some reason being socially suppressed from breeding. It is also possible that young females at Garamba have bred, but that some quickly lost their first calves. High mortality of first calves is common in many species, and has the same effect on population dynamics as a delayed start of (successful) breeding.

Preliminary modelling of the population (see Options document) assumed that females begin breeding at 7 years, and males begin breeding at 10. To explore the possible effects on population growth and stability of a later age of first breeding, models were examined also with first breeding occurring at 9 and 12 years for females and males, or at 11 and 15 years. It should be noted that the age of first breeding in the model is the age at which females first have the opportunity to breed. With 40% of females breeding each year, the actual age of first breeding for females in the modelled population would extend for a few years beyond the age at which they could first breed. (For example, 40% would breed at age 7, 40% would breed at age 8, etc.).

With the observed mortality rates, and in the absence of any poaching, a delay of first breeding until 9 years or even 11 years for females would be predicted to slow population growth, but not to cause noticeable vulnerability to extinction (see Table 1, top half of scenarios). The age of first breeding of males would have very little if any impact on population stability, because the species is polygamous and a few males could mate with many females.

Sensitivity of population growth and viability to variation in calf mortality, adult mortality, and breeding rates -- There is some uncertainty in the rates of mortality and breeding, both in the past and in the future as the habitat, population density, and social structure might change. With the ranges of values examined (40%, 30%, or 20% of adult females breeding; 10% or 20% calf mortality; 3% or 5% annual adult mortality), population growth and stability was most strongly impacted by the breeding rate, much less impacted by the rate of adult mortality, and still less by calf mortality (compare scenarios in Tables 1 and 2). Extinctions among the simulated populations did not occur except when only 20% of adult females produced young each year and there was 5% annual mortality of adults (scenarios 3, 6, 9, 12, 15, and 18 in Table 2). Also, it was only among these cases that there were scenarios in which the simulated populations failed to grow to more than 100 rhinos and failed to retain at least 90% of the original gene diversity. Overall, these results would suggest that the population at Garamba is now large enough so that it would be considered viable and secure, if at least 30% of females breed or adult mortality stays low. It is important to note, however, that *these conclusions assume that neither resumed poaching nor other catastrophes will again decimate the population.*

Effects of poaching -- Even moderate episodic poaching, with the loss of 25% of the rhinos (presently, 7 or 8 animals) every 10 years, could threaten the growth and persistence of the population at Garamba (see upper half of scenarios in Table 3). With such poaching, the population is not susceptible to random extinctions only if females begin breeding at 7 years, the breeding rate remains high (40% per year), and calf and adult mortality remain low (10% and 3%, respectively). Growth is slowed substantially and the population is vulnerable to extinction if there is moderate episodic poaching and any of the demographic rates drop below the more optimistic estimates.

Severe episodic poaching, with the loss of 50% of the population every 15 years substantially slows population growth and can cause population extinction (even within 25 years) regardless of whether reproduction remains high and natural mortality remains low (see lower half of scenarios in Table 3).

A continuous loss of animals to poaching can be even more destabilizing than the episodic poaching. A loss of about one rhino per year causes the population to be vulnerable to extinction unless breeding remains at 40% per year (scenarios 1, 4, and 7 in Table 4). However, even in these cases, a continuous loss of one rhino per year to poaching reduces population growth by about half relative to the growth possible if poaching continues to be prevented. At a higher rate of continuous poaching, causing a loss of 2 animals per year, the population does not grow, loses considerable genetic diversity, and is highly vulnerable to extinction.

It is very clear from the past history of the population, from the history of many other populations of rhinos, and from the analyses that poaching is the most critical threat to the population. Populations of long-lived, slow-breeding species such as the rhinoceroses cannot sustain more than very minimal rates of poaching.

Effects of removals -- In the absence of poaching, removal of 2, 4, 6, 8, 10, or 12 rhinos from the present population of 31 rhinos at Garamba would slow population growth slightly, but would not cause increased vulnerability to extinction, nor cause genetic diversity to drop below 90% (compare Tables 5, 6, and 7 to Table 1).

If the population at Garamba is destabilized by moderate episodic poaching, then the removal of some rhinos further destabilizes the population. The removal of even 2 pairs of rhinos slightly slows population growth and increases the probability of extinction (compare top half of Table 8 to the top half of Table 3). The removal of up to 12 rhinos further increases the rate of extinction and also causes faster loss of genetic diversity (compare Tables 9 and 10 to Table 3).

If episodic poaching occurs at the higher level in Garamba, then the removal of animals for translocation further increases the threat of extinction (Tables 11-13). This effect is most noticeable in the early years, because the removals leave a smaller population at

Garamba to withstand poaching. The effect is lessened in later years, especially when only a small number of rhinos are removed, and the population is highly vulnerable to extinction whether or not some animals were removed at the beginning. Similar effects are seen with removals from a population at Garamba threatened by continuous poaching (compare Tables 14, 15, and 16 to Table 4).

Thus, from a narrow biological perspective, the question of possibly translocating some rhinos to another area of natural habitat would seem to depend primarily on where the rhinos could be best protected from poaching or natural catastrophes, and where the habitat is optimal for reproduction, survival, and population growth. If the population in Garamba is kept secure from poaching, it could provide animals for translocation to a second population without incurring a considerable risk to the population remaining at Garamba. Unfortunately, if the population at Garamba is vulnerable to poaching, then removal of some animals further increases the threat of extinction. As recognized at the workshop, however, if the population at Garamba were tragically decimated by poaching (or other factors), then the removal of some animals might accelerate the decline at Garamba but thereby prevent the ultimate extinction of the taxon.

Numbers needed to establish a second population -- Because removing animals from Garamba involves a possible risk to those translocated animals, and makes the Garamba population more vulnerable to extinction if poaching resumes, there would not likely be any conservation value to translocating rhinos unless a second population that could be established had a high probability of growth and persistence.

A second population started with just 4 rhinos has a reasonable possibility of growing to carrying capacity and surviving, but is moderately to highly vulnerable to extinction even with the best rates of reproduction and survival (see Table 17). Not surprisingly, extinction of the new small population can occur quickly after establishment. An increased carrying capacity (from 20 to 50) of a new population does relatively little to protect it from extinction, but does allow for a larger population to be obtained if the population does not go extinct. A small population started from just four founders becomes quickly inbred and loses genetic diversity rapidly. The probability of failure of a second population with 4 founders is substantially increased if adult mortality is greater (5% rather than 3%; see Table 18).

The chance that a second population will survive is better when more founders are translocated (see Tables 17-24). With the best breeding and survival (first scenario in Tables 17, 19, 21, and 13), 8 founders are needed to ensure that the probability of extinction is kept below the 1% detectable by the model. The extreme vulnerability of populations started with just 4 founders can be illustrated by noting that a single population with 8 founders is more likely to persist than either of two populations of 4 founders each. (Compare PE values in Table 21 to the square of PE values from the same scenarios in Table 17: For example, with 30% breeding and first breeding at 9 years, a population started with 8 founders has a 1% probability of extinction within 100 years, while there is a 4% probability that two populations each started with 4 founders will both go extinct.) Thus, initiating additional populations with too few animals can be wasteful, risking translocated animals with little prospect for success. If adult mortality is kept to 3% and breeding rates are 30% or more, populations established with 10 founders appear to have a high probability of persistence

(Table 23). If breeding is poor (20%) or adult mortality is high (5%) at a new site, a population started with even 10 founders is vulnerable to extinction.

Although many of the hypothetical new populations survived in the simulations, they all become inbred and lost substantial genetic diversity. Populations started with 4, 6, 8, and 10 founders typically lost about 20%, 15%, 12%, and 10% of their gene diversity within the first few generations (25 years), with continuing losses (although at slower rates) subsequently. If a second population becomes inbred and loses genetic diversity, it may become at greater risk of extinction than indicated by the model results. Moreover, loss of fitness and adaptability could prevent the successful translocation of animals from that population back to Garamba or elsewhere. For example, Jiménez et al. (1994) found that inbred wild mice which had lost 25% of gene diversity had only about half the survivorship of non-inbred mice when released into their natural habitat. It is not known what the impact of inbreeding on rhinos might be, but the experimental population of mice was less susceptible to the effects of inbreeding in captivity than are most mammals.

Thus, a small second natural population of northern white rhinos would need to be managed interactively with the Garamba population (or, eventually, other populations), occasionally exchanging migrants to prevent inbreeding within the small population. Translocation of a few animals between the populations each generation would prevent rapid loss of adaptive genetic variation and genetic divergence of the populations. If the Garamba population were lost after a small second population had been established elsewhere, it would probably be extremely difficult to recover the taxon to large numbers living freely in natural habitats.

POSSIBLE FUTURE MODELLING

The above modelling was conducted to provide some guidance regarding the questions about population growth and probability of persistence that were asked at the White Oak meeting. It is hoped that these analyses will assist the conservation efforts on behalf of the northern white rhinos. Further modeling, with different parameters or testing different management options could be conducted if and when that is deemed useful by the governmental authorities and NGOs who have accepted the responsibility to ensure the future of the taxon. As monitoring and research provide more precise estimates of the biological parameters, and as the population continues to change in numbers, age and sex distribution, and biological characteristics, model predictions could be examined with revised estimates. Moreover, specific conservation actions that are suggested could be examined with simulation modelling to help identify the likelihood of success.

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Table Legend

INPUT VALUES

1st Yr Breed	Mean age at which females/males produce their first calf.
% A♀ Breed	Percent of adult females which breed in the average year.
Mort. C,A	Percent annual mortality of calves and adults.
K	Carrying capacity of the habitat.
Catastr. Frq.	Probability of a poaching catastrophe, per year.
Catastr. Sev.	Percent of animals killed in each poaching catastrophe.
Det. r	Deterministic population growth (r) predicted from the mean birth and death rates (as influenced by any poaching catastrophes)
Rem.	Number of males/females removed from the Garamba population.
Fndr ♂,♀	Number of translocated males/females used as founders of a hypothetical second free-ranging population.

Input columns left blank repeat the parameter values from the previous scenario.

MODEL PREDICTIONS

Stoc. r	Mean population growth (r) in the stochastic simulations.
PE	Probability of extinction, assessed by the percent of simulated populations extinct by that year.
N	Mean size of the simulated populations still extant at that year.
SD	Standard deviation in the population size across simulated populations.
H	Gene diversity (expected heterozygosity) of extant populations, as a percent of the initial gene diversity.

SCENARIO DESCRIPTIONS

High Repr.	Reproductive rates set at the level observed among the five breeding females at Garamba, with 40% of adult females breeding each year, or a mean intercalf interval of 2.5 years.
Mid Repr.	Reproductive rates set at 30% of adult females breeding each year, or a mean intercalf interval of 3.3 years.
Low Repro.	Reproductive rates set at 20% of adult females breeding each year, or a mean intercalf interval of 5 years.
Brd. Delay	Age of first breeding for females set at 9 years, for males at 12 years.
Long Brd. Delay	Age of first breeding for females set at 11 years, for males at 15 years.

Table 1. GARAMBA -- NO POACHING, NO REMOVALS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Rem	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C.A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,3	500	0	0	.072	0	.072	0	206	53	97	0	497	15	97	0	499	7	96
Mid Repr.		30					.054		.053	0	131	36	97	0	423	91	97	0	498	8	96
Low Repr.		20					.029		.028	0	73	19	97	0	152	64	96	0	416	110	95
Brd. Delay	9,12	40					.062		.062	0	156	37	97	0	484	42	97	0	497	6	96
		30					.046		.046	0	107	26	97	0	336	103	97	0	497	10	96
		20					.024		.023	0	65	17	97	0	117	47	96	0	324	132	95
Long Brd. Delay	11,15	40					.054		.054	0	126	29	97	0	430	83	97	0	498	7	96
		30					.039		.039	0	87	21	97	0	236	82	97	0	495	18	96
		20					.019		.018	0	56	13	97	0	91	36	96	0	219	112	94
High Calf Mortality	7,10	40	20,3				.065		.066	0	178	53	97	0	489	38	97	0	497	8	96
		30					.047		.047	0	114	33	97	0	358	113	96	0	496	11	96
		20					.023		.022	0	65	19	97	0	118	54	95	0	314	144	94
	9,12	40					.055		.057	0	135	36	97	0	452	75	97	0	497	8	96
		30					.039		.041	0	95	24	97	0	272	95	96	0	494	18	96
		20					.018		.018	0	59	15	97	0	96	41	96	0	223	121	94
	11,15	40					.048		.049	0	114	28	97	0	376	101	97	0	497	8	96
		30					.033		.035	0	81	19	97	0	204	73	96	0	486	38	96
		20					.014		.014	0	54	14	97	0	79	33	95	0	149	90	94

Table 2. GARAMBA -- NO POACHING, NO REMOVALS, HIGH ADULT MORTALITY

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Rem	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,5	500	0	0	.062	0	.059	0	159	56	97	0	455	83	96	0	494	16	96
Mid Repr.		30					.042		.040	0	98	37	96	0	269	124	96	0	477	55	95
Low Repr.		20					.017		.013	0	53	19	96	0	78	42	94	1	153	109	91
Brd. Delay	9,12	40					.052		.050	0	125	43	97	0	386	113	96	0	494	15	96
		30					.036		.033	0	82	26	97	0	196	91	96	0	461	75	95
		20					.013		.010	0	48	15	96	0	65	33	94	1	114	82	91
Long Brd. Delay	11,15	40					.045		.043	0	99	29	97	0	295	108	96	0	494	13	96
		30					.030		.028	0	71	20	97	0	149	67	96	0	410	116	95
		20					.010		.007	0	46	14	96	0	57	27	94	1	85	58	90
High Calf Mortality	7,10	40	20,5				.054		.054	0	139	50	97	0	416	105	96	0	490	21	96
		30					.035		.035	0	89	35	96	0	220	114	95	0	459	77	95
		20					.010		.006	0	47	18	96	0	62	39	93	4	93	84	89
	9,12	40					.045		.046	0	112	37	97	0	341	123	96	0	490	28	96
		30					.029		.029	0	75	27	96	0	165	84	95	0	414	114	95
		20					.007		.004	0	43	15	96	0	52	28	93	4	69	53	89
	11,15	40					.039		.039	0	92	30	97	0	257	108	96	0	482	45	96
		30					.024		.024	0	65	21	97	0	126	60	95	0	348	134	95
		20					.004		.002	0	42	13	96	0	48	23	94	3	58	44	89

Table 3. GARAMBA -- EPISODIC POACHING, NO REMOVALS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Rem	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
Moderate Poaching	7,10	40	10,3	500	.10	25	.047	0	.040	0	106	54	96	0	279	149	95	0	434	96	94
		30					.028		.021	0	68	35	95	0	136	101	94	1	275	162	91
		20					.004		-.006	1	39	20	94	4	44	33	90	20	48	54	84
	9,12	40					.037		.030	0	82	41	96	0	193	123	95	0	375	142	93
		30					.021		.014	0	58	28	95	1	95	72	93	4	196	152	90
		20					-.001		-.012	0	34	18	94	5	34	27	90	31	35	42	81
	11,15	40					.028		.021	0	66	33	95	1	130	97	94	1	287	168	92
		30					.014		.005	0	46	23	95	1	63	47	92	8	117	121	87
		20					-.006		-.017	0	29	15	94	7	26	20	89	40	23	25	81
Severe Poaching	7,10	40			.067	50	.038		.020	1	87	69	94	5	179	161	92	13	277	179	90
		30					.020		-.001	3	55	44	93	12	95	112	90	30	148	152	86
		20					-.005		-.029	9	31	24	92	25	29	34	85	68	36	52	79
	9,12	40					.028		.011	2	70	52	94	7	139	133	91	15	207	176	88
		30					.012		-.008	5	46	35	93	16	77	86	89	35	104	127	85
		20					-.010		-.029	4	29	23	92	27	28	32	86	68	26	33	79
	11,15	40					.020		.001	5	55	43	93	13	95	106	90	29	172	167	87
		30					.005		-.016	9	39	29	93	21	50	52	89	46	68	96	84
		20					-.015		-.035	9	26	19	92	33	22	24	86	75	22	34	77

Table 4. GARAMBA -- CONTINUOUS POACHING, NO REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
Low Poaching	7,10	40	10,3	500	1	3.3	.039	0	.036	0	88	28	96	0	224	100	95	0	475	67	94
		30					.020		.016	0	56	19	95	0	89	43	93	1	196	122	91
		20					-.004		-.013	0	31	10	94	2	27	15	89	28	20	15	78
	9,12	40					.029		.026	0	68	22	96	0	139	62	95	0	388	126	93
		30					.012		.008	0	45	15	95	0	59	28	92	1	93	64	88
		20					-.009		-.018	0	27	10	94	4	22	12	88	40	15	11	76
	11,15	40					.020		.017	0	53	16	96	0	86	36	94	0	214	116	92
		30					.006		.000	0	37	12	95	1	42	22	92	6	49	38	86
		20					-.014		-.022	0	25	8	94	4	17	10	88	50	11	8	74
Higher Poaching	7,10	40			1	6.7	.003		-.009	1	35	15	93	5	35	22	88	25	31	27	77
		30					-.016		-.032	1	22	9	91	17	15	10	82	78	9	6	66
		20					-.040		-.052	5	13	6	90	50	7	4	77	99	4	2	54
	9,12	40					-.007		-.020	0	28	12	93	7	23	15	86	49	17	13	74
		30					-.024		-.038	1	19	8	91	22	11	7	81	91	7	6	66
		20					-.045		-.059	6	12	6	89	62	6	3	76	100	--	--	--
	11,15	40					-.016		-.033	1	21	9	91	17	15	9	83	78	9	7	68
		30					-.030		-.047	2	15	7	90	42	9	6	79	95	5	5	66
		20					-.050		-.062	7	11	5	89	67	5	3	76	100	--	--	--

Table 5. GARAMBA -- NO POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
4 Rhinos Removed	7,10	40	10,3	500	0	0	.072	2,2	.071	0	171	49	97	0	494	26	96	0	499	7	96
		30					.054		.052	0	108	31	97	0	378	110	96	0	498	7	96
		20					.029		.027	0	61	19	96	0	123	53	95	0	372	131	94
	9,12	40					.062		.061	0	134	35	97	0	468	62	97	0	499	7	96
		30					.046		.044	0	90	23	97	0	279	99	96	0	497	11	96
		20					.024		.022	0	55	15	96	0	98	40	95	0	273	127	94
	11,15	40					.054		.053	0	104	23	97	0	386	96	97	0	499	6	96
		30					.039		.038	0	75	18	97	0	199	68	96	0	495	20	96
		20					.019		.018	0	48	12	96	0	78	30	95	0	192	100	93
6 Rhinos Removed	7,10	40					.072	3,3	.071	0	161	46	97	0	493	28	96	0	499	7	96
		30					.054		.052	0	103	30	96	0	366	113	96	0	498	9	95
		20					.029		.027	0	57	17	96	0	116	53	95	0	356	136	94
	9,12	40					.062		.061	0	123	3	97	0	455	77	96	0	499	7	96
		30					.046		.044	0	83	23	96	0	258	93	96	0	498	7	95
		20					.024		.021	0	50	14	96	0	88	38	95	0	244	124	93
	11,15	40					.054		.053	0	99	24	97	0	368	101	96	0	499	7	96
		30					.039		.038	0	71	17	96	0	187	66	96	0	493	30	95
		20					.019		.017	0	44	12	96	0	71	27	95	0	167	90	93

Table 6. GARAMBA -- NO POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
8 Rhinos Removed	7,10	40	10,3	500	0	0	.072	4,4	.070	0	146	42	96	0	486	45	96	0	499	7	95
		30					.054		.052	0	94	26	96	0	348	109	96	0	498	8	95
		20					.029		.026	0	52	15	95	0	107	47	94	0	336	143	93
	9,12	40					.062		.060	0	109	29	96	0	431	85	96	0	498	7	95
		30					.046		.044	0	74	20	96	0	236	90	95	0	496	15	95
		20					.024		.022	0	46	12	96	0	83	36	94	0	235	123	93
	11,15	40					.054		.052	0	90	22	96	0	341	101	96	0	499	6	95
		30					.039		.038	0	64	16	96	0	172	63	95	0	485	43	95
		20					.019		.017	0	40	11	96	0	65	27	94	0	148	84	92
10 Rhinos Removed	7,10	40					.072	5,5	.070	0	131	38	96	0	481	50	96	0	499	7	95
		30					.054		.051	0	84	26	96	0	305	115	95	0	498	9	95
		20					.029		.025	0	46	14	95	0	93	44	93	0	297	143	92
	9,12	40					.062		.060	0	100	26	96	0	414	95	96	0	499	7	95
		30					.046		.044	0	69	19	96	0	215	86	95	0	496	19	94
		20					.024		.020	0	41	12	95	0	74	32	94	0	202	121	92
	11,15	40					.054		.052	0	81	20	96	0	306	99	95	0	498	7	95
		30					.039		.037	0	58	15	96	0	154	58	95	0	478	61	94
		20					.019		.016	0	37	10	95	0	58	25	93	0	133	78	91

Table 7. GARAMBA -- NO POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
12 Rhinos Removed	7,10	40	10,3	500	0	0	.072	6,6	.069	0	117	36	95	0	467	68	95	0	499	7	95
		30					.054		.050	0	73	24	95	0	261	111	94	0	497	10	94
		20					.029		.025	0	41	13	94	0	84	40	93	0	279	139	91
	9,12	40					.062		.059	0	87	24	95	0	379	106	95	0	499	6	95
		30					.046		.043	0	60	17	95	0	191	76	94	0	491	35	94
		20					.024		.020	0	36	11	95	0	64	30	93	0	170	105	91
	11,15	40					.054		.051	0	70	20	95	0	263	97	95	0	499	10	95
		30					.039		.037	0	51	14	95	0	139	57	94	0	467	80	94
		20					.019		.016	0	32	9	95	0	52	23	92	0	116	70	90
2 Males Removed	7,10	40					.072	2,0	.072	0	205	56	97	0	498	13	97	0	499	7	96
		30					.054		.053	0	131	34	97	0	427	87	97	0	498	6	96
		20					.029		.028	0	71	19	96	0	146	58	95	0	412	114	95
	9,12	40					.062		.062	0	157	40	97	0	483	46	97	0	499	6	96
		30					.046		.046	0	105	25	97	0	328	101	96	0	498	7	96
		20					.024		.024	0	64	15	97	0	117	43	96	0	329	124	95
	11,15	40					.054		.053	0	123	29	97	0	424	88	97	0	499	7	96
		30					.039		.039	0	88	21	97	0	237	81	96	0	497	15	96
		20					.019		.019	0	56	13	97	0	88	33	95	0	213	106	94

Table 8. GARAMBA -- MODERATE EPISODIC POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
4 Rhinos Removed	7,10	40	10,3	500	.10	25	.047	2,2	.040	0	93	46	95	0	257	145	94	0	439	97	93
		30					.028		.020	0	59	30	95	1	117	90	93	3	270	172	90
		20					.004		-.007	1	33	18	94	6	37	29	89	25	46	52	82
	9,12	40					.037		.030	0	71	34	95	0	168	114	94	1	367	148	93
		30					.021		.012	0	50	24	95	1	79	57	92	6	166	144	89
		20					-.001		-.012	1	30	16	94	8	32	25	89	34	30	34	80
	11,15	40					.028		.021	0	58	30	95	1	114	84	93	2	276	165	91
		30					.014		.006	1	42	21	94	2	60	44	91	8	107	108	87
		20					-.006		-.017	1	27	15	94	9	24	19	88	45	23	25	80
6 Rhinos Removed	7,10	40					.047	3,3	.040	0	86	44	95	0	247	146	94	0	428	116	93
		30					.028		.019	1	54	27	94	1	104	82	92	4	244	171	89
		20					.004		-.009	2	30	16	93	7	33	26	88	31	42	61	80
	9,12	40					.037		.030	0	66	35	95	0	160	115	93	1	361	151	92
		30					.021		.011	1	45	24	94	2	73	58	91	6	152	143	87
		20					-.001		-.016	1	27	14	93	11	26	20	87	46	27	28	79
	11,15	40					.028		.021	0	53	26	95	1	101	74	93	1	258	166	90
		30					.014		.003	1	36	19	94	4	52	40	90	15	97	102	86
		20					-.006		-.018	2	24	13	93	12	23	18	87	49	22	25	79

Table 9. GARAMBA -- MODERATE EPISODIC POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
8 Rhinos Removed	7,10	40	10,3	500	.10	25	.047	4,4	.039	0	79	42	95	1	226	141	93	1	422	116	92
		30					.028		.020	0	50	27	94	2	104	79	91	5	245	173	89
		20					.004		-.009	1	26	14	92	9	30	24	87	36	38	47	79
	9,12	40					.037		.028	0	58	29	94	1	137	96	92	1	339	157	91
		30					.021		.010	1	41	21	94	3	67	54	91	10	141	131	87
		20					-.001		-.014	2	24	12	93	10	24	20	87	40	24	30	78
	11,15	40					.028		.020	1	47	23	94	2	95	66	92	4	251	165	90
		30					.014		.004	2	34	17	93	4	47	33	90	16	91	100	85
		20					-.006		-.019	3	21	11	92	14	19	15	86	55	18	17	76
10 Rhinos Removed	7,10	40					.047	5,5	.038	0	70	37	94	1	211	139	92	1	405	131	91
		30					.028		.018	1	44	24	93	3	87	73	90	5	206	161	87
		20					.004		-.010	1	26	15	92	10	29	25	86	38	33	44	78
	9,12	40					.037		.028	0	54	29	94	1	132	102	92	2	336	162	90
		30					.021		.010	1	36	18	93	3	59	44	90	10	127	119	85.
		20					-.001		-.015	2	23	12	92	14	23	18	86	47	23	24	77
	11,15	40					.028		.020	0	42	23	93	2	86	68	91	5	233	165	88
		30					.014		.004	1	31	16	93	6	46	35	90	16	83	92	85
		20					-.006		-.019	1	20	11	91	17	19	15	85	54	17	15	76

Table 10. GARAMBA -- MODERATE EPISODIC POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
12 Rhinos Removed	7,10	40	10,3	500	.10	25	.047	6,6	.037	0	62	35	93	1	185	129	92	2	399	138	90
		30					.028		.017	1	38	20	92	4	77	64	89	8	190	156	86
		20					.004		-.010	2	22	12	91	11	25	21	85	39	29	32	77
	9,12	40					.037		.027	1	48	26	93	2	111	90	91	3	308	167	88
		30					.021		.007	2	31	17	92	7	52	40	88	15	110	115	84
		20					-.001		-.015	3	19	11	91	19	20	16	85	52	20	23	76
	11,15	40					.028		.018	1	37	19	93	3	72	55	90	6	198	158	87
		30					.014		.002	2	27	14	92	9	38	29	88	21	65	65	83
		20					-.006		-.021	4	17	10	91	23	17	13	85	61	16	18	74
2 Males Removed	7,10	40					.047	2,0	.042	0	108	56	96	0	292	150	95	0	436	95	94
		30					.028		.023	0	66	34	95	1	139	100	93	2	302	161	92
		20					.004		-.005	0	38	20	94	3	44	36	90	21	55	60	84
	9,12	40					.037		.032	0	83	40	96	0	209	134	94	0	386	130	93
		30					.021		.014	0	55	27	95	1	94	69	93	4	189	152	90
		20					-.001		-.010	0	34	19	94	6	35	28	90	28	33	39	81
	11,15	40					.028		.022	0	68	32	95	1	136	97	94	2	298	161	92
		30					.014		.006	0	46	23	95	1	66	49	92	7	109	104	88
		20					-.006		-.016	1	31	15	94	7	26	19	89	39	24	29	80

Table 11. GARAMBA -- SEVERE EPISODIC POACHING, REMOVALS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Rem ♂,♀	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
4 Rhinos Removed	7,10	40	10,3	500	.067	50	.038	2,2	.018	4	81	64	94	7	170	160	90	15	260	188	88
		30					.020		-.001	5	50	38	92	15	82	92	89	31	137	148	85
		20					-.005		-.027	13	30	23	92	35	36	41	86	68	47	85	81
	9,12	40					.028		.010	3	61	47	94	8	118	124	91	18	187	169	87
		30					.012		-.009	7	41	31	93	19	62	73	88	44	98	125	85
		20					-.010		-.034	10	26	20	91	33	24	27	85	77	22	24	78
	11,15	40					.020		-.001	4	48	36	93	14	79	90	89	31	143	153	86
		30					.005		-.017	5	32	25	92	24	46	51	88	52	75	113	84
		20					-.015		-.034	13	23	16	91	36	21	21	85	76	25	34	78
6 Rhinos Removed	7,10	40					.038	3,3	.019	3	74	57	93	8	166	157	91	16	259	181	88
		30					.020		.000	5	47	35	92	14	80	94	88	31	137	154	84
		20					-.005		-.024	9	27	21	91	33	33	36	86	66	49	76	79
	9,12	40					.028		.008	5	53	40	93	14	107	110	90	24	190	169	86
		30					.012		-.011	5	36	28	91	21	57	67	87	45	92	125	83
		20					-.010		-.033	9	23	17	91	37	24	25	85	77	18	19	76
	11,15	40					.020		-.001	5	43	35	92	16	78	88	89	34	137	143	86
		30					.005		-.015	7	32	23	92	22	42	49	87	53	79	100	83
		20					-.015		-.036	12	22	16	91	39	19	18	85	79	14	15	76

Table 12. GARAMBA -- SEVERE EPISODIC POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem. ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
8 Rhinos Removed	7,10	40	10,3	500	.067	50	.038	4,4	.016	4	64	50	92	11	152	148	90	19	232	182	87
		30					.020		-.002	5	41	32	91	15	70	82	87	36	129	147	83
		20					-.005		-.030	12	23	19	90	36	25	31	83	74	28	42	77
	9,12	40					.028		.005	6	50	39	92	13	99	109	89	29	178	164	86
		30					.012		-.010	8	34	27	91	22	55	64	87	45	91	120	82
		20					-.010		-.031	10	23	17	91	36	22	20	84	74	22	28	77
	11,15	40					.020		-.003	9	40	31	92	18	70	82	88	39	136	147	84
		30					.005		-.017	8	29	21	91	26	37	42	86	58	69	99	82
		20					-.015		-.035	14	19	13	90	40	16	14	84	81	19	21	77
10 Rhinos Removed	7,10	40					.038	5,5	.016	4	57	46	91	10	129	130	89	21	244	182	87
		30					.020		-.002	7	40	31	91	19	71	73	88	38	120	139	84
		20					-.005		-.028	11	21	16	90	39	27	29	84	73	30	41	78
	9,12	40					.028		.007	9	46	36	91	16	97	109	88	29	178	169	85
		30					.012		-.012	11	30	23	90	27	49	59	86	49	84	121	80
		20					-.010		-.034	12	19	14	89	43	21	22	83	81	22	29	76
	11,15	40					.020		-.004	9	35	28	91	24	66	74	87	40	116	138	83
		30					.005		-.020	13	26	20	90	34	35	42	86	61	53	86	78
		20					-.015		-.038	15	18	13	90	47	17	18	84	86	20	33	76

Table 13. GARAMBA -- SEVERE EPISODIC POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem. ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
12 Rhinos Removed	7,10	40	10,3	500	.067	50	.038	6,6	.014	5	51	41	91	12	112	127	87	22	224	182	84
		30					.020		-.004	9	34	26	90	20	58	70	85	43	119	139	82
		20					-.005		-.029	13	20	16	89	40	24	24	83	76	26	35	75
	9,12	40					.028		.005	6	40	30	91	17	79	95	87	31	157	153	83
		30					.012		-.011	12	27	19	90	28	43	45	86	52	80	115	80
		20					-.010		-.036	18	17	12	89	46	18	18	81	85	21	51	76
	11,15	40					.020		-.004	10	33	25	90	24	68	78	87	43	130	141	83
		30					.005		-.019	12	23	17	90	31	33	36	85	61	59	92	78
		20					-.015		-.039	17	15	11	89	51	17	18	82	88	18	24	76
2 Males Removed	7,10	40					.038	2,0	.021	3	83	65	94	7	187	160	92	12	268	175	89
		30					.020		.002	4	60	43	93	11	103	112	90	26	157	162	86
		20					-.005		-.025	5	32	25	92	24	36	40	87	63	39	59	78
	9,12	40					.028		.010	3	64	50	93	8	119	124	91	20	211	174	88
		30					.012		-.008	5	46	37	93	17	67	76	89	38	106	135	84
		20					-.010		-.030	8	30	22	92	31	28	30	86	70	33	44	80
	11,15	40					.020		.003	4	60	46	93	11	95	105	90	24	165	161	87
		30					.005		-.015	4	38	29	92	19	48	56	88	48	66	90	84
		20					-.015		-.035	7	25	19	91	35	23	26	85	77	25	50	80

Table 14. GARAMBA -- CONTINUOUS LOW POACHING, REMOVALS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Rem. ♂,♀	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
4 Rhinos Removed	7,10	40	10,3	500	1	3.3	.039	2,2	.035	0	74	25	95	0	190	87	94	0	465	85	93
		30					.020		.015	0	48	17	95	0	79	40	92	2	175	120	90
		20					-.004		-.012	0	28	10	94	3	25	15	88	30	20	18	78
	9,12	40					.029		.025	0	57	19	95	0	116	56	94	0	349	142	92
		30					.012		.007	0	39	13	94	0	51	26	92	2	77	58	87
		20					-.009		-.019	0	24	9	93	5	18	10	87	45	12	9	74
	11,15	40					.020		.016	0	46	14	95	0	74	33	93	0	167	101	91
		30					.006		.000	0	33	11	94	1	38	19	91	10	45	32	85
		20					-.014		-.025	0	21	7	93	9	15	8	86	59	9	7	70
6 Rhinos Removed	7,10	40					.039	3,3	.035	0	68	24	95	0	171	81	94	0	458	88	93
		30					.020		.015	0	45	16	94	0	71	39	92	2	156	113	88
		20					-.004		-.016	0	24	10	93	8	21	13	86	38	16	13	74
	9,12	40					.029		.024	0	52	17	95	0	102	48	93	0	314	147	91
		30					.012		.006	0	36	13	94	0	48	26	91	4	71	54	85
		20					-.009		-.020	0	21	9	93	9	18	11	86	50	12	10	74
	11,15	40					.020		.015	0	42	13	94	0	68	33	92	1	154	105	90
		30					.006		-.001	0	31	10	94	1	35	18	90	11	40	30	83
		20					-.014		-.025	0	19	7	93	11	14	8	85	65	9	6	72

Table 15. GARAMBA -- CONTINUOUS LOW POACHING, REMOVALS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Rem. ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
8 Rhinos Removed	7,10	40	10,3	500	1	3.3	.039	4,4	.035	0	63	22	94	0	161	79	93	0	448	102	92
		30					.020		.014	0	40	15	94	1	64	36	91	3	138	102	87
		20					-.004		-.015	1	23	9	92	5	20	13	85	43	16	13	74
	9,12	40					.029		.024	0	49	17	94	0	96	49	92	1	288	150	91
		30					.012		.005	0	33	12	93	1	43	23	90	8	63	47	85
		20					-.009		-.022	1	19	7	92	10	15	9	84	58	11	7	72
	11,15	40					.020		.015	0	38	13	94	0	61	29	91	1	137	90	89
		30					.006		-.002	0	27	10	93	2	31	17	89	14	35	27	82
		20					-.014		-.026	1	18	7	92	14	13	8	84	70	8	7	68
10 Rhinos Removed	7,10	40					.039	5,5	.033	0	56	22	94	0	138	74	92	0	417	127	91
		30					.020		.012	0	35	13	93	1	56	32	90	4	116	95	85
		20					-.004		-.018	1	20	8	91	9	18	12	84	50	13	11	72
	9,12	40					.029		.022	0	43	15	94	0	82	42	91	0	247	146	89
		30					.012		.004	0	29	12	93	2	40	23	89	11	61	49	83
		20					-.009		-.022	1	17	7	91	13	14	8	83	65	10	8	69
	11,15	40					.020		.013	0	34	12	93	0	53	28	90	4	122	88	87
		30					.006		-.003	0	24	9	92	3	28	16	88	19	32	24	80
		20					-.014		-.026	1	16	6	91	15	11	7	82	73	8	6	69

Table 16. GARAMBA -- CONTINUOUS LOW POACHING, REMOVALS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Rem. ♂,♀	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
12 Rhinos Removed	7,10	40	10,3	500	1	3.3	.039	6,6	.032	0	50	19	93	0	122	70	91	0	387	139	90
		30					.020		.011	0	32	13	92	1	49	29	88	5	99	80	84
		20					-.004		-.018	1	18	8	90	13	16	10	82	60	14	13	71
	9,12	40					.029		.022	0	38	14	93	0	76	38	90	0	227	141	88
		30					.012		.003	0	26	10	92	3	33	18	88	13	48	37	81
		20					-.009		-.023	1	15	7	90	19	13	9	82	68	10	8	69
	11,15	40					.020		.012	0	30	11	92	1	48	26	89	4	99	72	85
		30					.006		-.006	0	22	8	92	4	24	15	86	26	27	22	79
		20					-.014		-.028	2	14	6	90	25	10	6	81	80	7	6	64
2 Males Removed	7,10	40					.039	2,0	.037	0	89	30	96	0	225	101	95	0	477	58	94
		30					.020		.016	0	55	18	95	0	88	42	93	1	190	119	91
		20					-.004		-.012	0	31	12	94	1	27	17	89	28	20	16	79
	9,12	40					.029		.027	0	68	22	95	0	135	57	94	0	385	129	93
		30					.012		.008	0	45	14	95	0	59	28	93	2	90	61	88
		20					-.009		-.019	0	27	10	94	4	20	12	88	41	12	10	74
	11,15	40					.020		.018	0	54	16	95	0	90	38	94	0	211	111	92
		30					.006		.001	0	37	12	95	0	43	23	92	7	48	35	86
		20					-.014		-.023	0	24	8	94	5	17	10	87	56	10	6	74

Table 17. NEW POPULATION, 4 FOUNDERS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,3	20	0	0	.072	2,2	.051	4	17	4	80	5	19	2	74	6	19	2	65
Mid Repr.		30					.054		.033	8	15	5	79	11	17	4	73	14	18	3	65
Low Repr.		20					.029		.010	15	10	5	77	29	13	6	70	47	14	5	63
Brd. Delay	9,12	40					.062		.043	6	16	5	80	7	18	3	74	9	19	2	65
		30					.046		.026	10	13	5	78	15	16	5	73	20	17	4	65
		20					.024		.005	15	9	4	78	33	12	6	71	53	12	5	62
Long Brd. Delay	11,15	40					.054		.035	7	14	5	79	11	18	4	75	12	18	3	67
		30					.039		.021	12	11	5	78	21	15	5	74	26	17	4	65
		20					.019		.002	19	9	4	78	38	11	6	72	60	12	5	63
Higher K	7,10	40		50			.072		.054	3	25	12	80	4	45	10	78	5	49	3	74
		30					.054		.035	8	17	9	79	11	35	15	75	14	45	10	71
		20					.029		.009	13	10	6	77	28	17	12	71	47	27	16	65
	9,12	40					.062		.047	6	21	10	81	9	42	12	78	9	48	6	74
		30					.046		.030	9	14	7	79	14	30	15	75	17	43	12	70
		20					.024		.005	16	9	4	77	30	13	9	70	54	21	14	65
	11,15	40					.054		.039	6	17	8	80	9	37	14	77	11	47	9	73
		30					.039		.023	10	12	6	80	17	25	15	76	24	40	14	71
		20					.019		.001	18	8	4	78	38	11	7	71	60	17	12	65

Table 18. NEW POPULATION -- HIGH ADULT MORTALITY, 4 FOUNDERS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,5	20	0	0	.062	2,2	.033	14	15	5	77	17	17	4	71	22	17	4	62
Mid Repr.		30					.042		.015	25	12	5	75	34	14	5	68	47	15	5	58
Low Repr.		20					.017		-.006	32	8	4	74	57	10	5	67	81	9	5	54
Brd. Delay	9,12	40					.052		.029	14	14	5	78	21	17	4	72	25	17	4	63
		30					.036		.010	26	10	5	76	38	13	6	70	53	14	6	60
		20					.013		-.009	36	8	4	75	60	9	5	68	83	9	5	57
Long Brd. Delay	11,15	40					.045		.023	17	12	5	78	23	16	5	72	29	16	4	63
		30					.030		.007	23	9	5	77	37	12	6	70	55	14	5	63
		20					.010		-.012	33	7	3	75	64	8	4	68	88	8	5	59
Higher K	7,10	40		50			.062		.038	14	20	12	78	17	36	15	74	19	45	9	69
		30					.042		.018	16	13	7	76	26	23	15	71	38	35	15	66
		20					.017		-.006	33	8	4	75	57	11	8	67	79	14	10	56
	9,12	40					.052		.030	14	15	9	77	21	31	16	73	26	43	11	69
		30					.036		.011	27	11	6	76	38	19	14	70	52	31	16	65
		20					.013		-.010	35	7	4	74	62	10	7	68	85	11	10	60
	11,15	40					.045		.025	19	14	8	78	27	29	16	74	32	41	13	70
		30					.030		.007	24	9	5	77	42	16	11	71	58	27	16	65
		20					.010		-.011	34	7	3	76	61	8	5	69	84	9	7	56

Table 19. NEW POPULATION, 6 FOUNDERS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
High Repr.	7,10	40	10,3	20	0	0	.072	3,3	.054	0	19	2	85	1	19	2	79	1	19	2	69	
Mid Repr.		30					.054		.037	2	17	4	85	4	18	3	79	5	18	3	69	
Low Repr.		20					.029		.013	3	13	5	83	9	15	5	77	21	14	5	67	
Brd. Delay	9,12	40					.062		.047	1	18	3	85	1	19	2	80	1	19	2	70	
		30					.046		.031	2	17	4	85	3	18	3	79	7	18	3	71	
		20					.024		.008	5	12	5	83	15	14	5	77	30	14	5	67	
Long Brd. Delay	11,15	40					.054		.039	2	17	4	85	3	19	2	80	3	19	2	71	
		30					.039		.025	3	15	5	85	4	17	4	80	8	18	3	71	
		20					.019		.004	5	11	5	84	17	13	5	78	34	13	5	68	
Higher K	7,10	40		50			.072		.059	0	35	12	86	1	48	6	83	1	49	3	78	
		30					.054		.039	2	24	10	85	3	42	12	82	4	48	5	78	
		20					.029		.014	4	14	7	84	11	23	13	78	22	34	16	72	
	9,12	40					.062		.050	1	29	11	86	1	47	8	84	2	49	2	79	
		30					.046		.034	2	21	9	85	4	39	13	82	7	47	8	78	
		20					.024		.009	4	13	6	84	15	20	13	78	28	28	16	71	
	11,15	40					.054		.043	1	24	10	86	2	44	11	84	2	48	5	80	
		30					.039		.028	2	17	7	85	4	33	15	82	6	44	11	78	
		20					.019		.005	5	11	5	84	16	16	10	78	38	24	15	72	

Table 20. NEW POPULATION -- HIGH ADULT MORTALITY, 6 FOUNDERS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,5	20	0	0	.062	3,3	.037	5	17	4	83	6	18	3	77	9	17	4	66
Mid Repr.		30					.042		.020	8	15	5	82	12	16	4	75	22	15	5	65
Low Repr.		20					.017		-.004	15	11	5	80	35	12	5	73	63	10	5	62
Brd. Delay	9,12	40					.052		.032	5	16	5	83	8	17	4	77	11	17	4	67
		30					.036		.015	8	14	5	82	15	16	5	77	26	15	5	67
		20					.013		-.006	17	10	5	80	40	11	6	73	66	11	5	64
Long Brd. Delay	11,15	40					.045		.026	6	15	5	83	10	17	4	78	14	17	4	69
		30					.030		.011	8	12	5	82	19	14	5	76	32	14	5	67
		20					.010		-.009	18	9	4	81	42	10	5	74	71	9	5	64
Higher K	7,10	40		50			.062		.043	5	28	13	84	6	43	12	81	7	46	7	76
		30					.042		.023	7	18	10	82	12	31	16	77	19	39	14	72
		20					.017		-.001	14	11	6	80	31	16	11	74	54	20	14	65
	9,12	40					.052		.036	6	23	11	84	9	39	13	81	9	46	8	76
		30					.036		.018	7	16	9	82	15	28	15	79	22	38	14	73
		20					.013		-.007	16	9	5	80	39	12	9	72	66	16	12	67
	11,15	40					.045		.031	5	19	10	84	8	36	15	81	11	45	10	77
		30					.030		.014	7	13	6	83	17	23	13	78	27	34	15	73
		20					.010		-.009	16	9	4	81	37	10	7	74	70	13	10	65

Table 21. NEW POPULATION, 8 FOUNDERS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,3	20	0	0	.072	4,4	.056	0	19	2	87	0	19	2	80	0	19	2	70
Mid Repr.		30					.054		.040	0	19	2	88	0	19	2	82	1	18	3	72
Low Repr.		20					.029		.016	1	16	4	88	3	16	4	82	10	15	5	71
Brd. Delay	9,12	40					.062		.047	0	19	2	88	0	19	2	82	0	19	2	72
		30					.046		.034	0	19	3	88	1	19	2	82	1	18	3	73
		20					.024		.012	1	16	4	87	6	16	4	82	14	15	4	72
Long Brd. Delay	11,15	40					.054		.042	0	19	2	88	0	19	2	83	0	19	2	74
		30					.039		.029	1	18	3	88	1	18	3	83	2	18	3	73
		20					.019		.009	2	15	4	88	7	15	5	82	18	14	5	72
Higher K	7,10	40		50			.072		.063	0	44	9	90	0	49	4	87	0	49	2	82
		30					.054		.044	1	32	12	89	1	46	8	86	1	48	4	82
		20					.029		.017	2	19	8	87	5	29	15	83	12	39	14	77
	9,12	40					.062		.055	0	39	11	90	0	49	4	87	0	49	2	83
		30					.046		.037	0	28	11	89	0	44	10	86	1	48	6	82
		20					.024		.014	2	18	7	88	4	27	13	84	10	35	14	77
	11,15	40					.054		.046	0	33	10	90	0	48	6	88	0	49	3	84
		30					.039		.032	0	24	9	89	1	40	12	86	2	47	6	83
		20					.019		.010	1	16	6	88	7	23	13	83	18	31	15	77

Table 22. NEW POPULATION -- HIGH ADULT MORTALITY, 8 FOUNDERS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,5	20	0	0	.062	4,4	.042	1	18	3	86	2	18	3	79	3	18	3	69
Mid Repr.		30					.042		.023	3	17	4	85	4	17	4	78	12	16	4	68
Low Repr.		20					.017		-.002	8	13	5	84	21	13	5	77	52	11	5	64
Brd. Delay	9,12	40					.052		.035	1	18	3	86	2	18	3	80	4	17	3	70
		30					.036		.020	2	16	4	86	5	16	4	80	14	15	4	70
		20					.013		-.003	5	13	5	85	18	13	5	78	49	11	5	66
Long Brd. Delay	11,15	40					.045		.030	2	17	4	87	3	18	3	81	6	17	3	72
		30					.030		.015	3	15	5	86	7	16	5	80	16	15	5	70
		20					.010		-.006	4	12	5	85	20	11	5	78	54	10	5	67
Higher K	7,10	40		50			.062		.048	0	36	13	88	1	46	8	85	1	47	5	80
		30					.042		.028	2	25	12	86	4	37	14	83	6	42	11	77
		20					.017		.000	6	15	8	85	18	18	12	77	42	21	14	71
	9,12	40					.052		.041	2	32	12	88	3	45	10	85	3	47	6	80
		30					.036		.022	3	22	11	86	5	34	15	83	10	41	12	78
		20					.013		-.001	5	14	7	85	16	17	11	79	41	20	14	71
	11,15	40					.045		.033	1	25	12	87	4	40	13	85	6	46	7	81
		30					.030		.018	2	18	9	87	7	30	15	82	13	39	13	78
		20					.010		-.005	9	13	6	86	23	14	9	79	51	17	12	72

Table 23. NEW POPULATION, 10 FOUNDERS

Input									Model Predictions													
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years				
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H	
High Repr.	7,10	40	10,3	20	0	0	.072	5,5	.057	0	19	2	88	0	19	2	82	0	19	2	71	
Mid Repr.		30					.054		.040	1	19	2	89	1	19	2	83	2	18	3	73	
Low Repr.		20					.029		.018	1	18	3	89	2	17	3	84	7	16	4	73	
Brd. Delay	9,12	40					.062		.049	0	19	2	89	0	19	2	83	0	19	2	73	
		30					.046		.035	0	19	2	90	0	19	2	84	2	18	2	74	
		20					.024		.014	0	17	3	90	1	17	4	84	7	15	4	74	
Long Brd. Delay	11,15	40					.054		.042	0	19	2	89	0	19	2	84	1	19	2	74	
		30					.039		.029	0	19	2	90	1	18	2	85	2	18	3	76	
		20					.019		.010	0	17	3	90	2	16	4	85	12	15	5	75	
Higher K	7,10	40		50			.072		.065	0	47	6	91	0	49	2	89	0	49	2	84	
		30					.054		.045	0	40	11	91	0	48	5	89	0	49	3	84	
		20					.029		.021	0	25	10	90	2	36	13	87	3	43	10	81	
	9,12	40					.062		.055	0	44	9	92	0	49	3	89	0	49	2	84	
		30					.046		.040	0	35	10	91	0	47	6	89	0	49	2	85	
		20					.024		.016	0	22	8	90	3	31	14	86	8	40	13	81	
	11,15	40					.054		.048	0	38	10	92	0	49	3	90	0	49	2	85	
		30					.039		.034	0	31	9	91	0	46	8	89	0	48	4	86	
		20					.019		.012	1	20	7	90	3	28	14	86	11	36	14	81	

Table 24. NEW POPULATION -- HIGH ADULT MORTALITY, 10 FOUNDERS

Input									Model Predictions												
Population Parameters					Catastr.		Det. r	Fndr ♂,♀	Stoc. r	25 Years				50 Years				100 Years			
Scenario Description	1st Yr Breed	% A♀ Breed	Mort. C,A	K	Frq	Sev				PE	N	SD	H	PE	N	SD	H	PE	N	SD	H
High Repr.	7,10	40	10,5	20	0	0	.062	5,5	.042	1	19	2	88	1	18	3	81	3	18	3	69
Mid Repr.		30					.042		.025	1	18	3	87	2	17	4	81	8	16	4	69
Low Repr.		20					.017		.001	2	15	5	87	10	14	5	80	36	12	5	67
Brd. Delay	9,12	40					.052		.037	0	18	3	88	1	18	3	82	3	18	3	70
		30					.036		.020	0	17	4	88	4	17	4	82	10	15	5	70
		20					.013		-.002	3	14	5	87	12	13	5	80	41	11	5	68
Long Brd. Delay	11,15	40					.045		.031	0	18	3	89	1	18	3	83	4	18	3	73
		30					.030		.016	1	17	4	88	5	17	4	83	11	15	4	72
		20					.010		-.002	2	14	5	88	10	13	5	81	36	11	5	70
Higher K	7,10	40		50			.062		.050	0	41	12	90	1	47	6	87	1	48	5	82
		30					.042		.031	1	30	12	89	2	42	12	86	3	44	9	81
		20					.017		.003	2	18	9	87	11	23	13	82	28	27	15	75
	9,12	40					.052		.043	1	37	12	90	1	47	7	88	1	48	5	83
		30					.036		.026	1	27	11	89	2	39	13	86	4	44	9	81
		20					.013		.001	2	17	7	88	9	21	12	82	28	24	15	75
	11,15	40					.045		.037	0	32	12	90	1	44	10	88	3	47	5	84
		30					.030		.021	0	23	10	89	3	36	14	87	6	43	11	82
		20					.010		-.001	2	16	7	88	10	19	11	83	35	22	13	76

Figure 1. Comparison of population growth in Garamba vs. model predictions. Population sizes are shown as of 1 January each year, except that "1996" numbers are from late October 1995. Populations were simulated with ages of first breeding for females modelled as 7, 9, or 11 years. Breeding was set at 40% of adult females producing calves each year. Infant mortality was set at 10% ± 10% SD, juvenile and subadult mortality was set at 1% ± 1% SD, and adult mortality was set at 3% ± 3% SD.