Genetic and Demographic Threats to the Black Rhinoceros Population in the Ngorongoro Crater

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Abstract: *A resident population of 13 black rhinoceros (*Diceros bicornis*) persist in Ngorongoro Crater, Tanzania. The effective population size (N_e) may be as few as 5 animals. Projected growth for this population suggests that the effective population size will remain small for the near future, threatening this local population with extinction due to the stochastic factors associated with small population size. A summary of historic and recent demographic data for this population reveals a population crash during the period of heavy poaching that affected this species throughout its range. Although poaching of this species has been brought under control, the population remains small. These data and models of projected population growth argue for consideration of more-intensive management within the framework of the small population paradigm. This case is an example of applied conservation resulting from this paradigm used in conjunction with rather than competing with the declining population paradigm. We identify additional monitoring, particularly of density-dependent behaviors, that will be necessary for designing a successful management program. Finally, the use of molecular markers for developing an accurate pedigree for this population is suggested in order to maintain a genetically healthy population. These strategies have broad applicability to black rhinoceros conservation throughout Africa.*

Amenazas Genéticas y Demográficas de la población de Rinocerontes Negros en el Cráter Ngorongoro

Resumen: *Una población de 13 rinocerontes negros (*Diceros bicornis*) aún persiste en el Cráter Ngorongoro, Tanzania. El tamaño poblacional efectivo (en) puede ser tan pequeño como 5 animales. Adicionalmente, el crecimiento proyectado para esta población sugiere que el tamaño efectivo de la población se mantendrá pequeño en el futuro cercano, amenazando de extinción a esta población local debido a factores estocásticos asociados con el tamaño pequeño de la población. Un resumen de los datos demográficos históricos y recientes de la población revelan un colapso durante el periodo de intensa caza, mismo que impacto a esta especie a lo largo de su rango. La caza de esta especie ha sido controlada, sin embargo la población se ha mantenido pequeña. Estos datos así como los modelos de poblaciones proyectadas arguyen la consideración de un manejo más intensivo dentro del marco del paradigma de una población pequeña. Este caso es un ejemplo de conservación aplicada resultado de su paradigma en conjunción en lugar de competir con el paradigma de la población en declive. Identificamos monitoreo adicional, particularmente de conductas densodependientes, que serán necesarias para diseñar un programa de manejo exitoso. Finalmente sugerimos el uso marcadores moleculares para desarrolar un pedigri preciso de esta población y así mantenerla genéticamente sana. Estas estrategias tienen una amplia aplicación en la conservación de los rinocerontes negros a través de Africa.*

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Introduction

The black rhinoceros (*Diceros bicornis*) has declined precipitously over the last 20 years from a population of approximately 70,000 to less than 2500 (Gakahu 1993). Hunting of rhinos for their commercially valuable horn is the major cause of this decline (Milner-Gulland & Leader-Williams 1992). Black rhinoceros occur as scattered, disjunct, small populations in areas of relatively intense protection. Because poaching has spread southward through sub-Saharan Africa, efforts to protect the animals in situ have generally been ineffective outside fenced reserves. Rhinoceros also face threats to their genetic and demographic health due to their small effective population size and isolation. These factors are likely to have a major impact on the probability that these populations will persist in the future.

In 1964-1966 Goddard (1967) individually identified 108 black rhinos in the Ngorongoro Crater. He considered this population resident in the crater and different from individuals observed on or adjacent to the rim of the crater. Poaching of black rhinoceros in the crater began in the early 1970s and was a major source of mortality until the late 1980s (Makacha et al. 1979; Kiwia 1989*a*). By 1990 the resident population had dropped to 10 animals. Although the population has grown over the last 5 years to between 11 and 14 animals, this small and apparently isolated population (Fig. 1) is extremely vulnerable, especially considering that the effective population size (N_e) may only be five.

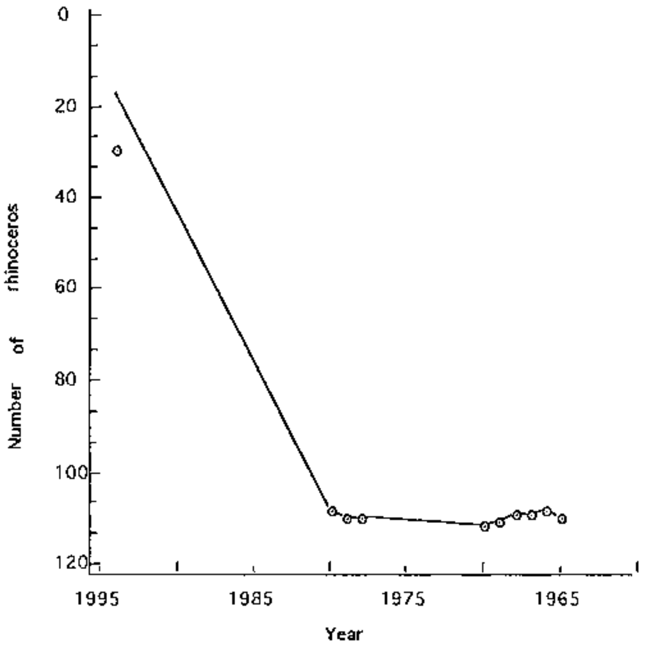

Figure 1. Resident population size of black rhinoceros in Ngorongoro Crater, Tanzania (1967-1995).

Caughley (1994) draws a distinction between what he terms the "declining population paradigm" and the "small population paradigm" as the current approaches used by conservation biologists to address species-driven conservation programs. He suggests that up until now only the declining population paradigm has provided useful, applied conservation information. Caughley's assessment is that the paradigm developed to address issues confronting the persistence of small populations had not been applied successfully to a current conservation issue. But the population of rhinoceros in the Ngorongoro Crater is an example of a population facing both an external threat—poaching for its commercially valuable horn—and the internal threats associated with small population size. Specifically, these factors include slow population growth due to density-dependent social interactions, high levels of inbreeding, and a variety of stochastic factors, including demographic shifts, disease, and the effects of even small increases in mortality on population growth and recruitment (Foose 1987; Conway 1989). These factors are likely to be applicable to other populations of black rhino that persist in scattered, small populations (e.g., in Maasai Mara, Nairobi, Hwange). We examined the population of black rhinoceros in the Ngorongoro Conservation Area to assess current demographic and genetic trends, and we discuss management options that may be necessary to conserve this species here and elsewhere.

History of the Ngorongoro Crater Black Rhinoceros Population

Although largely a self-contained ecological unit, Ngorongoro Crater is not entirely isolated. The crater is linked to the adjacent Serengeti Plains and Ngorongoro Highlands by the seasonal migration of several species of herbivores (Estes & Small 1981) and the immigration and emigration of predators (Kruuk 1972; Pusey & Packer 1987). Kiwia studied the Ngorongoro Crater black rhino population from December 1980 to May 1982 and for brief periods in September 1982, May 1984, and May 1988 (Kiwia 1989*a*, 1989*b*). From 1980 to 1982 he individually identified 14 resident and seven transient rhinos. During this period two adult females (one calf lost) and two adult males were poached. In 1983-1986 two additional black rhino were poached, and in 1988 another poached black rhino was found. Since 1988 no poached animals have been reported. In 1988 the Ngorongoro Ecological Monitoring Program, with the assistance of Kiwia, started to identify black rhinos resident in the crater and to record their movements and reproduction. Of five males present in the crater in 1981, only "John," born in 1977, was still present. "Hamisi," a transient male in 1981, had become a resi-

Table 1. Resident and transient black rhinoceros of Ngorongoro Crater (1973–6/1995).[a]

	Birth date	*1980*	*1981*	*1982*	*1983*	*1984*	*1985*	*1986*	*1987*	*1988*	*1989*	*1990*	*1991*	*1992*	*1993*	*1994*	*6/1995*
Males																	
Leo	pre-1973	R	—	—	—	—	D										
Mungaa	pre-1973	R	P/D														
Zakayo	pre-1973	R	P/D														
Saidi	pre-1973	T	—	D													
Hamisi[b]	pre-1973	T	—	—	—	—	—	—	—	R	—	—	—	—	—	R	T
Paolo[b]	pre-1973	T	—	—	—	—	—	—	—	—	—	—	—	—	—	—	T
John[c] (Betty[d])	1977	R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	R
Joseph	1978	R	—	D													
Ali (Mary[d])	1981		R	—	D												
Chabanga (Maggie[d])	1984					R	—	—	D								
Rajabu (Anna[d])	1985						R	—	—	—	—	—	—	—	E		
Runyoro (Maggie[d])	1990											R	—	—	—	—	R
Mikidati (Bahati[d])	1992													R	—	—	R
Females																	
Agnes	pre-1973	R	P/D														
Sada	pre-1973	R	—	P/D													
Filomina	pre-1973	R	—	—	D												
Lina	pre-1973	T	—	—	D												
Salima	pre-1973	T	—	—	D												
Stela	pre-1973	T	—	—	D												
Mary	pre-1973	R	C	—	D												
Salama?									R/C/D								
Kisura?									R/C/D								
Betty	pre-1973	R	C	—	—	—	—	—	D								
Fausta	pre-1973	T	—	R	—	C	—	—	—	—	—	—	—	—	—	—	R
Anna	pre-1973	R	C	C	—	—	C	—	—	—	—	—	—	—	—	—	R
Vicky[c]	pre-1973	R	—	C	—	—	—	C	—	—	—	—	C	—	C	—	R
Maggie[c] (Betty[d])	1976	R	—	—	—	C	—	—	C	—	—	C	—	C	—	—	R
Bahati[c]									R	—	—	—	—	C	—	C	R
Amina[c] (Vicky[d])	1986							R	—	—	—	—	—	—	—	C	R
Stella (Vicky[d])	1991												R	—	—	—	D
Patricia (Maggie[d])	1992													R	—	—	R
Mtoto (Vicky[d])	1993														R	—	R
Mdogo (Bahati[d])	1994															R	R
Mpya (Amina[d])	1994															R	R

[a] *R, resident; D, dead or disappeared; P, poached; T, transient; C, calf born.*
[b] *Reproductive transient.*
[c] *Reproductive resident.*
[d] *Mother.*

dent of the crater. "Paulo," a transient in 1981, continued to live outside the crater. Of eight adult and immature females identified in 1981, only three were still resident in 1988 (Table I). Also, one 1981 transient female (Fausta) had become a resident.

Individuals were recognized by means of photographs and line drawings that showed scars and unique tail and ear conditions. Full-sized individuals were classified as adult; individuals that had left their mothers but were not full-sized were classified as immature; an immature individual still with its mother was considered a calf (Goddard 1967). The Ngorongoro Ecological Monitoring Program, with Kiwia's assistance, identified some individuals that had been resident in the crater in 1980. This information made it possible to construct limited pedigrees based on observed mothers and calves.

Demographic Viability

Total population size has not increased since 1980 (Table 2). These numbers are especially troubling in relation to the demographic health of this small population. But it is important to examine this period of time in greater detail. Between 1980 and 1988 mortality due to poaching was responsible for the loss of at least seven adults and one calf in the resident population (Kiwia 1989*a*; Ngorongoro Ecological Monitoring Program [NEMP] 1990). Since 1990 the resident population has grown from 10 to 13 individuals, with seven calves born, one young adult male emigrating, one adult male becoming transient, and one immature female disappearing ($\lambda = 0.084$, $r = 1.088$). Thus, at a finer level of resolution we see the decline of the rhino population

Table 2. Historical population size and sex/age composition of black rhinoceros resident in Ngorongoro Crater.*

Reference	*Year*	*Total population*	*M*	*F*	*IM*	*IF*	*CM*	*CF*	*?C*	*C/F*	*T*
Goddard (1967)	1966	108	37	29	9	12	10	8	3	21/29	
Makacha et al. (1979)	1978	19	3	2	3	9			2	2/2	7
Kiwia (1989*a*)	1980	14	3	7	2	1	1			1/7	7
Kiwia (1989*a*)	1981	12	1	6	2	1		1	1	2/6	8
Kiwia (1989*a*)	1982	12	1	6	2	1		1	1	2/6	7
NEMP (1990)	1990	10	2	5	1	1	1			1/5	1
NEMP (1990)	1991	11	2	5	1	1	1	1		2/5	1
NEMP (1992)	1992	13	2	6	2		1	2		3/6	1
NEMP (1995)	1993	13	2	6	1	1	1	2		3/6	1
NEMP (1995)	1994	15	2	6	2	1	1	3		4/6	3
NEMP (1995)	1995	13	1	6	2			4		4/6	4

**M, adult male; F, adult female; IM, immature male; IF, immature female; C, calf; T, transient.*

Table 3. A historical comparison of fecundity rates and inter-birth intervals in the resident black rhinoceros population of Ngorongoro Crater.*

Fecundity measure		*1963*	*1964*	*1965*	*1966*	
Goddard						
C/F		8/29	8/29	6/29	7/29	
C/yr	7.2					
C/yr/F	0.25					
C/yr/Adult	0.11					
C/yr/pop	0.07					
		1990	*1991*	*1992*	*1993*	*1994*
Nemp						
C/F		1/5	1/5	2/6	1/6	2/6
C/yr	1.4					
C/yr/F	0.25					
C/yr/adult	0.18					
C/yr/pop	0.11					

**C/F, calf/female; C/yr, calf/year; C/yr/F, calf/year/female; C/yr/pop, calf/year/population. From 1963-1966 the mean calving interval was 2.3 years (n = 3). From 1990-1994 the mean calving interval was 2.0 years (n = 3).*

between 1980 and 1988 as part of the same precipitous, continent-wide decline of black rhino due to poaching for horn, and we see a positive growth period starting in 1989 and continuing to the present. Reproductive performance (calves per female, $p = 0.938$, df $= 1$) of the present population is not significantly different from the much larger population that Goddard studied (Table 3). The current sex ratio of approximately three males to 10 females should provide a good starting point for demographic recovery. But because five individuals are not sexually mature and two females may be post-reproductive, the effective population size is much smaller than the already alarmingly small total population size. A loss of animals due to resumption of poaching, increased emigration, or other unidentified threats could cause rapid deterioration of this situation.

To explore the likelihood of this population persisting into the future, we projected growth curves by constructing a deterministic life table and by means of the population viability model VORTEX (Lacy & Kreeger 1993). Parameter values for a post-breeding life table were taken from a number of previous studies (Goddard 1967; Schenkel & Schenkel-Hullige 1969; Joubert & Eloff 1971; Hitchens & Anderson 1983; Hall-Martin 1986) as well as the summaries described in Smith & Reed (1992). We assumed a life span of 35 years, 5 years as age of first reproduction, continued reproduction to age 30, an inter-birth interval of 26 months, and survival probabilities of 0.90 for the first year, 0.96 for year 2,

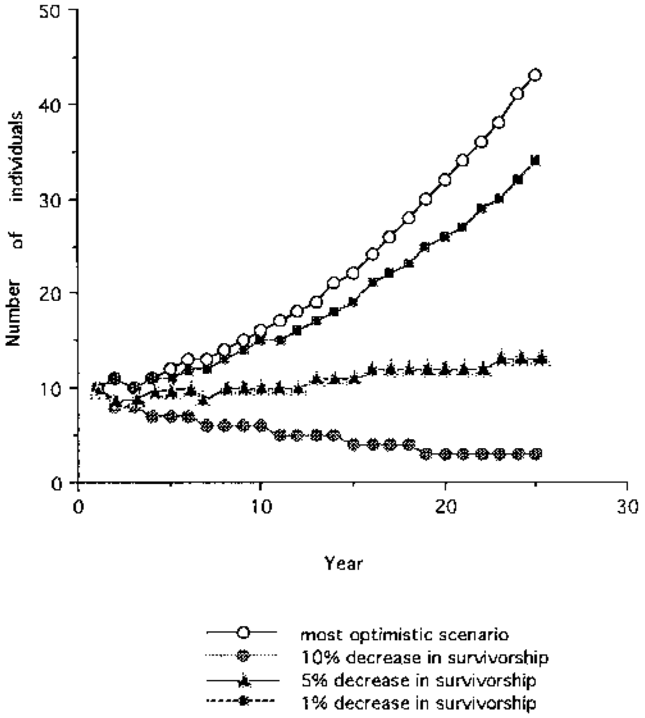

Figure 2. Post-breeding deterministic life table for the Ngorongoro black rhino population. Optimistic parameter values assumed a life span of 35 years, 5 years as age of first reproduction, continued reproduction to age 30, an inter-birth interval of 26 months, and survival rates of 0.90 for year 1, 0.96 for year 2, 0.94 for year 3, 0.97 for year 4, and 0.95 for subsequent years (Foose et al. 1993). Three additional projections were performed by decreasing survival probabilities by 0.01, 0.05, and 0.1.

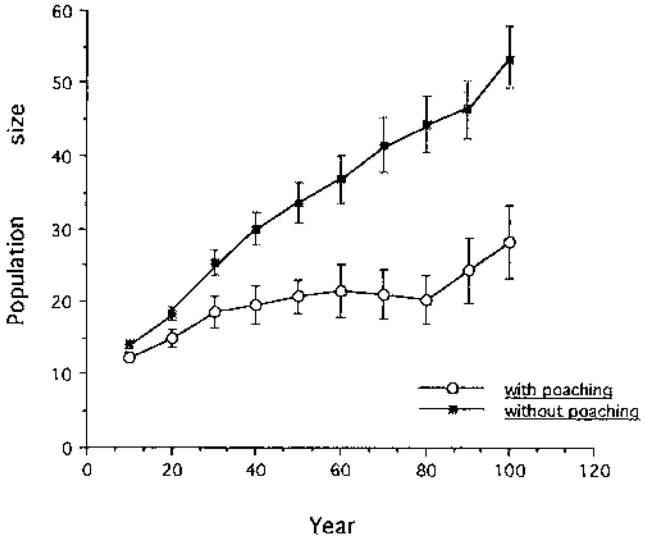

Figure 3. Life-table projection of population growth from VORTEX (Lacy & Kreeger 1993) (same parameter values as in Fig. 2). Included in the model is a modest level of poaching, 5% of population every third year.

0.94 for year 3, 0.97 for year 4, and 0.95 for subsequent years (Foose et al. 1993). Under these assumptions the population grew at an average annual rate (λ) of 1.047. After 25 years, life-table projections indicated that this population would grow from 12 to 46 (Fig. 2). Many of these parameter values, however, are unrealistically optimistic (especially the estimates of survivorship). If we decrease survivorship by just 0.1, the population drops to six animals by year seven, and three animals by year 21 (Fig. 2). With only a 0.05 decrease in survivorship the population would consist of only 13 animals at the end of 25 years. Even a 0.01 decrease in survivorship resulted in a population of only 36 animals at the end of 25 years (Fig. 2).

These projections point to the likelihood of this population remaining small for an extended period of time. What is not included in these projections are the large number of other stochastic factors that endanger all small populations. To address these stochastic factors to some extent, we used the same parameter values in an analyses with VORTEX (Lacy & Kreeger 1993) (Fig. 3). Vortex also allowed us to compare results with inclusion of a modest level of poaching (losing 5% of the population every 3 years; Foose et al. 1993). The result was a population size of less than 20 after 40 years (Fig. 3).

Genetic Viability

Because of their small population size, the black rhinoceros in the Ngorongoro Conservation Area face two genetic threats: inbreeding depression and loss of genetic variation due to random genetic drift (Allendorf & Leary 1986). Jimenez et al. (1994) recently demonstrated that inbreeding depression may be a more serious threat to wild populations than to captive populations, in which inbreeding depression has already been empirically demonstrated (Ballou & Ralls 1982). Although the current fecundity rate and inter-birth intervals of the Ngorongoro black rhino are similar to those observed in the 1960s, there is concern that future generations will display decreased fitness due to high levels of inbreeding.

The current resident adults are the survivors of intense poaching in the 1970s and 1980s that removed large numbers of animals instantaneously and randomly. Thus, the remaining adults are few but are no more likely to be related than individuals in the original large population. So it is not surprising that there is currently no detectable inbreeding depression. In Southern Africa, Swart et al. (1994) demonstrated the persistence of genetic variation in small populations of black rhinoceros that approximates the levels likely to have occurred in populations before the recent sharp decline. These levels of variation are significantly greater than would be expected based on current effective population sizes. The relatively long generation time for black rhinos has been suggested as the factor responsible for mitigating the possible bottleneck effect on current levels of heterozygosity (Swart et al. 1994). But because rhinos are difficult to census in swamp, brush, and woodland environments, it is likely that in many instances rhino numbers were underestimated and that current protected populations may not have passed through the severe reduction in population size suggested by some authors.

In the Ngorongoro Crater, the resident population of immature animals consists of a large number of half-sibs (or possibly full-sibs) in addition to the resident males that are likely to be the fathers of all young rhinos born in the last 5 years. Within the next few years the probability of father-daughter and full-sib matings will increase. The extent of this problem could best be assessed by determining a more accurate pedigree for the population by means of molecular genetic markers (Jefferys 1985; Chakraborty et al. 1988; Morin et al. 1994). This could be accomplished, without immobilizing animals, by DNA extraction from fecal material (Hoss et al. 1992).

Inbreeding depression is likely if the effective population size grows slowly, remains the same, or declines. This threat could be greatly ameliorated by accurately ascertaining the presence of transient breeding animals living in the Northern Highland Forest adjacent to the crater rim or by interactive management of animals selected with the aid of molecular genetic markers (Amato et al. 1993; Conway 1995). Such information should be gathered in the next 2-4 years before the current immature animals reach breeding age.

Although the genetic future of the population might be less threatened if there are four or five unrelated, transient animals that are part of the gene pool residing outside of the crater, it seems likely that such peripheral animals are related and would not reduce the inbreeding concerns we have for the strictly resident population. Also, if transient animals are not part of the gene pool, then immature animals that emigrate out of the crater are essentially lost even if they are not poached. This information is extremely important because the greatest threat to the genetic health of small black rhino populations is the length of time these populations persist at low effective population levels. A rapid increase in population would insure the maintenance of current levels of genetic diversity. Molecular genetic markers are powerful tools for addressing these and other related conservation questions for rhinoceros (Amato et al. 1993). Intensive management strategies based on empirical data such as DNA profiling is clearly not the answer to preserving most of the world's biodiversity, but these sophisticated methodologies may be necessary in order to conserve certain high-profile taxa.

Density-Dependent Behavior and Management Implications

Another factor that compounds the genetic and demographic threats of small population size is the effect of density on rhino behavior. In the 1960s Goddard (1967) individually identified a resident population of over 100 individuals and additional transient animals. This density of rhinos within the crater is likely to have been influenced by the density of rhinos outside of the crater. Given the substantially larger number of adult males and females (Goddard 1967; Kiwia 1989*b*), subordinate males would have had a better opportunity to breed with estrous females, with a possible concurrent effect on demography and genetics resulting in higher heterozygosity. Even though current densities are low and there presumably is plenty of space to accommodate more rhinos, individuals are leaving. In 1993 when only three adult males were resident in the crater, male aggressiveness may have been responsible for one individual (Rajabu, aged 8 years) emigrating out of the crater. Lower densities may allow for more-persistent aggressive interactions between resident and maturing or foreign males. Also, areas of even lower density (essentially empty) outside of the crater may encourage emigration.

This has important implications for some proposed management strategies. Translocating animals from other areas into the crater would be ineffective if the animals emigrated to less secure areas. This would be an expensive exercise if it resulted in the loss of the translocated animals without positively affecting demographic and genetic problems. Alternatively, to insure genetically healthy populations it may be necessary to move resident males and replace them with other males. To reduce the chances of introducing foreign parasites and diseases, such a move should involve individuals from neighboring ecosystems, as long as they were distant enough to be clearly unrelated. Also, if offspring continue to emigrate out of the population into less secure areas, it may be necessary to consider moving them into secure reserves. Otherwise, continued reproduction will not have a substantial positive impact on the persistence of rhinos in Tanzania.

A better understanding of density-dependent factors needs to be assessed through behavioral research on the Ngorongoro Crater rhinos in comparison with fenced-in populations. Such density-dependent factors may be responsible for the loss of certain species when they decline to small numbers (e.g., passenger pigeons, *Ectopistes migratorius*) or explain why certain taxa do not seem to recover from low population size even after the causative factors for their decline have been identified and removed (e.g., northern right whale, *Balaena glacialis*).

Discussion and Conclusions

The black rhinoceros population in Ngorongoro Crater is a small, isolated relict of what was historically a common and widespread group distributed throughout many habitat types in eastern and southern Africa. Although the most important threat to the survival of this species is hunting for its horn, the small, fragmented populations that persist face additional threats due to their size and degree of isolation. It is necessary to consider small-population management options to increase their likelihood of survival (Conway 1989).

Anecdotes concerning the rapid recovery of rhino populations from small numbers have been used to argue for the likely recovery of small populations if they can be protected from poaching. The primary examples have been the southern white rhinoceros (*Ceratotherium simum*) and the Indian rhinoceros (*Rhinocerus unicornis*). It is important to note that in both of these cases the founding population numbers were probably over 100, and not less than 20 (Owen-Smith 1974; Laurie 1978; Lacy 1987), as is the case for many current black rhinoceros populations.

A relevant example of a population of rhinoceros increasing from a small number is provided by the Garamba population of white rhinos, which has grown from 15 to over 28 in the last 10 years (Smith & Smith 1993). But it is premature to judge whether this population is likely to escape the threats inherent in its small size. We must carefully evaluate the likelihood of the long-term persistence of rhino populations started from very small numbers (Hall-Martin 1986; Foose 1987; Lacy 1987).

The Ngorongoro Crater black rhino population has remained small since 1980. The situation has been dynamic, with measurable improvement since 1988. It is likely that the improved financial and law enforcement capacity of the Ngorongoro Conservation Area, along with individual monitoring, has contributed significantly to this improvement. From 1988, the Ngorongoro Ecological Monitoring Program individually identified black rhinos in the crater. The program provided the antipoaching patrol with identification books and trained them to recognize individuals. Thus, it was possible to record information on individual fecundity, inter-birth intervals, and emigration. Such data suggest that the population is not suffering inbreeding depression, is in a positive growth period, but also is very small, unlikely to become demographically and genetically secure in the near future. These studies also point out that additional information about density-dependent factors, and an accurate pedigree, should be obtained before translocation project is proposed.

To further assess the appropriate management options, we must accurately determine the current population of the Ngorongoro Crater and the adjacent Northern Highland Forest Reserve. If the current population of 13 resident and 2 transient individuals is larger and reproductively interactive, then the potential for demographic and genetic viability is greatly improved. Concurrently, data on individual degrees of relatedness, obtainable with genetic fingerprinting, would allow a more accurate projection of the potential for inbreeding in this population. It would also provide a history of breeding partners. This information could be incorporated into any plans to move rhinos between reserves should that option be deemed necessary.

Thirty-three percent ($n = 6$) of the resident adult females have not produced observed calves in the last 7 years. Similar reproductive failure was observed over a 4-year period in the 1960s, but at a lower rate (28%, $n = 29$; Goddard 1967). It would be useful to determine if the observed absence of calves in the two adult females is due to abortion, early calf mortality, or lack of estrus, copulation, or fertilization. Such data are important for determining effective population size and in evaluating management options.

Research on individual movement patterns, feeding ecology, nutrition, and social interactions would provide the data needed to determine how this black rhinoceros population is utilizing resources at current densities according to sex and age class. Such data would indicate whether individuals resident in the crater use the adjacent Northern Highland Forest Reserve and whether forage availability plays a significant role in individual spacing patterns and the potential for emigration. Individual social histories would provide information on the development of breeding pairs and the role of aggression in individual movement patterns.

This population can serve as an important model for designing management strategies for black rhinoceros throughout their range. The long-term monitoring data reported by Goddard (1967), Kiwia (1989*a*), and this paper provide important background information for evaluating current trends and the effects of any proposed new management initiatives. This program, which combines ecological monitoring with proposed empirically tested assessments of intrinsic and extrinsic factors affecting the likely persistence of this species, is clearly necessary if we are to conserve rhinos into the next century.

Note Added in Proof

In September, 1995, the adult female Amina was poached and her male calf was lost to the population. By December, 1995, rhino carcasses were found that may have been the adult male Hamisi and the subadult female Stella.

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Literature Cited

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 77–104 in M. E. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Amato, G., M. V. Ashley, and J. Gatesy. 1993. Molecular evolution in living species of rhinoceros: implications for conservation. Pages 114–122 in O. A. Ryder, editor. Proceedings of the international conference on rhinoceros conservation and biology. Zoological Society of San Diego, San Diego.

Amato, G., D. Wharton, Z. Z. Zainal, and J. R. Powell. 1995. Assessment of conservation units for the Sumatran rhinoceros (*Dicerorhinus sumatrensis*). Zoo Biology 14:395–402.

Ballou, J., and K. Ralls. 1982. Inbreeding and juvenile mortality in small populations of ungulates: a detailed analysis. Biological Conservation 24:239–272.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Chakraborty, R., T. R. Meagher, and P. E. Smouse. 1988. Parentage analysis with genetic markers in natural populations. I. The expected proportion of offspring with unambiguous paternity. Genetics **118**:527-536.

Conway, W. G. 1989. The prospects for sustaining species and their evolution. Page 204 in D. Western and M. Pearl, editors. Conservation for the twenty-first Century. Oxford University Press, New York.

Conway, W. 1995. Wild and zoo animals interactive management and habitat conservation. Biodiversity and Conservation **4**:573-594.

Estes, R. D., and R. Small. 1981. The large herbivore populations of Ngorongoro Crater. African Journal of Ecology **19**:175-185.

Foose, T. J. 1987. Long term management of small rhino populations. Pachyderm **9**:13-15.

Foose, T. J., R. C. Lacy, R. Brett, and U. S. Seal. 1993. Kenya black rhino metapopulation workshop (workshop report). World Conservation Union/SSC Captive Breeding Specialist Group, IUCN, Gland, Switzerland.

Gakahu, C. G. 1993. African rhinos: current numbers and distribution. Pages 160-163 in O. A. Ryder, editor. Proceedings of the international conference on rhinoceros conservation and biology. Zoological Society of San Diego, San Diego.

Goddard, J. 1967. Home range, behavior, and recruitment rates of two black rhinoceros populations. East African Wildlife Journal **5**:133-150.

Hall-Martin, A. J. 1986. Recruitment in a small black rhino population. Pachyderm **7**:6-8.

Hitchens, P. M., and J. L. Anderson. 1983. Reproduction, population characteristics and management of the black rhinoceros, *Diceros bicornis minor*, in the Hluhuwe/Corridor/Umfolozi Game Reserve Complex. South African Journal of Wildlife Research **13**:78-85.

Hoss, M., M. Kohn, and S. Paabo. 1992. Excrement analysis by PCR. Nature **359**:199.

Jeffreys, A. J., V. Wilson, and S. L. Thein. 1985. Individual-specific fingerprints of human DNA. Nature **316**:76-79.

Jimenez, J. A., K. A. Hughes, G. Alaks, L. Graham, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. Science **266**:271-273.

Joubert, E., and F. C. Eloff. 1971. Notes on the ecology and behavior of the black rhinoceros, *Diceros bicornis*, Linn. 1758 in South West Africa. Madoqua **1**:5-53.

Kiwia, H. D. 1989*a*. Black rhinoceros (Diceros bicornis (L.)): population size and structure in Ngorongoro Crater, Tanzania. African Journal of Ecology **27**:1-6.

Kiwia, H. D. 1989*b*. Ranging patterns of the black rhinoceros (*Diceros bicornis* (L.)) in Ngorongoro Crater, Tanzania. African Journal of Ecology 1989 **27**:305-312.

Kruuk, H. 1972. The spotted hyena. A study of predation and social behavior. University of Chicago Press, Chicago.

Lacy, R. C. 1987. Further genetic and demographic analyses of small rhino populations. Pachyderm 9:16-19.

Lacy, R. C., and T. Kreeger. 1993. VORTEX: A computer simulation model for use in population viability analysis. Wildlife Research **20**: 45-65.

Laurie, W. A. 1978. The ecology of the greater one-horned rhinoceros. Ph.D. thesis. Cambridge University, Cambridge, United Kingdom.

Makacha, S., C. L. Mollel, and L. Rwezaura. 1979. The conservation status of the black rhinoceros (*Diceros bicornis*, L.) in the Ngorongoro Crater, Tanzania. African Journal of Ecology **17**:97-103.

Milner-Gulland, E. J., and N. Leader-Williams. 1992. A model of incentives for the illegal exploitation of black rhinos and elephants: poaching pays in Luangwa Valley, Zambia. Journal of Applied Ecology **29**:388-401.

Morin, P. A., J. J. Moore, R. Chakraborty, L. Jin, J. Goodall, and D. S. Woodruff. 1994. Kin selection, social structure, gene flow, and evolution of chimpanzees. Science **265**:1193-1201.

Ngorongoro Ecological Monitoring Program. 1990. Annual report. Ngorongoro Conservation Area Authority, Ngorongoro, Tanzania. Unpublished.

Ngorongoro Ecological Monitoring Program. 1992. Annual report. Ngorongoro Conservation Area Authority, Ngorongoro, Tanzania. Unpublished.

Ngorongoro Ecological Monitoring Program. 1995. Research and ecological monitoring annual report. Ngorongoro Conservation Area Authority, Ngorongoro, Tanzania. Unpublished.

Owen-Smith, R. N. 1974. The behavioral ecology of the white rhinoceros. Ph.D. thesis. University of Wisconsin, Madison.

Pusey, A. E., and C. Packer. 1987. Philopatry and dispersal in lions. Behavior **101**:275-310.

Schenkel, R., and L. Schenkel-Hulliger. 1969. Ecology and behavior of the black rhinoceros (*Diceros bicornis* L.): a field study. Verlag Paul Parey, Hamburg.

Smith, R. L., and D. Read. 1992. Management parameters affecting the reproductive potential of captive, female black rhinoceros, *Diceros bicornis*. Zoo Biology **11**:375-383.

Smith, K., and F. Smith. 1993. Conserving rhinos in Garamba National Park. Pages 166-177 in O.A. Ryder, editor. Proceedings of the international conference on rhinoceros conservation and biology. Zoological Society of San Diego, San Diego.

Swart, M. K. J., J. W. H. Ferguson, R. Dutoit, and J. R. B. Flamand. 1994. Substantial genetic variation in southern African black rhinoceros (*Diceros bicornis*). Journal of Heredity **85**:261-266.