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PAST AND FUTURE BREEDING OF THE INDIAN RHINOCEROS IN CAPTIVITY

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Summary

We analyzed the demography and breeding history of captive greater one-horned, or Indian, rhinoceroses (*Rhinoceros unicornis*), and evaluated its genetic consequence on the zoo population, using the studbook data up to 31 December 1996. *R. unicornis* – one of the most endangered large mammals – is kept in captivity in zoological gardens and animal parks worldwide. Nowadays, 85 of the 129 captive individuals are zoo-born. Until recently, however, little attention was paid to the genetic health of the zoo population.

In captivity, males and females have reached a maximum age of 42 years, but only males have reproduced beyond the age of 32 years. We found high juvenile mortality in both sexes (23% for males and 30% for females). Offspring of primiparous dams suffered higher juvenile mortality (40%) than those of multiparous dams (17%). In the data available, we could not find any inbreeding effects. The sex ratio of zoo-born *R. unicornis* was male-biased (60% males v 40% females). Despite the male-biased sex ratio, more females than males reproduced in captivity.

At present, 48.4% of the genes of all zoo-born *R. unicornis* stem from three founder individuals, whereas another 30 founders contributed to the remaining 51.6% of the genes. This unequal distribution leads to a low founder equivalent of 10.52. For a viable zoo population, a founder equivalent of at least 20 is considered to be necessary. Furthermore, 97% of all genes stem from founder individuals from a single, possibly highly inbred population in Assam, India.

We evaluated future breedings and show that as few as two offspring in a single zoo can influence the genetic health of the worldwide captive population. The difference in founder equivalents between the two hypothetical worst-case breedings and the two best-case breedings amounts to almost 10%.

Introduction

The World Conservation Union (IUCN) has recognized the potential contribution by zoos and other institutions keeping endangered animals in captivity, and recommends that vertebrate taxa numbering fewer than 1,000 individuals in the wild should be considered for captive breeding (IUCN, 1987). Today, the Indian rhinoceros is one of the most endangered large mammals, with about 2,000 individuals in the wild

(Martin and Vigne, 1996).

At present, 129 Indian rhinoceroses are kept in captivity and are distributed in 51 zoological gardens and animal parks in Asia, America and Europe (Wirz-Hlavacek *et al.*, 1997). With regard to the entire zoo population recorded in the studbook, 96 rhinos have been imported from the wild, and some 143 have been born in captivity since 1956, when the first rhino was born and brought up in Basel Zoo. In recognition of the species' precarious conservation status, cooperative breeding programmes have been set up in North America and Europe to provide a sound basis for long-term captive breeding (Khan, 1989; de Boer, 1991; Dee *et al.*, 1994).

The aims of the present study were (1) to present the history of the captive Indian rhinoceros population, (2) to evaluate life-history data, (3) to examine the demographic and genetic structure of the living zoo population, (4) to analyze the historical development of the genetic status of the zoo population, and (5) to evaluate the effects of five hypothetical breeding programmes of a single zoo onto the genetic health of the whole captive population.

Methods

Data were taken from the latest (31 December 1996) edition of the international studbook (Wirz-Hlavacek *et al.*, 1997). For the compilation of the population history, additional data were taken from Reynolds (1961) and Rookmaaker and Reynolds (1985). Data were analyzed by means of a studbook analysis program written by S. Zschokke (unpublished). Demographic and genetic models are based on Krebs (1978), Ballou (1983), Crow (1986), Lacy (1989), Stearns (1992) and Ballou and Lacy (1995).

Inbreeding coefficients and mean kinship coefficients based on pedigrees were calculated using the additive relationship method (Ballou, 1983). The mean kinship coefficient method allows to identify potential breeders that would maximize gene diversity in a given population. The kinship coefficient is defined as the probability that alleles drawn randomly from each of two individuals are identical by descent (Falconer, 1989). The mean kinship of an individual is then defined as the average of the kinship coefficients between that individual and all living individuals, including itself (Ballou and Lacy, 1995). Individuals with few living relatives probably carry alleles that are less common. Hence, a low mean kinship coefficient may indicate an important individual.

All founders were assumed to be unrelated, as were individuals introduced to captive herds at a later date. This may well not have been justified in all cases, and therefore the inbreeding coefficients represent minimum estimates. Founder equivalents were calculated following Lacy (1989).

The data on the origin of the founders were compiled from Reynolds (1961), Buechner *et al.* (1975), Tobler (1993), Wirz-Hlavacek *et al.* (1997), and from personal communications with the mammal curators of Dierenpark Planckendael and Antwerp Zoo.

Statistical analyses were performed with the StatView v4.51 program package.

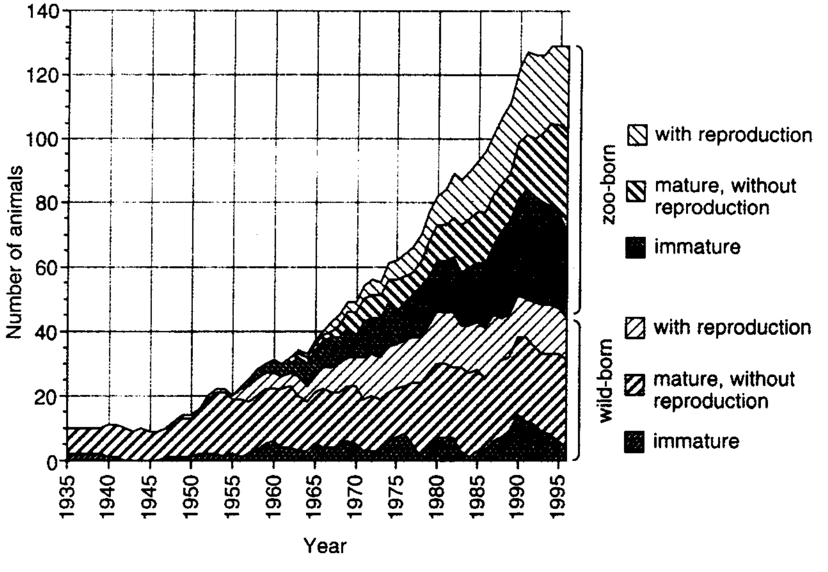
Results

History of the zoo population

Indian rhinoceroses were taken into captivity for the first time in the first century B.C. by the Romans (Reynolds, 1961). Several specimens were brought to Europe from the 16th century onwards. In the 19th century, single individuals of *R. unicornis* attracted numerous visitors to early zoos, travelling circuses and menageries in Europe and the United States (Reynolds, 1967). The first birth in captivity occurred in a menagerie in Kathmandu in 1824 (Rookmaaker, 1979). The modern breeding tradition was started at Basel Zoo in 1956 (Lang, 1961).

The size of the captive population increased steadily between 1950 and 1991, but has remained fairly stable in the nineties (Figure 1). The increase in population size was due partly to the continued introduction of wild-caught animals and partly to successful breeding in many zoos around the world. Of the 129 *R. unicornis* currently living in captivity, 85 (66%) were born in a zoo or animal park. However, 18 wild-caught animals were introduced into zoo populations over the last ten years, indicating that captures from the wild are still of importance. The last introduction of a wild-caught *R. unicornis* into a zoo population occurred in 1993 at Stuttgart Zoo.

Figure 1. Increase of the captive population of the Indian rhinoceros *Rhinoceros unicornis*. Note the large proportion of wild-born individuals without reproduction. Age at sexual maturity was defined as 4y 4m in females and 7y 9m in males.



Sex ratio and demographic structure of the living zoo population

In zoo-born *R. unicornis*, the sex ratio is male-biased from birth to the age of five years (Table 1). At sexual maturity (which occurs at different ages in the two sexes, see below), there is still a tendency towards a male-biased sex ratio, whereas in 20-year-old individuals, males and females occur in more similar proportions. In contrast, a female-biased sex ratio was found in the wild population of Royal Chitwan National Park, Nepal (Table 1; Laurie, 1982; Dinerstein and Price, 1991). A slight (but non-significant) tendency towards a female-biased sex ratio can also be observed in wild-born animals currently alive in zoos (Table 1). This partly counterbalances the male-biased sex ratio observed in zoo-born animals.

Table 1. Sex ratios in the captive population of *R. unicornis*. The sex ratios given for the Kaziranga populations are not very reliable because a large proportion (53% and 23% respectively) of the individuals could not be sexed in these censuses.

Data for the wild populations were taken from Laurie (1982), Dinerstein and Price (1991), Spillett (1967) and Lahan and Sonowal (1973).

	Male	Female	n	p[a]
zoo-born				
live births	59.5 %	40.5 %	126	0.040
6 months	60.4 %	39.6 %	106	0.030
5 years	63.2 %	36.8 %	87	0.018
maturity[b]	58.2 %	41.8 %	79	0.177
20 years	54.5 %	45.5 %	22	0.832
currently alive in zoos				
wild-born	47.7 %	52.3 %	44	0.880
zoo-born	57.6 %	42.4 %	85	0.193
overall	54.3 %	45.7 %	129	0.379
mature	51.0 %	49.0 %	98	0.920
wild populations (adult animals)				
Chitwan (1975)	38.1 %	61.9 %	118	0.013
Chitwan (1988)	43.4 %	56.6 %	205	0.069
Kaziranga (1966)	44.7 %	55.3 %	150	0.221
Kaziranga (1972)	51.9 %	48.1 %	391	0.479

[a] binomial test

[b] age at sexual maturity was defined as 4y 4m in females and 7y 9m in males

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Figure 2. Age distribution of male and female *R. unicornis* kept in captivity on 31 December 1996. ■= wild-born individuals, □= zoo-born individuals. Arrows indicate sex-specific age at sexual maturity.

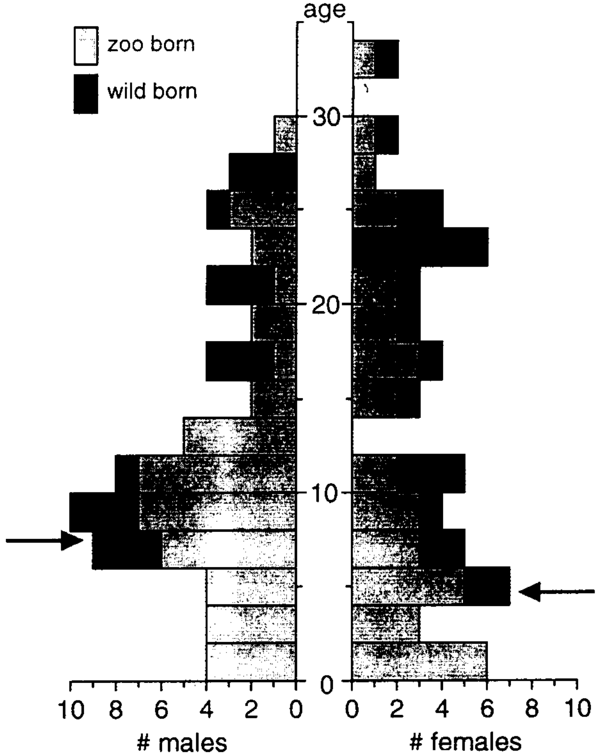


Figure 2 shows the age distribution of male and female *R. unicornis* kept in captivity. Of the 70 males, 50 (71%) have attained sexual maturity. However, only 15 (30%) of these mature males have successfully reproduced. In contrast, 48 (81%) of the 59 females have reached sexual maturity, and 25 (52%) of them have given birth to at least one offspring. This indicates a significant ($\chi^2 = 4.94$, df = 1, p = 0.026) difference between males and females in the proportion of mature individuals that have reproduced.

Life history of Rhinoceros unicornis *in captivity*

The survivorship of live-born *R. unicornis* in captivity is shown in Figure 3. Infant survivorship (live-birth to six months) was 87.7% for males and 85.7% for females. If stillbirths are included, infant survivorship (birth to six months) was 66.9% for males and 70.4% for females. Seventy-five per cent of all juvenile deaths (n = 16, excluding stillbirths) occurred on the day of birth or on the following day. Juvenile and young adult survivorship (age 6 months to 12 years) was high (on average > 99% p.a.). Males and females did not differ in survivorship (Mantel-Cox, χ^2 = 0.465, p = 0.495).

According to the studbook, the maximum age that animals reached in captivity was approximately 42 years for both sexes. However, according to Reynolds (1961), a female lived for 47 years, first in a private menagerie and then in a zoo, in India in the 19th century.

Figure 3. Survivorship of live-born *R. unicornis* kept in captivity. Stillborn individuals have been omitted from this graphic. If they were included, the mortality of age class 0 (0-to-2 years old) would be 23.1% in males and 29.6% in females.

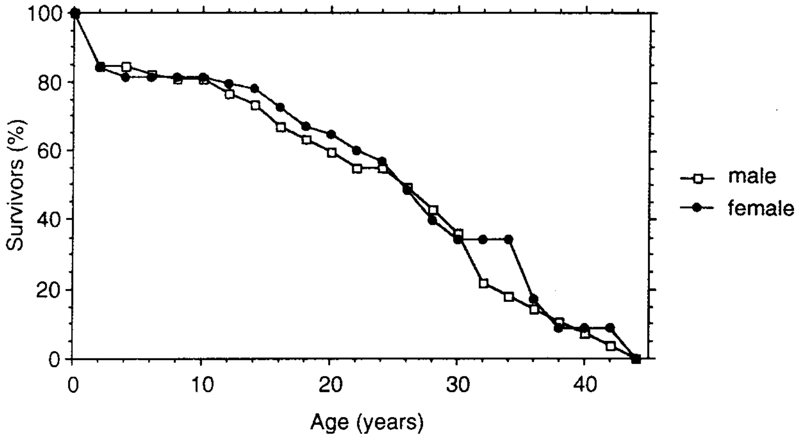
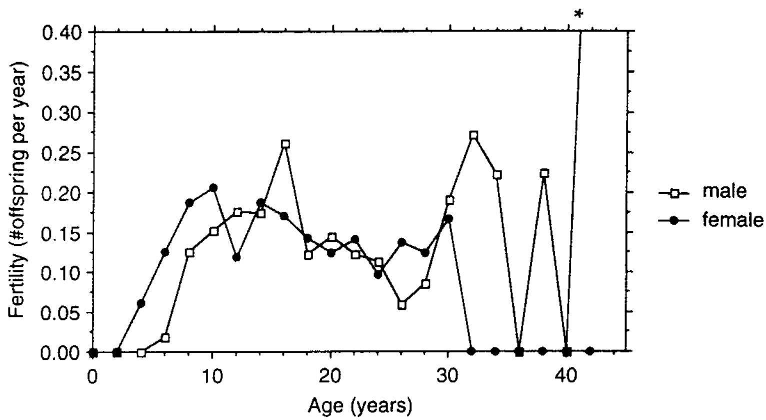


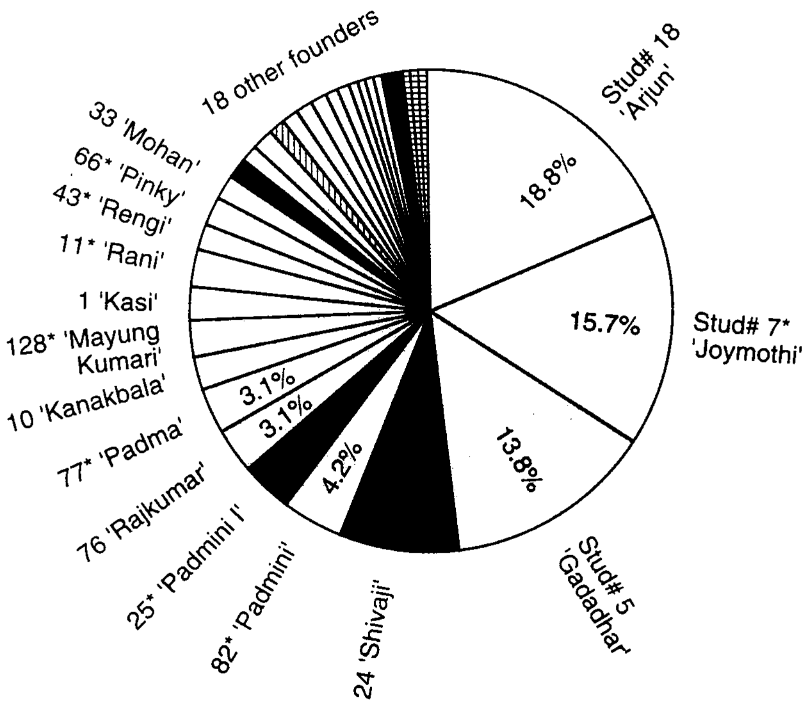
Figure 4. Age-specific fertility. Fertility was defined as the number of offspring per female or male per year. Data for ages > 30 are very unreliable due to small sample sizes. * This data point (0.76) results from the low sample size.



We found no correlation between juvenile mortality (including stillbirths) and the inbreeding coefficient of the offspring or that of either of its parents. Furthermore, there was no association between juvenile mortality and the season of birth. However, we found a difference in juvenile mortality between the offspring of primiparous (juvenile mortality = 40%, n = 43) and multiparous (juvenile mortality = 17%, n = 96) mothers (χ^2 = 8.578, df = 1, p = 0.034).

The age-specific fertility of captive *R. unicornis* females showed a concave shape (Figure 4). In contrast, no age-specific decline in male fertility could be detected in the data so far available.

Figure 5. Distribution of founder contributions to the living zoo-born population. The three best represented founders (Stud ## 5, 7 and 18) contributed almost half (48.4%) of all the genes found in the living zoo-born population. The other 30 founders contributed the other half of the genes. □ = captured in Assam ■ = probably captured in Assam, ▥ = captured in eastern India (Bihar State), ⊟ = captured in Nepal. * indicates females.



First reproduction occurred earlier in females (median: 9y 2m, n = 39) than in males (median: 10y 5m, n = 31; U = 378.0, p = 0.007). The youngest dam giving birth was Studbook #99 at an age of 4y 4m. Studbook #86 was the youngest sire of exactly known age (8y 4m) whose offspring was live-born (#152 was 7y 7m old when his offspring was stillborn two months prematurely). The oldest dam to give birth was #29 at the age of 31y 5m. The oldest sire to become a father was the approximately 42-year-old #10 (Wirz-Hlavacek et *al.*, 1997).

Current genetic structure

One way of looking at the genetic health of a population is to analyze the distribution of origins of all genes (derived from founder animals) present in zoo-born living animals. In an ideal situation, there would be many founders who had made equal contributions to this gene pool. In the case of *R. unicornis* kept in captivity, there are 33 founders and the distribution of founder contributions is highly skewed (Figure 5). The three best represented founders account for almost half (48.4%) of the genes and the other 30 founders account for the other half. Considering the distribution of founder genes among the living animals, we found that 25 (29.4%) of the 85 zoo-born living individuals carry exclusively genes from the three best represented founders, and another 35 individuals (41.2%) carry some genes from these founders. In contrast, only 25 individuals (29.4%) are not related to the three best represented founders.

Origin of founders

In the wild, there are two major populations of *R. unicornis* (Laurie, 1978). One population lives in Assam (north-east India), in and around the Kaziranga National Park, and the other lives in the Royal Chitwan National Park in Nepal. Of the 33 founders of the current captive population, 24 (including the three best represented ones) were caught in Assam. All in all they have contributed 84.7% of the genes in the captive population (Figure 5). The origin of another five founders (with a combined founder contribution of 13.9%) is uncertain, but probably also in Assam (following capture, four of the five were held at Assam State Zoo, Guwahati, and one was given to Antwerp Zoo as a present from the Assam government). One founder (#157, with a founder contribution of 1.2%) was caught in eastern India (Bihar State, just south of Nepal), and three founders (who have contributed 1.8% of the genes) were caught in Nepal.

Development of the genetic status of the captive population

Lacy (1989) defined the founder equivalent as a concept to quantify the genetic status of a population. The founder equivalent (FE) of a population is the number of equally contributing founders that would be needed to produce the observed genetic diversity. The founder equivalent is usually lower than the actual number of founders, because unequal genetic contributions of founders lower the genetic diversity.

The founder equivalent is mainly influenced by the actual number of founders and the evenness of their contribution to the living offspring. In the case of the captive *R. unicornis* population, the founder equivalent is negatively correlated with the sum of the founder representations of the three best represented founders ($z = -2.91$, $n = 37$, $p = 0.0036$; cf. Figure 6).

In the captive *R. unicornis* population, the founder equivalent rose in parallel with the breeding success of additional wild-born animals (Figure 6). After 1974, the founder equivalent dropped because of the death of the only two descendants of the founders #8 and #13, and an increasing over-representation of the three best represented founders (## 5, 7 and 18). After 1980, the founder equivalent slowly recovered, but did not attain its former level until 1995. At present, the founder equivalent (FE = 10.52) is probably still too small to maintain a viable captive population over a longer period. Specialists agree that the genetic contribution of at least 20 individuals is required to maintain a viable population (Foose *et al.*, 1986; Soulé *et al.*, 1986).

Effects of future breeding

To assess the impact of the breeding management of a single zoo on the genetic status of the entire captive population, we evaluated, as a case study, hypothetical births of two additional offspring with different parentages at Basel Zoo. Basel Zoo currently (31 December 1996) houses one adult female (Ellora, #110), one adolescent female (Quetta, #210), one adolescent male (Jaffna, #220) and one juvenile male (Tarrh, #240). The former male (Chitawan, #100), who was closely related to both females and to Tarrh, had to be euthanased because of foot problems in autumn 1995. The adolescent male Jaffna was purchased in spring 1996 from San Diego Wild Animal Park.

We analyzed the effects of five possible breeding programmes on the inbreeding coefficients and the mean kinship of the resulting offspring (Table 2). In the first breeding programme (programme A), the two females currently housed at Basel Zoo were 'mated' with the recently-born Tarrh (#240). This kind of breeding with close relatives would be a continuation of the former breeding system, using animals that are easily available, i.e. animals that were born in Basel Zoo. The resulting offspring would have high inbreeding coefficients and high mean kinships (Table 2).

Programme B, the currently planned breeding programme, tests the outcome of matings between Jaffna and the two females. One of the reasons for purchasing Jaffna was to decrease the inbreeding coefficient in future offspring (cf. Baur and Studer, 1995). In fact, the offspring of the planned matings will have relatively low inbreeding coefficients, which means that they have good chances of being genetically healthy. However, these offspring will still have a high proportion (62.5%) of their genes deriving from the three best represented founders (see above). Therefore, they will have a relatively high mean kinship (between 0.090 and 0.091). As a consequence, it will be hard to find suitable mating partners for the offspring from a genetic point of view. At the same time, the genetic health (measured in terms of founder equivalents) of the entire captive population will deteriorate if Jaffna reproduces successfully with Ellora and Quetta, because the overall share of the three best represented founders will further increase (Figure 6).

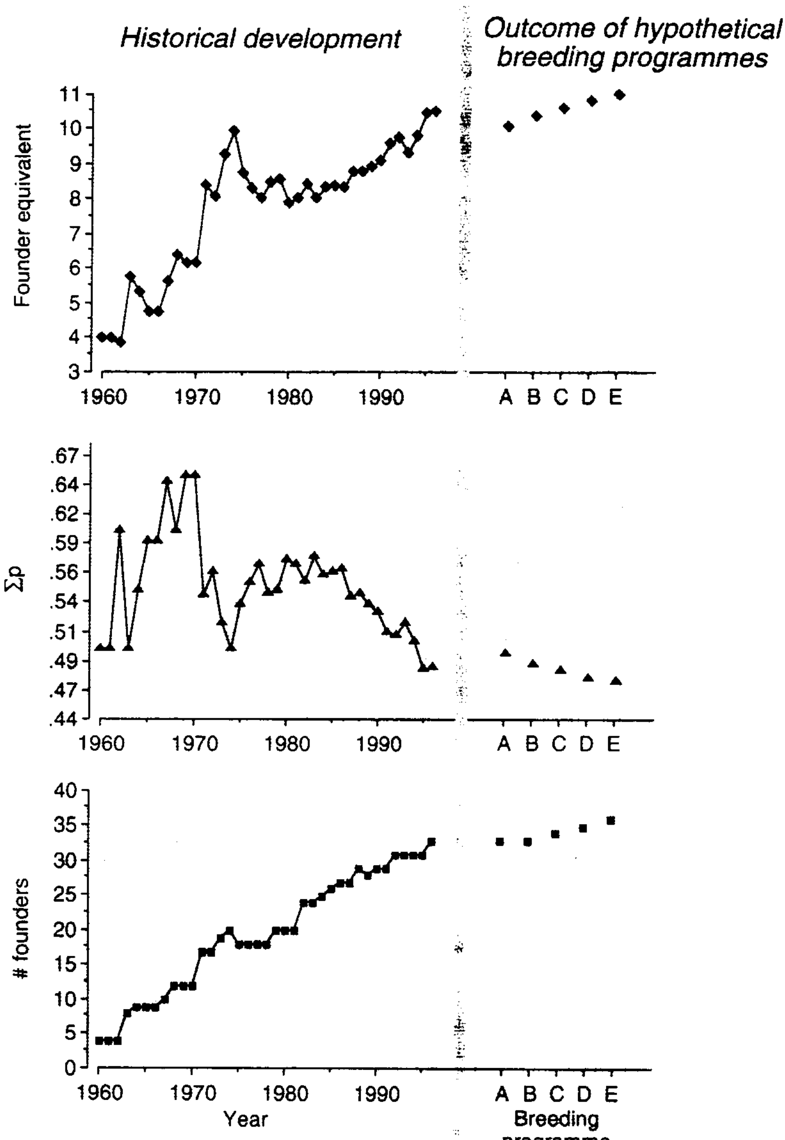
From a genetic point of view, a better solution for Basel Zoo would be to introduce a wild-born female into the Basel group. In programme C, Jaffna is mated with Ellora (#110) and with a wild-born female. In programme D, he is mated twice with the same wild-born female. The offspring of matings between Jaffna and a wild-born female would have an inbreeding coefficient of 0 and a relatively low mean kinship (Table 2). The programmes C and D would – in contrast to the programmes A and B – increase the founder equivalent of the entire zoo population (Table 2, Figure 6).

Table 2. List of analyzed (hypothetical) breeding programmes A–E for Basel Zoo with the inbreeding coefficient (F) and mean kinship coefficient (MK) of the resulting offspring and the founder equivalent (FE) of the worldwide captive population when these two offspring are added. The current FE is 10.522. Note that the MK of each individual depends on the whole population. Therefore, the MK of the first offspring of programme B differs slightly from the first offspring of programme C, even though they have the same parents, because the second offspring is different in the two programmes.

	Sire(s) (Stud#)	Dam(s) (Stud#)	F	MK	FE	Comment
A	240	110	0.500	0.121	10.085	continuation of old breeding system
	240	210	0.500	0.122		
B	220	110	0.016	0.090	10.373	these matings are planned
	220	210	0.016	0.091		
C	220	110	0.016	0.088	10.599	requires introduction of a wild-born female
	220	new ♀	0.000	0.036		
D	220	new ♀	0.000	0.036	10.831	requires introduction of a wild-born female
	220	new ♀	0.000	0.036		
E	new ♂	new ♀	0.000	0.007	10.999	requires introduction of a wild-born male & a wild-born female
	new ♂	new ♀	0.000	0.007		

An even better solution (and more difficult, since wild-born animals are difficult to acquire) would be to breed with a wild-born male and a wild-born female (programme E). This would produce offspring with no inbreeding and very low mean kinships. This solution would also mean a substantial improvement of the genetic health of the population. The resulting founder equivalent (11.00) would be almost 10% higher than the worst case, that is programme A (FE = 10.08), and much better than today's situation (FE = 10.52) or the currently planned programme B (FE = 10.37).

Figure 6. Development of founder equivalents, the founder dominance of the three founders Stud ## 5, 7 and 18 (Σp) and the number of founder animals between 1961 and 1996 (on the left-hand side). On the right-hand side, the influence of the different hypothetical breeding programmes (A–E) at Basel Zoo on the entire captive R. unicornis population is shown.



Discussion

Sex ratio

The reason for the male-biased sex ratio of zoo-born *R. unicornis* is not known. It is possible that this ratio is fixed and coupled with a lower survival rate of male offspring in the wild. Alternatively, it could be a functional adaptation to favourable conditions in the zoos. Since male *R. unicornis* fight for access to females (Ullrich, 1964; Dutta, 1991), females in good condition are expected to produce male offspring, whereas females in worse conditions should produce female offspring (Clutton-Brock and Harvey, 1991).

The female-biased sex ratio observed in the wild population of Nepal is probably the result of intraspecific fights among males or of sex-specific poaching (Lahan and Sonowal, 1973; Laurie, 1982; Dinerstein and Price, 1991).

Life history

All studies carried out in the wild (Lahan and Sonowal, 1973; Laurie, 1982; Dinerstein and Price, 1991) state that the mortality of calves is approximately 10% and that a large proportion of this mortality is caused by tiger predation. In captivity, juvenile mortality is higher, even though there is no tiger predation. We suspect that a proportion of neonatal deaths escaped observation in the wild (Dinerstein and Jnawali, 1993).

In the present paper, we measured the observed fertility, which is based on all animals recorded in the studbook, including those animals that have never been given the chance to reproduce. If all animals had been allowed to reproduce, the measured fertility would probably be higher.

Laurie (1982) reported that in Royal Chitwan National Park the mean age of females at first parturition is about 7.1 years. Thus, on average, females reproduce earlier in the wild than in captivity. In contrast, Dinerstein and Price (1991) reported that 'all but one' of the breeding males observed in Chitwan were older than 15 years, which is much older than the captive breeding males.

Genetic variability

The important question about the extent of the natural genetic variability in *R. unicornis* is so far unanswered. Both major populations in the wild (Nepal and Assam) went through bottlenecks; the population in Assam was reduced to 10–30 individuals before hunting was banned in 1908 (Ryhiner, 1961; Laurie, 1978; Molur *et al.*, 1995). The population in Nepal was reduced to 60–80 individuals in the early 1960s (Dinerstein and McCracken, 1990). So far, only two studies have been undertaken to analyze the genetic diversity of *R. unicornis*. Merenlender *et al.* (1989) found no differentiation between three zoo-born individuals (## 85, 111, 116), all of them descended from founders caught in Assam. Dinerstein and McCracken (1990) reported on high levels of genetic variation among individuals sampled in Royal Chitwan National Park.

The severe bottleneck reported in the Assam population could have caused a high degree of homozygosity with the consequent loss of deleterious alleles, similar to that found in the northern elephant seal (Bonnell and Selander, 1974; Hoelzel *et al.*, 1993) and the cheetah (O'Brien *et al.*, 1983; O'Brien *et al.*, 1985). Since almost all zoo-born *R. unicornis* descend from the Assam population, we could then expect that there are no, or only very few, deleterious alleles left in the captive population. This might explain the absence of observed inbreeding depression within the captive population.

It would be interesting to analyze the genetic variability of the captive *R. unicornis* population and to compare it with those of wild populations in Kaziranga National Park and Royal Chitwan National Park. The results of such a study would be very important for future captive-breeding strategies.

Conclusions

If we want to secure a viable captive population, future breeding programmes must consider not only the genetic health of individuals (as expressed by their inbreeding coefficient), but also their genetic status within the population (as expressed by their mean kinship) and the genetic status of the entire population (as expressed by founder equivalents).

Ideally, all individuals should reproduce equally. This basic rule was rarely considered in the past. In the future, care must also be taken to reduce the representation of the over-represented founder individuals by reducing reproduction of their offspring.

It is obvious that zoos cannot contribute in isolation from *in situ* conservation efforts, and that captive breeding is not sufficient in itself to save endangered taxa (Ebenhard, 1995). Captive breeding specialists and field conservationists need to cooperate and complement each other's efforts, with the ultimate goal of creating self-sustaining zoo populations.

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References

Ballou, J.D. (1983): Calculating inbreeding coefficients from pedigrees. In *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations* (eds. C.M. Schonewald-Cox, S.M. Chambers, B. MacBryde and W.L. Thomas), pp. 509–520. Benjamin/Cummings, Menlo Park.

Ballou, J.D., and Lacy, R.C. (1995): Identifying genetically important individuals for management of genetic variation in pedigreed populations. In *Population Management for Survival and Recovery*

(eds. J.D. Ballou, M. Gilpin and T.J. Foose), pp. 76–111. Columbia University Press, New York.
Baur, B., and Studer, P. (1995): Inbreeding in captive Indian rhinoceros. *International Zoo Yearbook* 34, pp. 205–211.
Bonnell, M.L., and Selander, R.K. (1974): Elephant seals: genetic variation and near extinction. *Science* 184, pp. 908–909.
Buechner, H.K., Mackler, S.F., Stroman, H.R., and Xanten, W.A. (1975): Birth of an Indian rhinoceros *Rhinoceros unicornis* at the National Zoological Park, Washington. *International Zoo Yearbook* 15, pp. 160–165.
Clutton-Brock, T., and Harvey, P. (1991): Parental investment. In *Behavioural Ecology, an Evolutionary Approach* (eds. J.R. Krebs and N.B. Davies), pp. 234–262. Blackwells, Oxford.
Crow, J.F. (1986): *Basic Concepts in Population, Quantitative, and Evolutionary Genetics*. W. H. Freeman and Co., New York.
de Boer, L.E.M. (1991): *European Zoos Care about the Conservation of Endangered Animal Species*. National Foundation for Research in Zoological Gardens, Amsterdam.
Dee, M., Foose, T., and Willis, K. (1994): *AZA SSP Masterplan Indian / Nepalese Rhino (*Rhinoceros unicornis*)*. Los Angeles.
Dinerstein, E., and Jnawali, S.R. (1993): Greater one-horned rhinoceros populations in Nepal. In *Rhinoceros Biology and Conservation* (ed. O.A. Ryder), pp. 196–207. Zoological Society of San Diego, California.
Dinerstein, E., and McCracken, G.F. (1990): Endangered greater one-horned rhinoceros carry high levels of genetic variation. *Conservation Biology* 4, pp. 417–422.
Dinerstein, E., and Price, L. (1991): Demography and habitat use by greater one-horned rhinoceros in Nepal. *Journal of Wildlife Management* 55, pp. 401–411.
Dutta, A.K. (1991): *Unicornis: the Great Indian One-horned Rhinoceros*. Konark Publishers, Delhi.
Ebenhard, T. (1995): Conservation breeding as a tool for saving animal species from extinction. *Trends in Ecology and Evolution* 10, pp. 438–443.
Falconer, D.S. (1989): *Introduction to Quantitative Genetics*. Longman, New York.
Foose, T.J., Lande, R., Flesness, N.R., Rabb, G., and Read, B. (1986): Propagation plans. *Zoo Biology* 5, pp. 139–146.
Hoelzel, A.R., Halley, J., O'Brien, S.J., Campagna, C., Arnbom, T., Le Boeuf, B., Ralls, K., and Dover, G.A. (1993): Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. *Journal of Heredity* 84, pp. 443–449.
IUCN (1987): *The IUCN Policy Statement on Captive Breeding*. IUCN, Gland, Switzerland.
Khan, M. (1989): *Asian Rhinos: an Action Plan for their Conservation*. IUCN/SSC Asian Rhino Specialist Group, Gland, Switzerland.
Krebs, C.J. (1978): *Ecology: the Experimental Analysis of Distribution and Abundance*. Harper and Row, New York.
Lacy, R.C. (1989): Analysis of founder representation in pedigrees: founder equivalents and founder genome equivalents. *Zoo Biology* 8, pp. 111–123.
Lahan, P., and Sonowal, R.N. (1973): Kaziranga Wildlife Sanctuary,

Assam. A brief description and report on the census of large animals (March, 1972). *Journal of the Bombay Natural History Society* 70, pp. 245–278.
Lang, E.M. (1961): Beobachtungen am Indischen Panzernashorn (*Rhinoceros unicornis*). *Der Zoologische Garten* (N.F.) 25, pp. 369–409.
Laurie, A. (1982): Behavioural ecology of the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Zoology, London* 196, pp. 307–341.
Laurie, W.A. (1978): The ecology of the greater one-horned rhinoceros. Ph.D. thesis, Cambridge.
Martin, E.B., and Vigne, L. (1996): Numbers of greater one-horned rhinos continue to rise. *Oryx* 30, pp. 163–165.
Merenlender, A.M., Woodruff, D.S., Ryder, O.A., Kock, R., and Váhala, J. (1989): Allozyme variation and differentiation in African and Indian rhinoceroses. *Journal of Heredity* 80, pp. 377–382.
Molur, S., Sukumar, R., Seal, U., and Walker, S. (1995): *Workshop Report: Population and Habitat Viability Assessment of the Great Indian One-horned Rhinoceros*. CBSG, Coimbatore.
O'Brien, S.J., Roelke, M.E., Marker, L., Newman, A., Winkler, C.A., Meltzer, D., Colly, L., Evermann, J.F., Bush, M., and Wildt, D.E. (1985): Genetic basis for species vulnerability in the cheetah. *Science* 227, pp. 1428–1434.
O'Brien, S.J., Wildt, D.E., Goldman, D., Merril, C.R., and Bush, M. (1983): The cheetah is depauperate in genetic variation. *Science* 221, pp. 459–462.
Reynolds, R.J. (1961): Asian rhinos in captivity. *International Zoo Yearbook* 2, pp. 17–42.
Reynolds, R.J. (1967): Some photographs of rhinos exhibited by American circuses between 1855 and 1926. *Der Zoologische Garten* (N.F.) 34, pp. 279–292.
Rookmaaker, L.C. (1979): The first birth in captivity of an Indian rhinoceros (*Rhinoceros unicornis*): Kathmandu, May 1824. *Der Zoologische Garten* (N.F.) 49, pp. 75–77.
Rookmaaker, L.C., and Reynolds, R.J. (1985): Additional data on rhinoceroses in captivity. *Der Zoologische Garten* (N.F.) 55, pp. 129–185.
Ryhiner, P. (1961): *Auf Tierfang durch die Welt*. Horst Erdmann, Herrenalb.
Soulé, M., Gilpin, M., Conway, W., and Foose, T. (1986): The millennium ark: how long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5, pp. 101–113.
Spillett, J.J. (1967): A report on wild life surveys in North India and Southern Nepal, Jan.–June 1966. *Journal of the Bombay Natural History Society* 63, pp. 492–628.
Stearns, S.C. (1992): *The Evolution of Life Histories*. Oxford University Press, Oxford.
Tobler, K. (1993): *International Studbook for the Great Indian Rhinoceros* Rhinoceros unicornis *(Linné 1758)*. Zoological Gardens Basel, Switzerland.
Ullrich, W. (1964): Zur Biologie der Panzernashörner (*Rhinoceros unicornis*) in Assam. *Der Zoologische Garten* (N.F.) 28, pp. 225–250.
Wirz-Hlavacek, G., Zschokke, S., and Studer, P. (1997): *International*

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