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Inbreeding in captive Indian rhinoceros

Rhinoceros unicornis

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Since the 1950s the Indian rhinoceros *Rhinoceros unicornis* has bred successfully in captivity. An analysis of the international studbook has revealed a high incidence of inbreeding in some captive populations. This paper discusses the effects of inbreeding in relation to other factors, such as parity, birth weight and gestation length, and calls for the introduction of an international co-operative breeding programme to minimize inbreeding and to maintain genetic diversity within the captive population.

Inbreeding increases homozygous genotypes which together with the general tendency for deleterious alleles to be recessive, provides the genetic basis of adverse effects (Falconer, 1981). Studies on laboratory and domestic animals have shown that inbreeding often leads to a reduction in viability and fertility (Wright, 1977; Lasley, 1978) and this has also been documented for a variety of zoo animals (Ralls *et al.*, 1979, 1980, 1988; Ballou & Ralls, 1982; Ralls & Ballou, 1982a,b, 1983; Laikre & Ryman, 1991; Lacy *et al.*, 1993). The need for genetic management of small populations has been recognized and co-operative breeding plans have been developed for a number of taxa (Ralls & Ballou, 1983). Our analysis of the Indian rhinoceros *Rhinoceros unicornis* studbook has revealed a dramatic increase in inbreeding within the captive population over the past 30 years. We also examined the breeding of this species at the Zoological Gardens of Basle which at the time of writing housed the most successful breeding group.

The Indian rhinoceros is one of the most endangered large mammals. In the early 1980s only two populations exceeded 80 individuals (Laurie, 1982; Dinerstein & McCracken, 1990) and earlier this century both faced extinction. This situation has been improved by habitat protection. The population in what is now the Royal Chitwan National Park, Nepal, was reduced to an estimated effective population size of 21–28 (60–80 individuals) in 1962 but recovered to almost 400 animals by 1988 (Dinerstein & Price, 1991). In Kaziranga National Park, Assam, the population declined to less than 100 in 1912 (Laurie, 1982) but recovered to 1500 animals by the late 1980s. Poaching has been a serious problem in Assam where at least 233 rhinoceroses were killed between 1982 and 1985 (Martin *et al.*, 1987).

METHODS

Data on parentage, juvenile mortality, birth weight and gestation length were obtained from the 6th edition of the Indian rhinoceros studbook (Tobler, 1991; data to 31 December 1990). Inbreeding coefficients based on pedigree were calculated with a computer program (THINK-PASCAL on MacIntosh, available from the authors on request) using the additive relationship matrix method (Ballou, 1983). All founders were assumed to be unrelated, as were individuals introduced to herds at a later date. This may not have been justified in all cases and therefore the inbreeding coefficients represent minimum estimates. Individuals with an inbreeding coefficient of zero were classified as 'non-inbred' and those with an inbreeding coefficient greater than zero as 'inbred'. The terms inbred and non-inbred are relative and levels of inbreeding can only be quantified with respect to a base population (Falconer, 1981). Because the founder animals were used as the base population the inbreeding coefficients reflect only the situation that has occurred in captivity. It was not possible to calculate inbreeding coefficients for three individuals whose parentage was unknown and these animals have been excluded from the analyses.

Following Ralls *et al.* (1979, 1980) offspring that survived longer than six months were classified as having 'lived' and all others, including still births, as 'died'. Offspring were further classified as to whether the dam was wild-caught or captive-born, primiparous or multiparous, inbred or non-inbred. Two offspring that could not be classified by any of these criteria were excluded from these particular analyses. Offspring were also grouped by the month and season of birth, which allowed us to compare inbred and non-inbred calves born during the same month or season regardless of the year.

POPULATION GROWTH AND INBREEDING

The captive population of Indian rhinoceros has increased steadily from six in 1951 to 114 in 1990 as a result of successful breeding and the importation of wild-caught animals (Fig. 1). Between 1951 and 1980 an average of 2·0 wild-caught animals per year were either introduced to existing herds or used to establish new breeding groups in the captive population. Imports of wild-caught animals declined during the 1980s and the number of births in captivity increased, with a mean 5·3 young born each year.

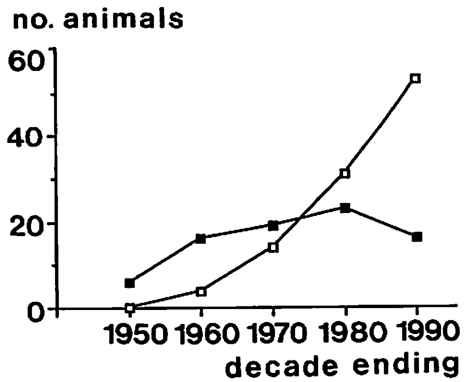

Fig. 1. Total number of imports (black squares) and births (open squares) of Indian rhinoceroses *Rhinoceros unicornis* per decade from 1950 to 1990.

Despite the importation of new founder stock the mean inbreeding coefficient of calves born in captivity increased from zero in the 1950s to 0·084 (range 0–0·375) in the 1980s (Fig. 2). Of 53 calves born between 1981 and 1990, 16 (30%) were inbred. The level of inbreeding varied greatly among zoos between the 1960s and time of writing. The data presented here relate only to the 1980s. At San Diego Wild Animal Park the mean inbreeding coefficient was 0·068 (range 0–0·250, $n=11$); at Stuttgart Zoo the mean inbreeding coefficient was 0·188 ($n=5$); at Basle Zoo the mean inbreeding coefficient was 0·333 (range 0·250–0·375, $n=6$). These values represent minimum estimates.

BREEDING REGIME AT BASLE

The population at Basle Zoo was founded with one ♂ (Gadadhar, stdbk no. 5) acquired in 1951 and one ♀ (Joymothi, stdbk no. 7) acquired in 1952. Both animals were obtained from the same source but it is not known whether they were related. The first birth in captivity occurred on 14 September 1956 (Rudra, stdbk no. 14) (Lang, 1961; Lang *et al.*, 1977). Up to 1965 six offspring were the result of matings between Gadadhar and either Joymothi or Gadadhar's daughter (Moola, stdbk no. 17). In 1965 a wild-caught ♂ (Arjun, stdbk no. 18) was acquired and he sired all 14 young born at Basle up to 1984. Since 1988, Chitawan (stdbk no. 100), the son of Arjun and Arjun's daughter (Tanaya, stdbk no. 56), has sired all offspring. By December 1990 24 young had been born from four ♀♀ and sired by three ♂♂. As a result of repeated mating between related animals the mean inbreeding coefficient of offspring at Basle increased from zero in the 1950s to 0·333 in the 1980s (Fig. 2). All offspring born since 1988 have an inbreeding coefficient of 0·375. Of the 13.11 rhinoceroses born at Basle, eight out of nine ♀♀ (89%) have given birth to at least one calf, at Basle, Stuttgart, Berlin, Antwerp, Philadelphia or Los Angeles, whereas only three of 12 ♂♂ (25%) have been allowed to reproduce (by 1990 1.2 had not yet reached the age of sexual maturity). Of 84 calves born in captivity between 1971 and 1990 43 (51%) have at least one parent that originated from the Basle line.

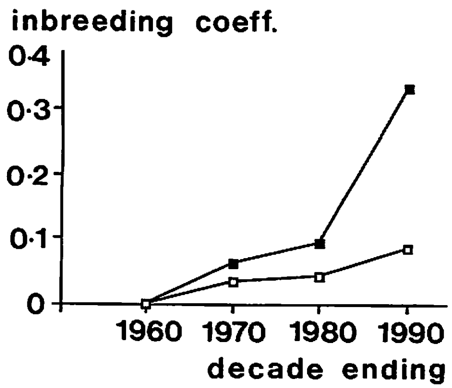

Fig. 2. Mean inbreeding coefficient of Indian rhinoceroses for all calves born in captivity (open squares) and calves born at Basle Zoo (black squares).

INBREEDING AND JUVENILE MORTALITY

Using the data from all captive rhinoceros a three-way table analysis (Sokal & Rohlf, 1981) that considered juvenile mortality, inbreeding and parity indicated the presence of a three-way interaction. Individual Freeman-Tukey deviates suggested that the degree of association between level of inbreeding and juvenile mortality differed between offspring of primiparous ♀♀, which had a higher mortality, and offspring of multiparous ♀♀. Independent of parity, inbred and non-inbred animals did not differ in juvenile mortality (inbred: 8%, $n=24$; non-inbred: 22%, $n=77$; $\chi^2=2·26$, df$=1$, $P>0·1$). However, the offspring of ♀♀ which were inbred tended to have a higher juvenile mortality (23%, $n=13$) than those born to non-inbred ♀♀ (18%, $n=88$; $\chi^2=0·18$, df$=1$, $P>0·1$). Calves with an inbreeding coefficient $>0·25$ appeared to have a higher juvenile mortality (33%, $n=6$) than calves with an inbreeding coefficient <0·25 (22%, $n=54$).

PARITY, BIRTH WEIGHT AND GESTATION

Independent of the degree of inbreeding, the offspring born to captive-born ♀♀ had a higher juvenile mortality rate (23%, $n=60$) than those born to wild-born ♀♀ (12%, $n=41$), although this difference is not statistically significant ($\chi^2=1{\cdot}98$, df=1, $P=0{\cdot}15$). Furthermore, independent of the degree of inbreeding, offspring of primiparous ♀♀ had a significantly higher juvenile mortality rate (38%, $n=26$) than those of multiparous ♀♀ (10%, $n=67$; $\chi^2=9{\cdot}84$, df=1, $P<0{\cdot}001$). This may reflect a lower maternal capability in young or inexperienced ♀♀, a smaller birth weight or something other than inbreeding associated with a first-born calf. Available data indicate that birth weight is important for juvenile survival: mean birth weight of calves that did not survive was 54·9±2·6 kg (mean±SD), range 51–57 kg, $n=4$; mean birth weight of calves that survived was 67·4±5·9 kg, range 59–79, $n=18$ ($t=4{\cdot}12$, $P<0{\cdot}001$). Inbred and non-inbred animals did not differ in birth weight ($t=0{\cdot}68$, $P>0{\cdot}5$) and thus birth weight was not correlated with the inbreeding coefficient of the calves ($r=0{\cdot}11$, $n=22$, $P>0{\cdot}6$). Gestation tended to be shorter for inbred young (474·1±9·7 days, $n=10$) than for non-inbred young (479·5±5·8 days, $n=14$; $t=1{\cdot}71$, $P=0{\cdot}1$). Gestation length was negatively correlated with the coefficient of inbreeding of the young ($r=-0{\cdot}43$, $n=24$, $P=0{\cdot}03$).

BIRTH SEASON

The distribution of births by month for inbred and non-inbred young is given in Table 1. There was no difference in the monthly distribution of inbred and non-inbred births. Independent of the degree of inbreeding, offspring born during the colder months (October to March) had a significantly higher juvenile mortality rate (25%, $n=51$) than those born in the warmer months (April to September: 10%, $n=49$, $\chi^2=3{\cdot}96$, df=1, $P<0{\cdot}05$).

MONTH OF BIRTH	INBRED CALVES		NON-INBRED CALVES	
	LIVED	DIED	LIVED	DIED
Jan	4	1	6	3
Feb	1	0	3	1
Mar	2	0	3	1
Apr	0	0	6	0
May	2	0	5	1
Jun	1	0	4	1
Jul	2	0	5	2
Aug	3	0	11	1
Sep	2	0	3	0
Oct	2	0	6	3
Nov	2	0	3	2
Dec	1	1	5	1
Total	22	2	60	16

Table 1. Distribution of juvenile mortality in inbred and non-inbred Indian Rhinoceros *Rhinoceros unicornis* calves according to month of birth. No date of birth was available for one non-inbred stillborn calf. Primiparous ♀♀ had 25% of inbred and 29% of non-inbred calves. The young from primiparous ♀♀ had a significantly higher juvenile mortality than those from multiparous ♀♀.

DISCUSSION

Captive breeding should be utilized to develop a self-sustaining population which preserves as much as possible of the genetic variability present in the wild (Franklin, 1980; Frankel & Soulé, 1981; Frankham *et al.*, 1986; Soulé *et al.*, 1986; Willis, 1993). Many existing captive populations, including those of the Indian rhinoceros, were founded before the need for genetic management was recognized. These populations may already have characteristics that are unsuited to the development of self-sustaining populations. Inbreeding in the captive Indian rhinoceros population has increased significantly even though this species has been bred for only two or in a few cases three generations (the generation interval of the Indian rhinoceros is six to ten years).

Many animal breeders believe that inbreeding rates should not exceed 2 or 3% per generation because higher rates of inbreeding fix deleterious genes more quickly than selection can eliminate them (Soulé, 1980). Soulé (1980) recommends that the more conservative value of 1% inbreeding per generation should be used as an upper limit for most zoo animals (sustained sire-daughter mating would result in an inbreeding rate of 25% per generation). In the Indian rhinoceros inbreeding increases by more than 4% per generation (Fig. 2).

The level of inbreeding depression in a small population may be dependent on a number of factors such as the breeding system of the species, its genetic load, the time the population has been genetically isolated and the environment in which inbreeding depression is measured (Ralls *et al.*, 1979; Pray *et al.*, 1994). Theoretically, the Indian rhinoceros may be adapted to high levels of inbreeding and therefore the population might not suffer from inbreeding depression. If Indian rhinoceros regularly inbreed in the wild, much of the genetic load would have been eliminated and there should be fewer deleterious effects of inbreeding in captivity (Templeton & Read, 1983). Dinerstein & McCracken (1990) found a high heterozygosity in 23 *R. unicornis* in the Chitwan Valley, despite a population bottle-neck early in the 1960s.

Inbreeding has been shown to reduce viability and fertility in such taxonomically distant organisms as insects and plants (Wright, 1977). Ralls *et al.* (1979) predicted that these effects may be expected in the majority of ungulate species. Ballou & Ralls (1982) documented adverse effects of inbreeding in 12 species of captive ungulates and all herds of the species examined had a mean inbreeding coefficient that exceeded 0·196. World-wide inbreeding in the captive Indian rhinoceros population has not yet reached this level, except in the breeding groups at some zoos. The present study does not show any significant deleterious effects in captive Indian rhinoceros, although calves with an inbreeding coefficient larger than 0·25 tended to have a higher juvenile mortality than calves with an inbreeding coefficient smaller than 0·25. However rather than wait for significant results, action should be taken to minimize further inbreeding.

Managed captive-breeding programmes, such as the American Zoo and Aquarium Association Species Survival Plan (SSP), the European Endangered Species Program (EEP) and the Joint Management of Species Programme (JMSP) of the Federation of Zoological Gardens of Great Britain and Ireland, are used to retain as much original genetic variation in a population as possible, given the practical limitations of space and resources (Flesness, 1977; Foose, 1983; Foose *et al.*, 1986; Ralls & Ballou, 1986; Soulé *et al.*, 1986; Foose & Ballou, 1988; Lacy, 1989). Geneticists and population biologists have developed recommendations for achieving this goal, such as maximizing effective population size and equalizing the genetic contribution of the founder animals within the captive population. These strategies may help to maintain genetic diversity in a population, enabling it to adapt to new environments and preserves future management options.

The IUCN/SSC Asian Rhino Specialist Group has compiled a list of recommendations for the conservation of the Indian rhinoceros (Khan, 1989), including increasing the captive population from 75 to at least 150 individuals and managing the world captive population as a single unit. We suggest that the captive-breeding programme in North America (Khan, 1989) be extended to a world-wide co-operative breeding programme under the guidance of the appropriate organization. The time has come to institute sound genetic management of small populations to minimize inbreeding and maximize genetic diversity.

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Hand-feeding a Black rhinoceros *Diceros bicornis* calf at Dvur Kralove Zoo

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In December 1992 a Black rhinoceros *Diceros bicornis* was born to a 22-year-old ♀ at Dvur Kralove Zoo. Because this was her first calf and she appeared to have an under-developed udder, preparations were made for hand-rearing. The tolerant behaviour of the dam allowed us to hand-feed the calf which remained with its mother until weaning at 15 months. This paper describes the feeding formula, feeding technique and veterinary care involved.

Hand-rearing Black rhinoceros *Diceros bicornis* in captivity has not been attempted often and only if the calf is weak or if the dam has died or is aggressive towards the calf. Calves have been separated for hand-rearing from a few days to several weeks old but on most occasions the animal has failed to survive (Kreag, 1966; Maruska *et al.*, 1986). Successful hand-rearing has been reported at Cincinnati Zoo for a calf weighing 37·3 kg at birth (Maruska *et al.*, 1986) and at London Zoo where an 18 kg newborn was extremely weak (Kirkwood *et al.*, 1989). At Dvur Kralove the calf had a low birth weight and appeared to be weak. In addition, the dam failed to produce sufficient milk and the calf required hand-feeding.

BIRTH

At 0300 hours on 14 December 1992, after successful hormone induction of oestrus using an oral application of synthetic progesteron allyl trenbolone (Regumate), consequent mating and a gestation period of 469 days, the 22-year-old primiparous Black rhinoceros ('Jarča', stdbk no. 178) gave birth to a ♀ calf (stdbk no. 456). As this was her first calf and because of her age, she was monitored using closed-circuit TV 24 hours a day for two weeks before parturition. Female rhinoceroses usually begin to secrete milk about 14 days prior to parturition but because Jarča's udder was poorly developed and as she appeared to be producing only a small amount of milk, preparations were made for hand-rearing.

DAYS	MEAN VOLUME FORMULA FED PER DAY (litre)	COMMENTS
1	1·71	
2	3·81	
3	4·11	
4	5·21	
5–8	6·51 (5·2–7·5)	
9–26	9·75 (9·4–10·5)	a reduced volume of food was ingested on days 12–21 (mean 7·65 litre) associated with a bout of diarrhoea and treatment
27–40	10·55 (9·7–11·7)	
41–215	13·55 (9·7–16)	a reduced volume of food was ingested on days 74–78 (mean 10·5 litre) associated with a bout of diarrhoea and treatment
216–225	14	intake stabilized at 14 litre per day
226–451		the volume of milk offered was gradually decreased by 0·5 litre in 10 day intervals until weaning at 15 months. Last volume 2·5–3·5 litre

[1]Ranges in parentheses.

Table 1. Mean volume of formula fed per day to a Black rhinoceros *Diceros bicornis* calf until weaning at 15 months of age.

There were no complications with the birth as the calf had a caudolongitudinal presentation with upper positioning. The newborn was markedly weaker than calves previously born at Dvur Kralove and after four hours it was still not able to stand, even with help from a keeper. The calf first stood at six hours and appeared to search for a teat. Keepers fed the calf 20 ml of colostrum using a syringe and at ten hours gave a second small feed of colostrum mixed with milk from another ♀ ('Elvira', stdbk no. 244) that had given birth successfully six days earlier. From the following morning the calf was fed totally by hand. The small quantity of colostrum produced by the dam was combined with horse colostrum and milk from two other ♀♀ (stdbk no. 244 and also stdbk no. 282 which had given birth 11·5 months previously). Milking of these two females was attempted daily. One keeper would feed and scratch the animal while another keeper milked her through the enclosure barrier. This required constant vigilance and a good knowledge of the ♀'s temperament to ensure safety. Not all attempts at milking were successful and the quantity of milk obtained varied: it was possible to milk up to 2 litres from Elvira.

FEEDING

Preparations for hand-feeding included obtaining a reserve of horse colostrum which was collected during veterinary health checks from mares at the horse breeding centre in Slatiňany. On days 1 and 2 the calf was fed Black rhinoceros colostrum and milk, and horse colostrum. From day 3 reconstituted dried, centrifuged domestic cow's milk (Laktino) was gradually introduced to the mixture. The feed was offered in a metal-plated bottle with a 100 mm calf nursing nipple. Substitute milk was prepared from 50 g of dried milk (Laktino), 40 g of glucose and 4 ml of radicle (corn sprout) oil/Klickovy olej (a mixture of unsaturated butyric acids with vitamin E, 0·26 mg in 100 g of oil), diluted in one litre of boiled water. Although the volume of formula offered increased, the frequency of feeds decreased and the proportion of rhinoceros milk and milk substitute varied (Tables 1, 2 and 3), the proportion of