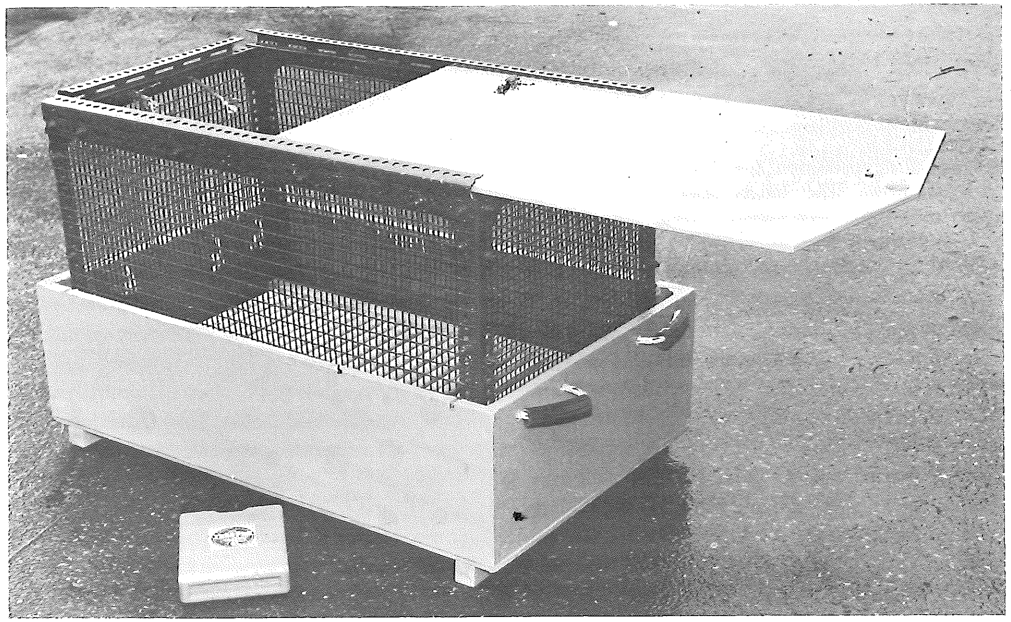

Plate 1. Transport cage for Sea otters *Enhydra lutris,* showing the sliding lid, wooden dowlings on the floor and the outer casing or carrying box. *Vancouver Public Aquarium.*

wooden case was necessary only on the long air trip.

The basic cage measured 91 × 56 × 56 cm high. The frame was made of lightweight plastic-coated slotted angle L-bar. All four sides were covered by plastic-coated 2·5 × 1·3 cm wiremesh, which allowed maximum ventilation. The floor was made of 1·9 cm diameter wooden dowling placed 1·2 cm apart to allow faecal matter to drop through. This is most important as the otter is unable to groom out of the water and if the fur becomes soiled it loses its waterproofing and insulation qualities, resulting in stress and chilling when the animal finally has access to water for swimming.

The sliding lid of the cage was made of 1 cm thick plywood. It fitted into a slot and could be closed much faster than a hinged lid; an important factor at the capture site. The slotted frame for the lid was constructed of two L-bar sections bolted one above the other about 1·27 cm apart. Once closed the lid was secured with a nut and bolt.

The wooden outer casing measured 140 × 66 × 28 cm high. It was waterproofed with a fibreglass coating and had carrying handles at either end. Several plastic freezer packs were placed on the bottom and covered with ice to a depth of about 15 cm. The cage was then lowered to rest on the ice. With the slatted wooden floor of the cage above, the arrangement provided maximum cooling without the animal coming into direct contact with the ice. Another advantage was that the attendants could lift the cage out of the box and remove any excreta and/or change the ice during the journey without opening the animal's cage.

The cabin temperature in the aircraft was lowered and all fans turned on. During a total transport time of 14 hours the Sea otters remained calm, clean and, to all outward appearances, unstressed. Within minutes of their arrival at the Aquarium all the animals began to groom and feed, and all seven are alive and thriving at the time of writing.

It is the opinion of the authors that the use of this cage contributed in large part to the successful transport of the animals.

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Demographic survey of the Black rhinoceros *Diceros bicornis* in captivity

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There is a growing awareness in zoos that rare and endangered species in captivity should not be managed as solitary collections but as entire populations to which demographic methods can be applied (Foose, 1980). The eventual aim of such procedures would be to make more species self-sustaining in captivity. Pinder & Barkham (1978) assess that of the 229 rare mammal species in zoo collections between 1962 and 1 January 1976 only 26 species could be considered self-maintaining, and of these only eight had achieved this status after 1970. In previous years there has been a lack of accurate analysis in zoos of their contribution to conservation, and also of serious self-criticism (Pinder & Barkham, 1978) but this state of affairs is gradually changing. Several attempts have been made recently to discuss the management of endangered species both demographically (Foose, 1977, 1980; Goodman, 1980) and genetically (Benirschke, 1977; Flesness, 1977; Chesser *et al.*, 1980; Senner, 1980) with a view to making recommendations for its possible improvement.

Demographic methodology has long been used to describe wild populations. Survival curves have been constructed by Goddard (1970) for Black rhinoceroses *Diceros bicornis* in the Tsavo National Park, Kenya. The most time-consuming and difficult part in the constitution of life tables for wild populations is the determination of age. This is not such a problem for species in captivity, especially if there is a studbook available since here the estimated age, at least, of each individual is recorded. Without a studbook, age determination is obviously more difficult but relatively accurate data can often be obtained from zoo records.

It seems evident from the birth and death rates given in the Black rhinoceros studbook (Klös & Frese, 1981) that the captive population is decreasing. Since recording started in 1969 there have been a few years where the number of births have balanced the number of deaths, but the overall picture is one of diminishing stocks. Before 1977 it was possible to replace stock deficits by importation from the wild but since the numbers of wild Black rhinoceroses are now seriously depleted (Hillman & Martin, 1979) and there are a number of restrictions on trade, future importations will be difficult to justify. If the species is to remain a part of zoo collections it seems necessary that the population already in captivity is managed with the aim of making it eventually self-sufficient. At present our calculations show that captive numbers are decreasing at a rate of *c.* 7% per year and if this trend is allowed to continue the number in ten years' time will be only half of what it is today. To calculate the rate of population decrease, and to discover how propagation might be improved, the following demographic analysis has been carried out.

MATERIALS AND METHODS

Information on 145 Black rhinoceroses which died between 1969 and 1980 was obtained from the studbook and from data received through answers to questionnaires. In 12 cases the age at which the animal died had to be estimated on the basis of the date at which it had arrived at the zoo. The same sources have also provided data on the total number of captive births and on the number of animals still living in captivity. Following methods described by Krebs (1978) the material has been divided into age groups for the construction of generation life tables, fertility tables and survivorship curves. The following symbols have been used:

x: age interval;

n_x: number surviving at the start of age interval x;
l_x: scale of proportion, or probability, of surviving to the start of age interval x (i.e. age-specific survival rate);
d_x: number dying during the age interval x to $x+1$;
q_x: mortality rate during the age interval x to $x+1$;
e_x: mean expectation of life for those alive at the start of age interval x;
m_x: number of offspring of the same sex as the parent expected from an individual at age interval x per time unit (five years);
R_o: net reproductive rate;
r_m: innate capacity of a population for increase (or decrease) for a particular set of environmental conditions;
G: generation time (mean period of time between the birth of an animal and the birth of its progeny);
λ: annual rate of change.

The symbol l_x given here is expressed on the basis of 1·00 as a starting point, which is the scale of proportion surviving to a given age or the probability of survival. A number of other starting points can be used (e.g. 100, the scale of percentage survival, or 100 000, used for human populations). Survival rate can be calculated as

$$l_{x+1} = l_x\,(1 - q_x)$$

Since knowing the chances of survival in the first few years of life is of particular interest an age interval of one year has been selected for the first five years, after which ages are given in five-year groups. It has been possible to give the ages of most of the young animals accurately since almost all were captive bred. Life tables usually start with a complete survival at birth (Krebs, 1978) but in this study

x	n_x	l_x	d_x	q_x	e_x
0'	145	1·000	10	0·069	
0–1	135	0·931	16	0·119	12·2
1–2	119	0·820	2	0·017	12·7
2–3	117	0·807	15	0·128	12·0
3–4	102	0·703	1	0·010	12·7
4–5	101	0·697	3	0·030	11·8
5–10	98	0·676	25	0·255 (0·051)	11·1
10–15	73	0·503	28	0·384 (0·077)	9·1
15–20	45	0·310	19	0·422 (0·084)	8·2
20–25	26	0·179	13	0·500 (0·100)	
25–30	13	0·090	4	0·308 (0·062)	7·1
30–35	9	0·062	7	0·778 (0·156)	4·1
35–40	2	0·014	1	0·500 (0·100)	4·8
40+	1	0·007	1	1·000	1·7

Key: x. age interval (years); n_x. number surviving at start of age interval x; l_x. probability of surviving to start of age interval x; d_x. number dying during age interval x to $x+1$; q_x. rate of mortality during age interval x to $x+1$ (numbers in parentheses are yearly rates); e_x. mean expectation of further life (years).

Table 1. Life table for the Black rhinoceros *Diceros bicornis* population in captivity, compiled from data on animals which died between 1969 and 1980.

x	d_x	n_x	l_x	q_x
0'	4	67	1·000	0·22 (0'–0–1)
0–1	10	63	0·940	
1–2	0	53	0·791	0·00
2–3	8	53	0·791	0·15
3–4	0	45	0·672	0·00
4–5	0	45	0·672	0·00
5–10	6	45	0·672	0·13 (0·03)
10–15	16	39	0·582	0·41 (0·08)
15–20	11	23	0·343	0·48 (0·10)
20–25	6	12	0·179	0·50 (0·10)
25–30	1	6	0·090	0·17 (0·03)
30–35	4	5	0·075	0·80 (0·16)
35–40	0	1	0·015	0·00
40–48	1	1	0·015	1·00
48+		0	0·0	

Table 2. Life table for 67 captive ♀ Black rhinoceroses which died between 1969 and 1980 (for a key to the symbols see Table 1).

an additional group 0' is included, consisting of ten animals which were either stillborn or died within 24 hours of birth (Table 1). Life tables for ♂♂ and ♀♀ are given separately (Tables 2 and 3).

One method of predicting how a population will change is to discover the net reproductive rate R_o by combining mortality l_x and net reproduction m_x rates:

$$R_o = \sum_{x=0}^{\infty} l_x m_x$$

To do this it is necessary to know the probability of an animal surviving to a specific age (l_x) and to know how many offspring it will produce within the corresponding age interval (m_x). If the survival rate was 100% then R_o would simply be the sum of the offspring born to each age group, or the sum of the m_x column.

To find m_x for each sex it is necessary to discover the number of births of each sex. In the case of the Black rhinoceros it can be done by counting all the captive births (based on the records available) and dividing the number by two (Figs 1b and 2b) since the sex ratio in the 131 known births in captivity was roughly equal (65.63.3). In addition to the live births information is available on two abortions, where the young were carried to almost full term, which have been included in Figs 1 and 2 but not in the life tables of Table 1.

The number of ♀♀ in Fig. 1a is made up from all ♀♀ surviving to each particular age group, including ♀♀ which are still alive and therefore not among the 67 ♀♀ in Table 2. The age of an individual in 1981 has been the basis for calculating the age of the living ♀♀ (e.g. a ♀ aged 11 years in 1981 will count as one in the 5–10 year age group but as only 0·20 in the 10–15 year age group). Since no

x	d_x	n_x	l_x	q_x
0'	3	75	1·000	0·12 (0'–0–1)
0–1	6	72	0·960	
1–2	2	66	0·880	0·03
2–3	7	64	0·853	0·11
3–4	1	57	0·760	0·02
4–5	3	56	0·747	0·05
5–10	19	53	0·707	0·36 (0·07)
10–15	12	34	0·453	0·35 (0·07)
15–20	8	22	0·293	0·36 (0·07)
20–25	7	14	0·187	0·50 (0·10)
25–30	3	7	0·093	0·43 (0·09)
30–35	3	4	0·053	0·75 (0·15)
35–40	1	1	0·013	1·00
40+		0	0·0	

Table 3. Life table for 75 captive ♂ Black rhinoceroses which died between 1969 and 1980 (for a key to the symbols see Table 1).

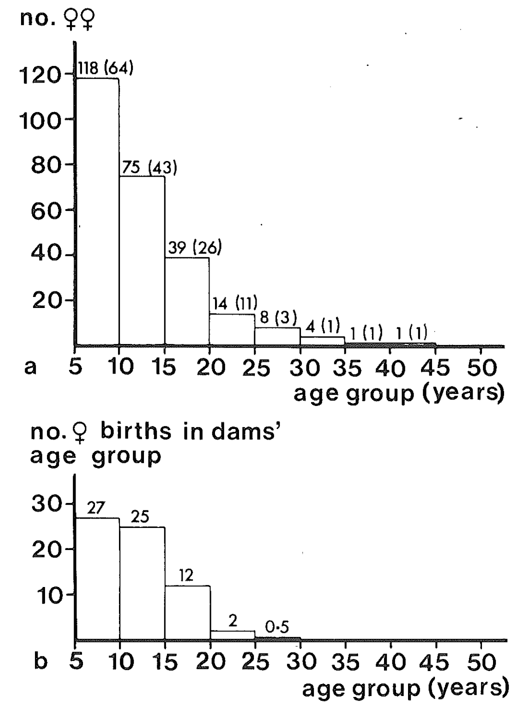

Fig. 1. Total number of ♀ Black rhinoceroses *Diceros bicornis* in captivity up to 1981, based on records available: a. number of ♀♀ in each group (numbers in brackets represent ♀♀ which have bred); b. number of ♀ calves in dams' age group (♀ calves = all calves divided by two).

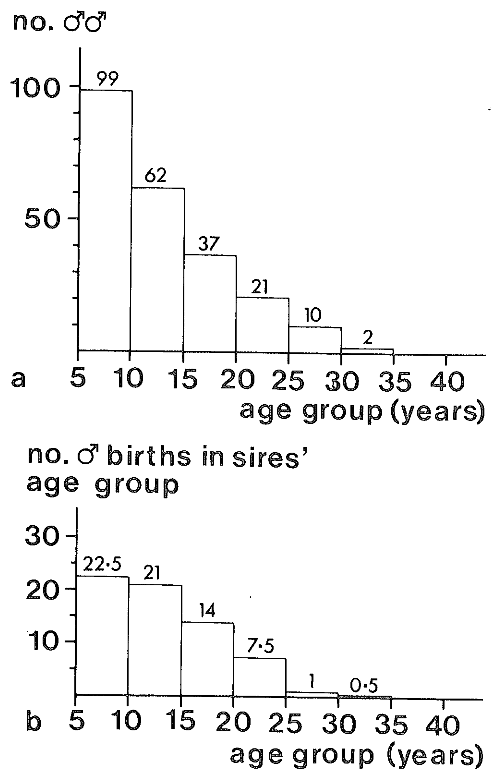

Fig. 2. Total number of ♂ Black rhinoceroses in captivity up to 1981, based on records available: a. number of ♂♂ in each age group; b. number of ♂ calves in sires' age group (♂ calves = all calves divided by two).

birth has been attributed to ♀♀ (or ♂♂) younger than five years this age group is not included in the calculations. The 118 ♀♀ listed in the first column of Fig. 1a is the total figure whereas the 64 ♀♀ indicated in brackets are the ones which actually produced the 133 calves. The figures for ♂♂ have been worked out in a similar fashion (Fig. 2).

Once the number of births and the total number of animals are known the m_x value for each sex is found by dividing the number of births of one sex in each age group by the number of animals of that sex in the group (Table 4). It must be noted that the accuracy of the m_x results for ♂♂ is not as high as that for ♀♀ because in 17 cases the sires of the calves were not known. Since in those cases the births could not be attributed to the ♂♂ of any particular age group they were distributed proportionally over the entire range, which means that it is not possible to indicate breeding ♂♂ in Fig. 2a.

To calculate the net reproduction rate the l_x value is represented as the probability of surviving to the midpoint or pivotal age of each age interval (Krebs, 1978). The l_x value in Table 5 has been calculated on the basis of all the animals in Table 1, including three calves of unknown sex, and hence is the most complete. The m_x value used in Table 5 is the more accurate value for ♀♀ (Table 4). This

x	PA	l_x		m_x		V_x	
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
5–10	7·5	0·580	0·627	0·2272	0·2288	0·1318	0·1435
10–15	12·5	0·373	0·463	0·3387	0·3333	0·1263	0·1542
15–20	17·5	0·240	0·261	0·3784	0·3077	0·0908	0·0803
20–25	22·5	0·140	0·135	0·3571	0·1429	0·0410	0·0193
25–30	27·5	0·073	0·083	0·1000	0·0625	0·0073	0·0052
30–35	32·5	0·033	0·045	0·2500	0·0	0·0083	0·0
						$R_o=0·4055$	$R_o=0·4025$

Key: x. age interval (years); PA. pivotal age; l_x. probability of surviving to pivotal age; m_x. number of offspring per animal aged x per time unit (five years); V_x. product of l_xm_x; R_o. net reproductive rate.

Table 4. Survivorship table (l_x), fertility table (m_x) and the product (V_x) for ♂♂ and ♀♀ separately in the captive Black rhinoceros population. The m_x figure is based on all known births and all individuals, alive and dead, for which records are available to the end of 1981.

x	PA	l_x	m_x	V_x
5–10	7·5	0·590	0·2288	0·1350
10–15	12·5	0·407	0·3333	0·1357
15–20	17·5	0·245	0·3077	0·0754
20–25	22·5	0·135	0·1429	0·0193
25–30	27·5	0·076	0·0625	0·0048
30–35	32·5	0·038	0·0	0·0
				$R_o=0·3702$

Key: x. age interval (years); PA. pivotal age; l_x. probability of surviving to pivotal age; m_x. number of ♀ offspring per ♀ aged x per time unit (five years); V_x. product of l_xm_x; R_o. net reproductive rate.

Table 5. Survivorship table (l_x) and fertility table (m_x) for the Black rhinoceros in captivity. The m_x value is given for ♀♀ only since this is the more accurate figure (see text).

is a commonly used procedure since from a demographer's point of view a population can be seen as ♀♀ giving rise to more ♀♀ (Krebs, 1978).

An alternative method of calculating how a population will change is to use the parameter r_m, which is the innate capacity for increase (or decrease) for one particular set of environmental conditions, in this case conditions in zoos. To do this it is first necessary to find the multiplication rate per generation, which is R_o, and then to find the generation time (G) which is defined as the mean period between the birth of a parent and the birth of its progeny. This is only an approximate definition, however, since offspring are born over a period of time and not all at once. A crude estimation of G can be found using the formula

$$G=\frac{\sum l_xm_xx}{R_o}$$

When generations overlap, r_m is determined using the equation

$$\sum_{x=0}^{\infty} e^{-r_mx}l_xm_x=1$$

Since r_m is an instantaneous rate it must be converted to a finite rate, the annual rate of change, using the formula

$$\lambda=e^{r_m}$$

where e is a constant at 2·71828 (base of natural log). Any change in the birth or death rates will of course affect the r_m value.

RESULTS AND DISCUSSION

Values for d_x, n_x, l_x and q_x are given for the population of Black rhinoceroses in captivity as a whole, and for ♂♂ and ♀♀ separately (Tables 1, 2 and 3). The mean expectation of the remaining lifespan (e_x) has been calculated for each age group (Table 1) and the survivorship curve for the captive population is shown in Fig. 3 with the annual death rate for each age group (q_x) in Fig. 4. Calculations of R_o, G, r_m and λ have been made both for ♂♂ and ♀♀

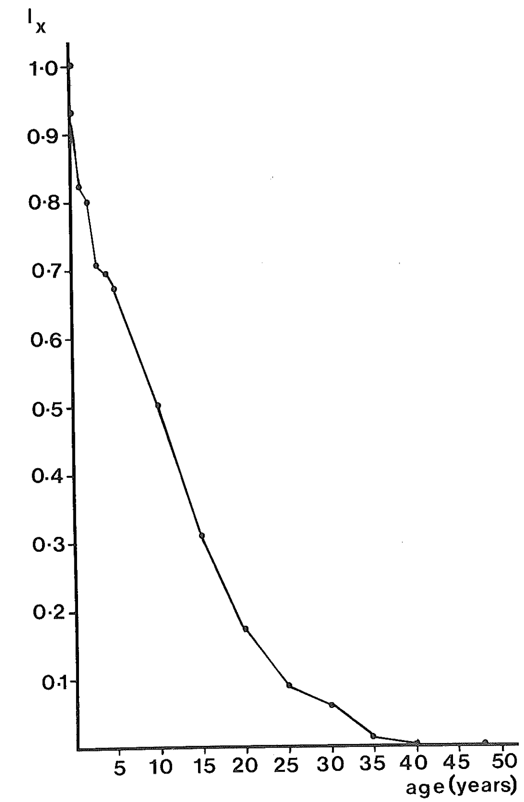

Fig. 3. Survivorship curve for Black rhinoceroses in captivity showing proportion surviving to start of each interval (Table 1). Perinatal losses (stillbirths and early deaths) are included, therefore the survival rate at birth is less than 1·0.

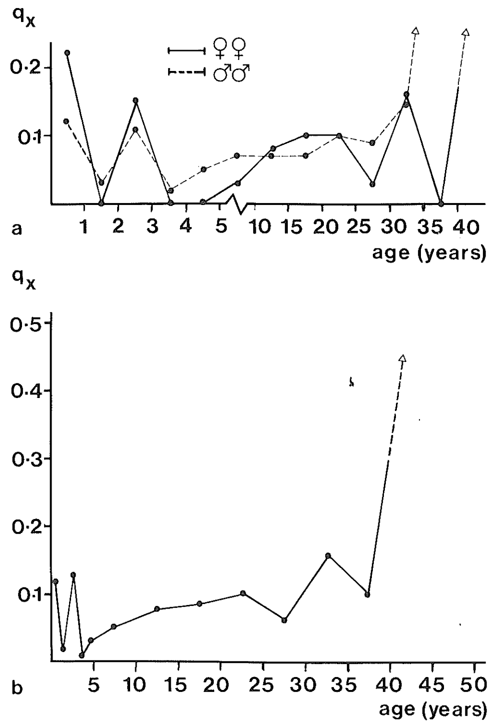

Fig. 4. Annual death rate (q_x) for Black rhinoceroses in captivity: a. annual death rate (q_x) for ♂♂ and ♀♀ separately, including perinatal losses; b. annual death rate (q_x) for the whole population, not including perinatal losses.

	R_o	r_m	λ	G
♂♂	0·4055	−0·0607	0·9411	13·7
♀♀	0·4025	−0·0689	0·9334	12·4
All	0·3702	−0·0746	0·9281	12·4

Table 6. Calculations for the Black rhinoceros population of the net reproductive rate, innate capacity for increase, annual rate of change and generation time.

and for the population as a whole (Table 6). All these figures show that the population is decreasing ($R_o<1$, $r_m<0$, $\lambda<1$); the decrease is *c.* 7% per year ($\lambda=0\cdot9281$). A projection of the decrease over 25 years is shown in Fig. 5.

Foose (1980) claims that it is important to treat the sexes separately as survival and ferti-

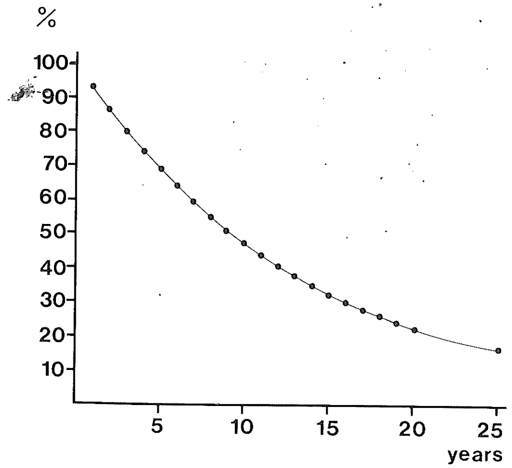

Fig. 5. A projection of the decrease over the next 25 years in the percentage of captive Black rhinoceroses (with an r_m of $-0\cdot0746$).

lity often differ significantly for ♂♂ and ♀♀. For the Black rhinoceros in captivity this is not the case, however, since there is no significant difference between the sexes in the number of deaths (d_x in Tables 2 and 3; Kolmogorov-Smirnov two-sample test $p>0\cdot05$). As the fertility values (m_x) for the ♂♂ are not very accurate fertility for the two sexes cannot be compared. The fertility rate and the reproductive values (V_x) from Table 5 are shown graphically in Fig. 6. The high apparent value for ♂♂ between 30 and 35 years (Fig. 6) is merely a result of the small sample size in this group (two individuals). A calf was sired by one of the ♂♂ in that age group but as all births were counted and divided by two, only 0·5 birth is listed (Fig. 2).

That R_o is less than one was the expected outcome of the calculations based on the studbook figures. One of the reasons for the population decrease is that more than one-third of the adult ♀♀ are not contributing to the next generation (Lindemann, 1982). In order to discover whether it is at all feasible to breed the Black rhinoceros successfully in captivity it is necessary to look exclusively at the 64 ♀♀ which have bred (Fig. 1a).

The minimum requirement for ensuring species' survival in captivity is that sufficient offspring are produced to maintain $R_o\geqslant1$. If,

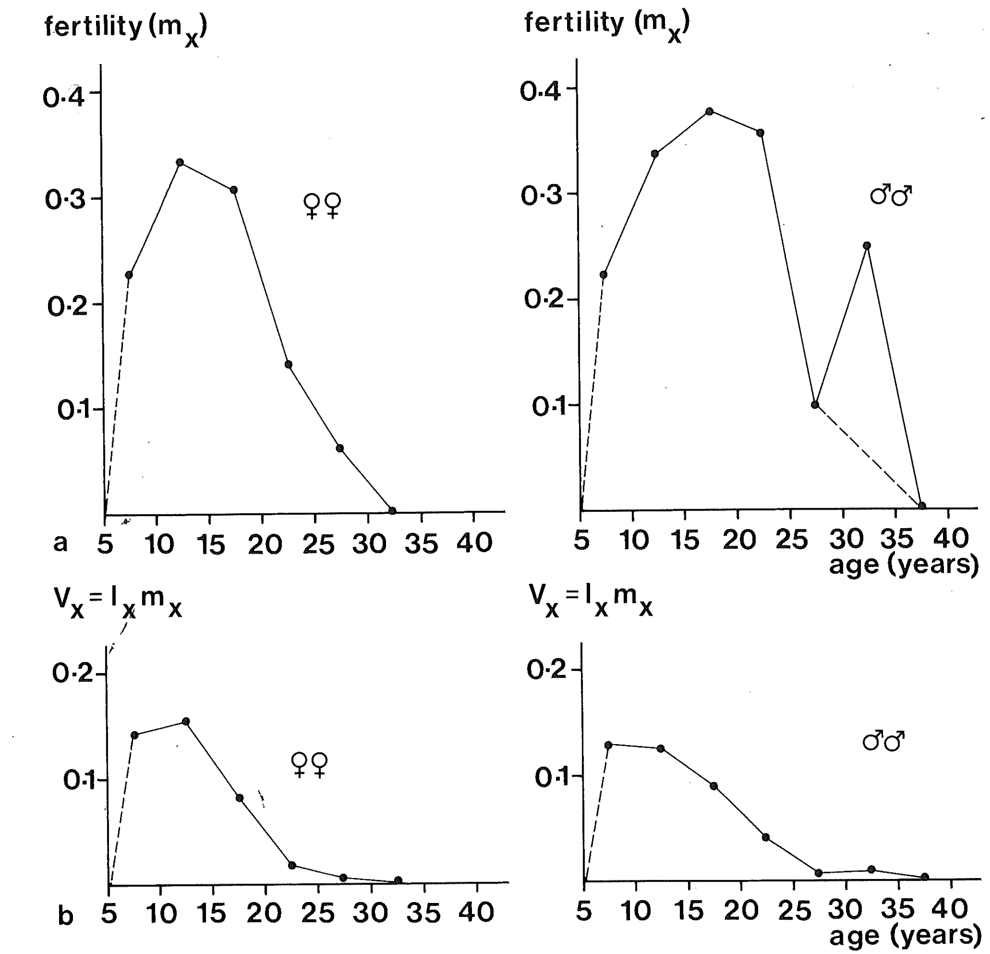

Fig. 6. Fertility (m_x) and reproductive value (V_x) for Black rhinoceroses in captivity. a. Fertility: number of offspring of the same sex as the parent per age group (five years); see text for an explanation of the high value of m_x for ♂♂ aged between 30 and 35 years. b. Reproductive value: the l_xm_x products from Table 5 are shown for each age group.

using the present material, the category of breeding ♀♀ only is considered (Table 7) R_o is still less than one, indicating that unless either the survival rate or the fertility rate is improved the captive Black rhinoceros population will not be able to reproduce in sufficient numbers to maintain itself. The sum of the m_x column in Table 7 is 1·8, meaning that the number would multiply 1·8 times in one generation if survival was 100%.

To hope for anything approaching complete survival would at the moment be too optimistic, but it is imperative that survival is improved. To increase the survival rates of all reproductive age groups by a certain amount is more effective than increasing the fertility in the same classes by the same amount (Goodman, 1980). To increase fertility rates might be an easier task, however (Foose, 1980), and is also important from a genetic point of view. Roughly, the greater the number of breeding animals the larger the effective population size and the smaller the rate of inbreeding.

x	PA	l_x	m_x	V_x
5–10	7·5	0·590	0·4219	0·2489
10–15	12·5	0·407	0·5814	0·2366
15–20	17·5	0·245	0·4615	0·1131
20–25	22·5	0·135	0·1818	0·0245
25–30	27·5	0·076	0·1667	0·0127
30–35	32·5	0·038	0·0	0·0
			1·8133	R_0=0·6358

Table 7. Survivorship table (l_x), fertility table (m_x) and the product (V_x) for breeding ♀♀ only in captivity (for a key to the symbols see Table 5).

It must be concluded that maximum breeding, both in the individual animal and in the population as a whole, should be attempted. Zoos should be asked not to keep single animals and even keeping a pair should be discouraged. Where practical larger groups should be favoured since this improves the likelihood of an individual being able to select a compatible mate, as well as reducing the risk of being left with a single animal after the death of its partner. The following example demonstrates the kind of breeding improvement which is needed. Of the 169 Black rhinoceroses alive in 1981 (Fig. 7), approximately 13 will die within one year (Table 8). Of the 94 living ♀♀ (Fig. 7) 20 are too young and 11 might be too old to breed, leaving 63 ♀♀ to produce the 13 calves required to sustain the population. This is 0·21 calves per year per adult ♀, or nearly twice the present rate of 0·11 calves (Lindemann, 1982). The average interbirth interval in captivity is 35 months (Lindemann, 1982) meaning that each breeding ♀ produces 0·34 calves per year. If all of the 63 ♀♀ of breeding age were producing calves at this rate 21 calves would be born in 1982.

Of the young Black rhinoceroses born 18% die in their first year (including perinatal losses), a death rate which might not be exceptionally high when compared to the wild population. Goddard (1970) gives mortality rates of 16% for both the first and the second year of life in a population in Tsavo, Kenya.

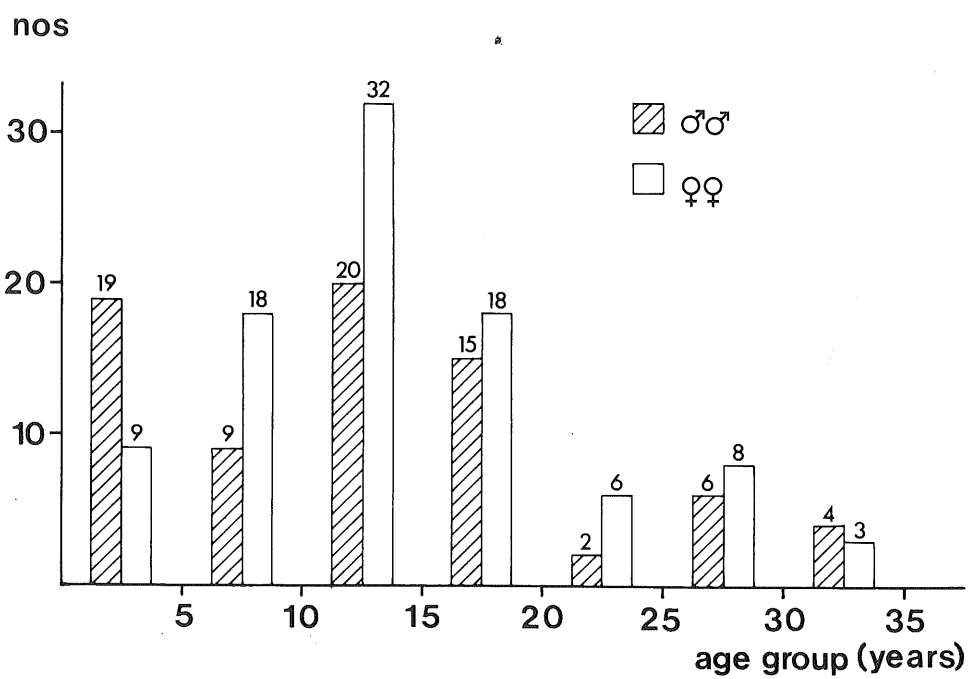

Fig. 7. Age distribution of the Black rhinoceros population in captivity, 1981; n=169 (75 ♂♂, 94 ♀♀).

AGE GROUP	NO. IN EACH AGE GROUP[1]	DEATH RATE[2]	NO. LOST (one year)
0–5	28	6·2[3]	1·7
5–10	27	5·1	1·4
10–15	52	7·7	4·0
15–20	33	8·4	2·8
20–25	8	10·0	0·8
25–30	14	6·2	0·9
30–35	7	15·6	1·0
			12·6

[1]taken from Fig. 7
[2]percent from life table (Table 1)
[3]average from six groups (Table 1)

Table 8. Actual number of Black rhinoceroses lost in 1981, from a population of 169.

Conway (1980), however, claims that zoos do better than nature in increasing recruitment rates and lowering death rates. Although death rates in older classes are not quite as high in captivity as in the wild, captive recruitment rates are far lower. The recruitment rate in Tsavo was 10·9% (Goddard, 1970) and in Ngorongoro and Olduvai it was 7% and 7·2% respectively (Goddard, 1967), while the mean annual recruitment rate in captivity was 4·9% in the years 1975–1980 (Lindemann, 1982). To put it another way, the ♀♀ at Ngorongoro and Olduvai were giving birth to one calf every four years on average, while the ♀♀ in captivity had on average one calf every nine years.

More important than the actual size of the recruitment is the question of whether recruitment equals mortality; in the case of the Black rhinoceros the answer is 'no'. The mean annual loss in captivity for the years 1975–1980 was 6·1% (Lindemann, 1982).

The fact that many juveniles (12·8%) died aged between two and three years (Table 1, Fig. 4) needs further investigation. Since in most cases these animals died from disease (Lindemann, 1982), it is strongly recommended that a veterinary study is undertaken to try to understand more fully the causes of death in this group.

ACKNOWLEDGEMENTS
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