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Black Rhinoceros (*Diceros bicornis*) in U.S. Zoos: II. Behavior, Breeding Success, and Mortality in Relation to Housing Facilities

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The captive population of black rhinoceros *(Diceros bicornis)* is not self-sustaining. The reasons for suboptimal reproduction and high mortality need to be investigated. This can only be achieved by cross-institutional analyses of environments, behavior, and performance. In this study, we collected data on 23 zoos with black rhinoceros to compare zoo environments with reproductive success, mortality, and behavior. Institutional variation was characterized by enclosure area, percentage of walls around enclosure perimeter, percentage of public access along enclosure perimeter, climate, noise level, number of years zoo has maintained black rhinoceros, frequency of chlorine use, and number of male and female black rhinoceros at a zoo simultaneously. Birth and death rates for each institution were calculated from studbook records. We found that the breeding success of a zoo since 1973 correlated positively with enclosure area, and zoos with two or more females had a lower reproductive rate than zoos with only one female. Females residing during their pre-reproductive years at a zoo with another reproductive female gave birth for the first time on average 3 years later than sole females. Mortality since 1973 correlated positively with percentage of public access. In Part I, we developed behavior profiles of 29.31 individual black rhinoceros from keeper ratings. Scores for males on the behavior trait *Fear* also correlated positively to percentage of public access, and we suggest that this aspect of black rhinoceros exhibits is a stressor for this species, especially the males. We found that different aspects of captive environments are associated with male and female black rhinoceros behavior. Male scores on the behavior trait *dominant* were higher in smaller enclosures, and female scores for a group of behaviors suggesting agitation (*chasing/stereotypy/mouthing)* were positively correlated with percentage of walls in their enclosure. These two behavior traits were found in Part I to be negatively correlated with the breeding success of an individual male or female. We re-surveyed the behavior and husbandry of 29

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black rhinoceros pairs in zoos 2 years after the original data were collected. The re-survey confirmed that compatible black rhinoceros pairs are those with assertive females and submissive males, and that enclosure area and a low percentage of concrete walls around the enclosure are positive predictors of a pair's reproductive success. We conclude that temperament traits of individuals and characteristics of their captive environments both have an impact on a pair's breeding success. Our study demonstrates that cross-institutional comparisons of zoo facilities, when integrated with behavioral assessments of individual animals, are a valuable tool for investigating potential causes of poor reproduction and well-being in zoo animals. Zoo Biol 18:35–52, 1999.

Key words: enclosure size; zoo visitors; dominant behavior; chlorine; olfactory behavior; stereotypy

INTRODUCTION

Habitat destruction and poaching of rhinoceros horn have decimated the natural populations of the world's five extant species of rhinoceros. Intensive management of wild and captive populations of rhinoceros has thus become critical for their survival. For the black rhinoceros (*Diceros bicornis*), the captive breeding populations are neither stable nor self-sustaining, with a failure of approximately one third of the captive population to breed, delayed age of first reproduction, long inter-birth intervals, and almost equal birth and death rates [Smith and Read, 1992; Wilson and Read, pers. comm.]. To persist, the captive population currently requires periodic infusion from the wild. Furthermore, captive black rhinoceros are prone to a number of unusual diseases unreported for their wild counterparts. Hemolytic anemia, mucocutaneous ulcers, fungal pneumonia, salmonellosis, hemosiderosis, encephalomalacia [Miller, 1994; Kriek, 1994], and most recently, hemorrhagic diathesis syndrome [Lung in Murray and Gamble, 1998] have limited the growth of the captive population. The causes of poor health and low reproductive rates in captivity are largely unknown and reflect a shortcoming in our knowledge of the basic biology of rhinoceros.

Captive black rhinoceros managers recommend "examination of husbandry practices, facility design, animal densities and sex ratios to determine the factors that are most critical for breeding success" [International Rhino Foundation, Cumberland, OH]. They also state that "stress has been implicated as an underlying causal factor for many of the disease syndromes identified in rhinoceros maintained in captivity" and that research to identify the stressors acting on black rhinoceros should be undertaken. Poor reproduction and stress-related disease syndromes of uncertain etiology imply that black rhinoceros are highly sensitive and respond negatively to the environmental and/or social conditions of captivity. The first step toward establishing the impact of zoo facilities and social densities on black rhinoceros is a cross-institutional comparison of environments and reproductive and behavioral performance.

Although there is a growing literature on the effects of environment on lab and farm animals, only a few studies examined the effects of zoo environments on reproduction and health of exotic mammal species. Miller-Schroeder and Paterson [1989] found that enclosure volume, enclosure complexity, and the availability of privacy were positively correlated with breeding success in lowland gorillas (*Gorilla gorilla*). A multivariate analysis of zoo husbandry survey data collected for the red panda (*Ailurus fulgens*) revealed that large enclosures and availability of several nest boxes were important factors in successful reproduction [Roberts, 1989]. Mellen's

[1991] study of small exotic felids in zoos indicated that group size and quality of caretaking by keepers were important environmental factors influencing breeding success.

However, to understand the mechanisms through which environmental factors affect zoo-housed species, we must also take into consideration the potential role of individual and gender differences between animals. For example, male and female reproductive strategies differ, which may lead to differential sensitivity to specific factors prevalent in captive conditions but absent in the wild. Also, individuals may differ in responsiveness to environmental change and challenge [e.g., Benus et al., 1987].

In Part I, we presented methods used to develop and validate a behavior profile for cross-institutional comparisons of black rhinoceros. The profile was based on keeper ratings of animal behavior and temperament. Differences between individual rhinoceros were described in terms of scores for six behavior traits: *olfactory behavior, chasing/stereotypy/mouthing, friendly to keeper, fear, dominant,* and *patrolling*. In the current study (Part II), we examined variation in black rhinoceros facilities, animal density, breeding success, and mortality for 23 North American zoos. Then, using the behavior profiles of individuals, we integrate data on behavior, environment, breeding success, and mortality to form hypotheses concerning the environmental factors that have an impact on captive black rhinoceros.

METHODS

Animals

We included in the study 60 black rhinoceros (29 males, 31 females) ranging in age from 1.5 to 29 (at the end of 1995). These represent the entire black rhino population, except for infants, at each of 19 U.S.zoos. Our sample includes both *Diceros bicornis minor*, the Southern black rhinoceros (5.7), and *Diceros bicornis michaeli*, Eastern black rhinoceros (24.24). Only one zoo had both subspecies; they were kept in separate exhibits but housed nightly in the same barn. Figure 1 presents the age distribution of males and females in the study, and their reproductive status at the end of 1995.

Environmental Variables

During 1994–1995, the 19 zoos were visited by a researcher as part of the Methods of Behavioral Assessment Project (MBA). Each researcher, following a standardized protocol, assessed a number of environmental features including physical facilities, climate, social environment, keeper staff, and general management routines. Medical and breeding histories of individual rhinoceros were collected from zoo and studbook records. To increase the sample size of institutions for our analyses, we added data from four other zoos that were surveyed via questionnaire during 1996–1997 (see below).

We measured or assessed a total of 60 environmental features that proved to be inter-correlated. Most of these were excluded from analysis because of highly skewed distributions among the 23 zoos. We finally used only six variables pertaining to the outdoor enclosure of black rhinoceros to describe variation between institutions: 1) Total enclosure area for black rhinoceros in square meters. 2) Frequency of chlorine use was the days per week keepers cleaned any part of the indoor or outdoor enclo-

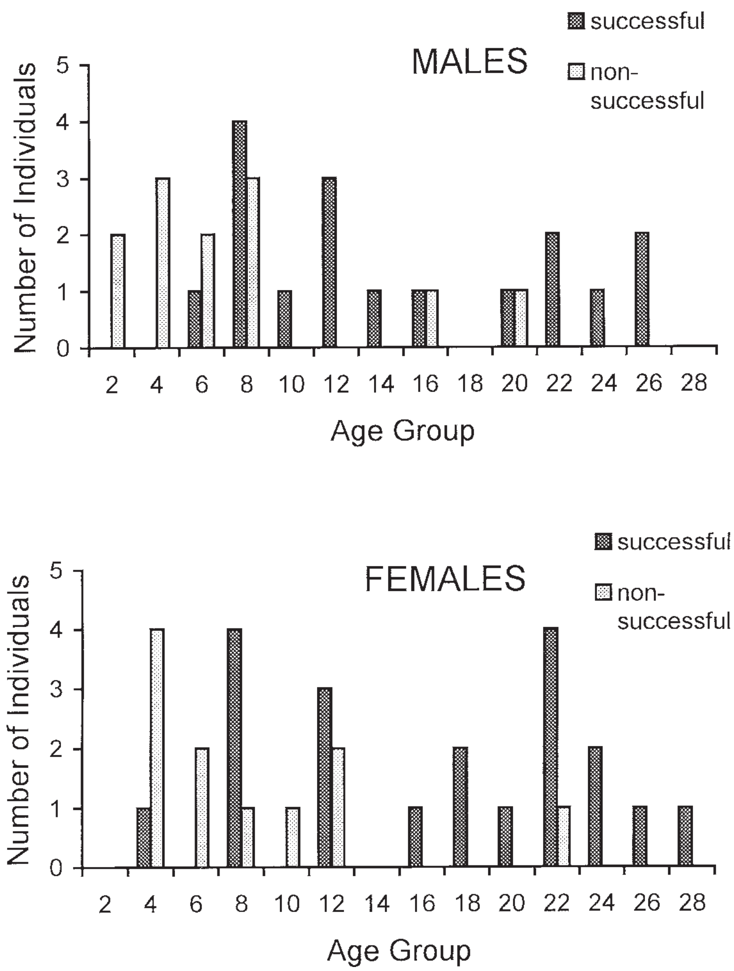

Fig. 1. Age distribution and breeding status of male and female black rhinoceros in this study at the end of 1995.

sures with a chlorine-based disinfectant. 3) Percentage of walls is the percentage of enclosure perimeter composed of concrete or gunnite walls over which the rhinoceros cannot see when near the wall. 4) Climate was measured on a scale of 1 to 14 based on the location of each zoo on a U.S. Department of Agriculture plant hardiness zone map. The scale generally varies from colder, harsher, fluctuating climates (low end) to warmer, more moderate climates (high end). 5) Noise level. One author (J.F.) visited 17 zoos and, in the center of each outdoor rhino yard, directly measured sound levels four times for 15 sec prior to opening near dawn, twice during operating hours, and once after closing. Sound was measured by its maximum, minimum, SPL (pressure), and L_{eq} (constant tone equivalent) levels in decibels using a Larson Davis 2800 Real Time analyzer (Provo, UT). Frequency range was measured in 11 one-third octave bands from 0 to 20 kHz. To compare the relative basal noise levels of each zoo, we reduced measured sound levels to a single value of basal sound condition throughout the day. We excluded measures of mechanical equipment and/or sudden sharp changes in sound levels (identified by maximum, minimum, and SPL measures) and then averaged all remaining L_{eq} values. 6) Percentage of public access is the percentage of the outdoor enclosure perimeter that allowed zoo visitors an unobstructed view into the enclosure at a distance of less than 10 m. 7) The number of years a zoo has kept black rhinoceros was included to take into account potential differences between zoos based on the amount of experience with the species. For zoos with more than one outdoor yard, measurements of noise level, percentage of walls, and percentage of public access for each enclosure were averaged. Descriptive statistics for each variable are given in Table 1.

We examined the North American Black Rhinoceros Studbook [Foose, 1995, 1996, 1997] to calculate institutional breeding success, defined as the number of births (surviving or not) divided by the sum of the years since 1973 that animals over the age of 2.5 were housed at the zoo (births/adult years). By 1973, 15 of the 23 zoos in this study were keeping black rhinoceros. Mortality was the total number of deaths or stillbirths divided by the sum of years that all black rhinoceros had been at the zoo since the zoo began keeping black rhinoceros. Table 1 also includes descriptive statistics for these two performance variables.

Animal Density

To analyze possible effects of animal density, we classified the number of adult (older than 3 years) males and number of adult females kept simultaneously at a zoo as being one or more than one. Generally each institution kept one or two breeding pairs, or one male and two females. We only analyzed animal density for zoos that had successfully bred black rhinoceros (n = 20 of the 23 at the end of 1995) to examine the effect of density on reproductive rate rather than success or failure. For females that had reproduced, we also examined the effect of the presence of another female on age of first reproduction. We compared females that were the only female

TABLE 1. Descriptive statistics for seven environmental variables, breeding success, mortality, and density of black rhinoceros at 23 (or 17) zoos

Variable	N (zoos)	Mean	SD	Range
Enclosure area (m^2)	23	2724.21	2926.95	433–12,037
Frequency of chlorine use (days/week)	23	2.14	2.54	0–7
% Walls along enclosure perimeter	23	39.56	33.72	0–93
Climate (plant hardiness zone)	23	7.63	2.16	3.5–11
Noise level, outdoor enclosure (avg. dB)	16	39.8	4.96	31–50
% Public access along enclosure perimeter	23	35.57	15.68	8.3–70
Years zoo has kept black rhino	23	26.51	16.73	4–61
Institutional breeding success (births/adult years since 1973)	23	.08	.05	0–0.21
Mortality (deaths/adult years)	23	.04	.03	0–0.10
	N	% Zoos		
Animal density (at successful zoos only)				
1 adult female	9	45		
>1	11	55		2–4
1 adult male	13	65		
>1	7	35		2

at a zoo at the time of their first reproduction (n = 8) to those that had spent their pre-reproductive years from age three in breeding situations at a zoo where there was another reproductive female already present, including the mother (n = 13). For the latter, we included four additional females in the North American Regional Black Rhinoceros Studbook but not in our study. We excluded females that were wild caught or had been moved between institutions more than twice before their first birth (n = 14).

Behavior

Behavioral profiles of individuals were developed in Part I. In the current analyses, we used scores for each black rhinoceros for six behavior traits: *olfactory behavior, chasing/stereotypy/mouthing, friendly to keeper, fear, dominant,* and *patrolling.*

Re-survey of Black Rhinoceros in 1996–1997

To test the repeatability of our results, 2 years after the original data collection period we distributed a modified behavior and husbandry questionnaire to keepers at 23 U.S. zoos and one Australian zoo. Only paired adult black rhinoceros in breeding situations were included in this survey; 17 of the pairs were from our original study and 12 were new in the re-survey. From the studbook, we calculated the breeding success of each pair as number of births/years together.

Statistical Analyses

We determined whether the environmental variables were a random sample from a normal distribution using the Shapiro-Wilk statistic W [Shapiro and Wilk, 1965]. Only frequency of chlorine use and total enclosure area deviated significantly from an normal distriubution. When calculating correlations we used natural log transformations of total enclosure area to remove positive skew from the distribution. Pearson correlation coefficients (r) were calculated between environmental variables and between environmental and behavioral variables. We compared environmental variables between zoos with a) one or b) more than one female and male using T-tests. Our samples of 60 black rhinoceros were not independent due to aggregation at 19 zoos. Therefore, to conduct statistical analyses of behavior and environment we considered animals living in separate enclosures as independent samples, irrespective of the zoo where the enclosures were. At most zoos, black rhinoceros pairs shared an enclosure with their partner. By analyzing males and females separately, we avoided including enclosures twice in the same analysis. However, for six females who shared an outdoor yard with another adult female, behavior scores of the paired females were averaged and treated as three data entries. We accepted a significance level of α of < 0.05. We made no adjustment to α for chance correlations because we are using correlation analysis only to identify interesting relationships for further investigation.

From the original survey data we developed an hypothesis of the environmental and behavioral effects on breeding success of black rhinoceros pairs. To test the predictive power of this hypothesis, we analyzed the data from the re-survey with multiple regression analysis. Collinearity diagnostics were examined to assess the degree of inter-correlation among the independent variables. All analyses were carried out with SAS for PC version 6.10 [SAS Institute, 1989].

RESULTS

Institutional Variation and Breeding Success

Table 2a presents correlation coefficients for environmental variables, institutional breeding success, and mortality. Total enclosure area is the only environmental variable that is significantly positively correlated with a zoo's breeding success. Thus, zoos with larger areas for their black rhinoceros have better reproductive results (Fig. 2). However, enclosure area is confounded by at least one other variable: it is significantly negatively correlated with frequency of chlorine use. The percentage of walls around an enclosure is significantly negatively correlated with climate, the more walled enclosures being found in colder climates. Mortality is significantly positively correlated with percentage of public access along the enclosure perimeter (Fig. 3). This environmental variable does not appear to be confounded by any of the other variables.

Also provided in Table 2b are the results of *T*-tests for all these variables compared between zoos with one or more than one female, and one or more than one male. Zoos that usually keep two or more females have significantly lower reproductive rates than zoos that keep only one female (Fig. 4). Zoos with two or more females have more experience with black rhinoceros, having kept this species significantly longer (mean, 37 ± 4.28 years, n = 11) than zoos with only one female (mean, 17 ± 3.73 years, n = 12). The mean age at which a female gives birth for the first time is significantly lower if she is the only female at the zoo (mean, 6.7 years, n = 8; range, 5–8) compared to females at zoos with other females or the mother already present (mean, 9.85 years, n = 13; t = –3.39, P = 0.003; range, 6.5–15). The extra-female effect does not appear to be related to the availability of male breeding partners, for among the 13 females at multi-female zoos, eight had their own male partner (mean age first birth, 9.7 years) and five shared a male with another female (mean, 11.7 yrs). These data strongly suggest that female black rhinoceros influence the reproductive rates of each other in a zoo environment.

Environment and Behavior

For males and females separately, correlation analyses between individual scores on six behavior traits and six environmental variables are given in Table 3a and b.

TABLE 2. a) Correlation coefficients for seven environmental variables, breeding success, and mortality, n = 23 zoos. b) Means (SEM) and T values for the same variables comparing zoos with one or more than one female and male

	Enclosure area	Frequency of chlorine use	% Walls around perimeter	Climate	Noise level (n = 16)	% Public access along perimeter	Years zoo has kept black rhinoceros	Breeding success	Mortality
a) Correlation coefficients									
Frequency of chlorine use	**–0.42**								
% Walls around perimeter	0.15	–0.25							
Climate	–0.21	0.33	**–0.41**						
Noise level (n = 16)	–0.42	–0.13	–0.01	0.04					
% Public access along perimeter	0.01	0.01	–0.04	–0.22	0.09				
Years zoo has kept black rhinoceros	–0.23	–0.04	0.23	–0.10	0.23	–0.02			
Breeding success	**0.43**	–0.23	–0.19	0.06	0.08	0.28	0.02		
Mortality	0.09	–0.11	–0.19	0.13	–0.38	**0.43**	0.35	0.18	
b) T values									
1 vs. >1 female at zoo	0.07	–1.33	–0.25	–0.33	–0.53	1.78	**–2.90**	**2.04**	–0.31
1 vs >1 male at zoo	–1.09	–0.26	–0.06	–0.97	0.23	–0.57	–0.26	0.44	0.34

n = 20 zoos that have bred black rhinoceros. Bold type indicates $P < 0.05$.

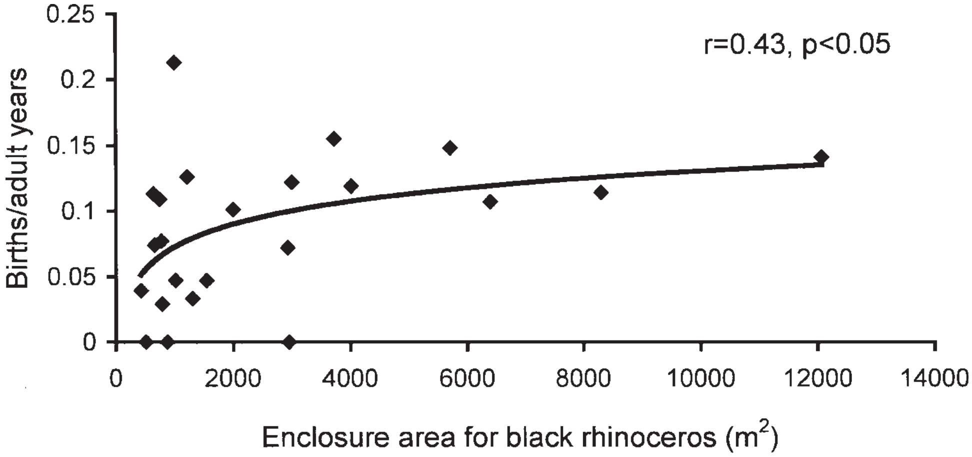

Fig. 2. Correlation between Total Enclosure Area and a zoo's Institutional Breeding Success since 1973. Each point represents one zoo (regression line, y=-.037+.035 log(x)).

Columns marked with an "a" indicate the behaviors that were found in Part I to be negatively correlated with individual breeding success. For males, *dominant* is significantly negatively correlated with enclosure area. *Olfactory behaviors*, as well as *chasing/stereotypy/mouthing* are significantly positively correlated with frequency of chlorine use. Therefore, even though enclosure area and frequency of chlorine use are confounded by being negatively correlated (Table 2a), these two environmental variables appear to be associated with different aspects of male black rhinoceros behavior.

For males there is also a significant positive correlation between *fear* and percentage of public access, illustrated in Fig. 5.

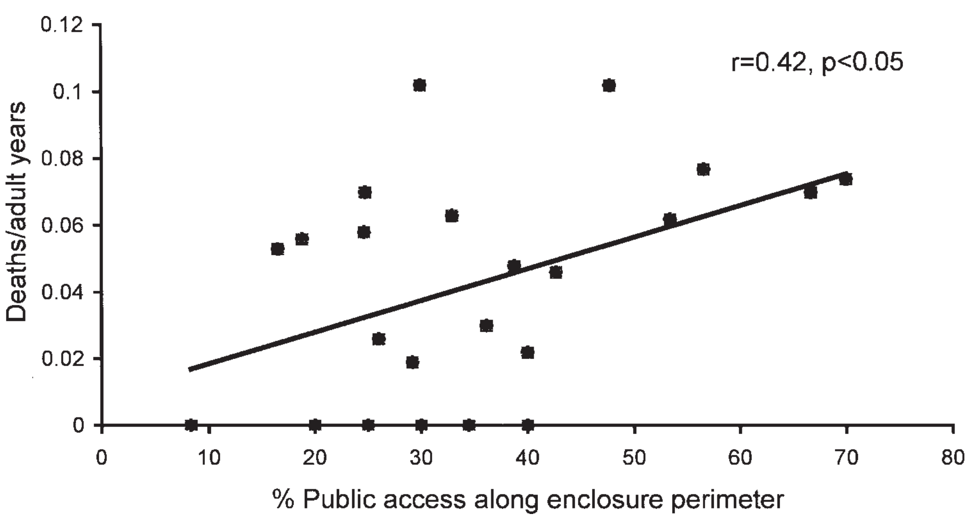

Fig. 3. Correlation between Percent Public Access along enclosure perimeter (to within 10 m) and Mortality. Each point represents one zoo (regression line, y=.009+.0009x).

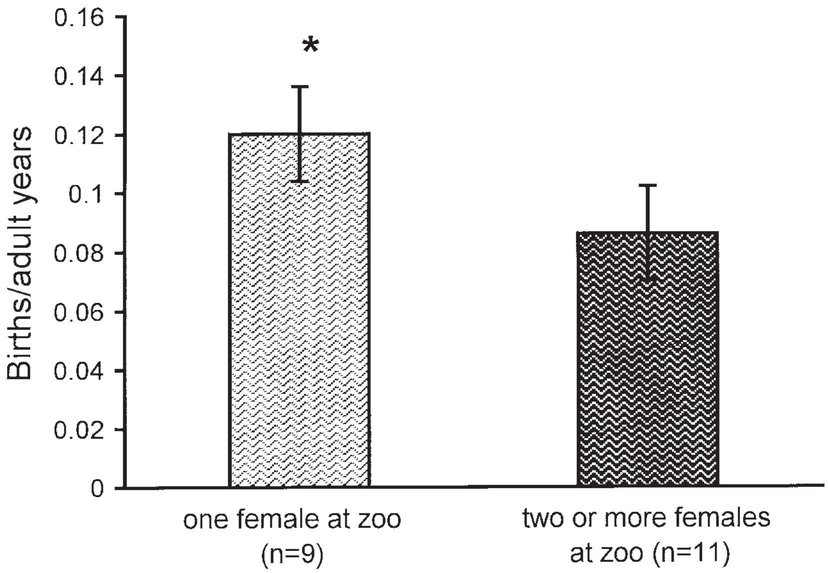

Fig. 4. Mean (± s.e.m.) reproductive rate (since 1973) of zoos breeding black rhinoceros that keep only one female or 2 or more females. * = <0.05.

For females, a different pattern of correlation emerges. *Chasing/stereotypy/mouthing*, the behavior trait that, in Part I, was associated with poor reproductive performance in females, is significantly positively correlated with percentage of walls. Scores for *patrolling* are also positively correlated with percentage of walls. Percent-

TABLE 3. Correlations between behavior ratings of individual black rhinoceros and environmental variables; a) males, b) females

a. Males (n = 26)	Olfactory behavior[a]	Chasing/ stereotypy/ mouthing	Friendly to keeper	Fear	Dominant[a]	Patrolling
Enclosure area	–0.36	–0.36	–0.22	–0.23	**–0.65****	0.18
Frequency of chlorine use	**0.40***	**0.50****	0.19	–0.11	0.18	–0.36
% Walls along perimeter	–0.13	0.20	0.06	–0.18	0.20	0.01
Climate	–0.19	0.20	0.17	0.27	–0.21	–0.10
Noise level (n = 23)	0.30	–0.04	–0.05	–0.04	0.28	0.01
% Perimeter with public access	–0.37	0.02	0.01	**0.50****	–0.20	–0.38

b. Females (n = 25)	Olfactory behavior	Chasing/ stereotypy/ mouthing[a]	Friendly to keeper	Fear	Dominant	Patrolling
Enclosure area	–0.18	–0.23	–0.34	–0.08	0.36	0.26
Frequency of chlorine use	0.18	0.25	**0.49***	–0.04	0.00	–0.09
% Walls along perimeter	0.23	**0.40***	0.15	0.15	–0.00	**0.42***
Climate	**–0.56****	–0.05	–0.19	–0.15	–0.00	–0.33
Noise level (n = 23)	0.16	0.01	0.18	0.36	–0.12	–0.04
% Perimeter with public access	–0.10	–0.05	–0.12	0.20	0.33	0.06

[a]Behaviors that were significantly negatively (males) or positively (females) correlated with individual breeding success in Part I.
*$P < 0.05$; **$P < 0.01$

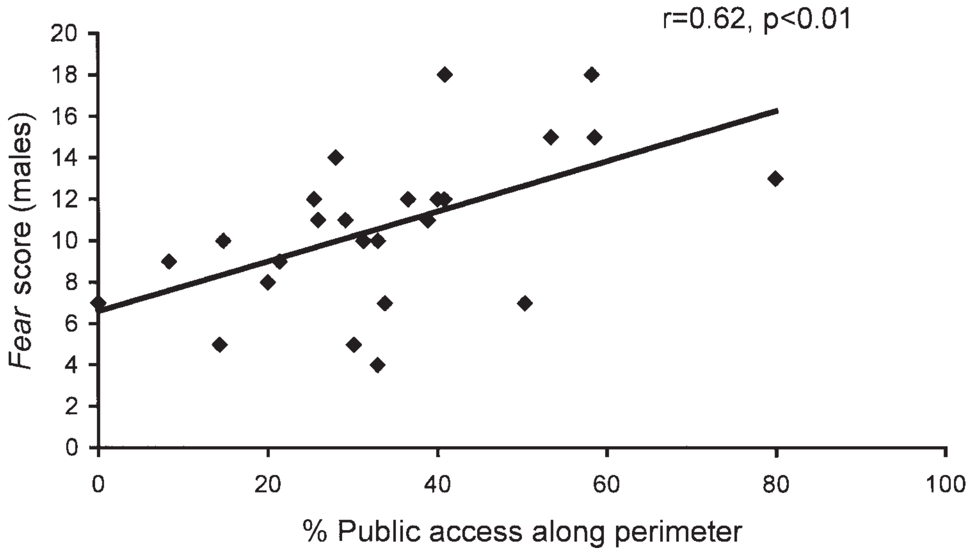

Fig. 5. For male black rhinoceros (n=26 adults), correlation between Percent Public Access along enclosure perimeter and score on Fear (regression line, y=6.6+.12x).

age of walls was confounded by climate (Table 2a), and we found a significant negative correlation between *olfactory behavior* and climate for females (Table 3b); the warmer the climate the lower females were rated on performing urination and olfactory investigation behaviors. Therefore, features of concrete walls and climate appear to be most associated with the behavior of female black rhinoceros.

For females, we also found a significant positive correlation between *friendly to keeper* and frequency of chlorine use. This could be a spurious correlation, or it could be due to the frequency of chlorine use and enclosure area being confounded. Large enclosures are cleaned less frequently with chlorine, but keepers working with rhinoceros in large enclosures also tend to rate males and females with lower *friendly to keeper* scores (although these relationships did not reach significance, Table 3a and b).

We summarize all these relationships into pathways in Fig. 6. The top two rows describe the three environmental correlates of zoo performance variables that we found: the number of females at a zoo is negatively associated with the zoo's reproductive rate with successfully breeding pair(s), the size of its outdoor enclosures is positively associated with the amount of breeding success and/or failure, and the degree to which the public surrounds the rhino enclosures is positively associated with its mortality rate. The former two relationships are portrayed as bi-directional because it is possible that zoos with very productive rhinoceros pairs purposely keep only one female, or that zoos with higher breeding success have intentionally enlarged their rhinoceros enclosures. The second row in Fig. 6 also includes an additional environmental variable, percentage of walls around an enclosure, that was found to be negatively associated with the individual breeding success of females. Rows 2 and 3 describe correlations between environments and the behavior profiles of individuals living in them. From these relationships, we are able to suggest several hypotheses for the mechanism of the environmental effects on a zoo's performance with black rhinoceros: a) In Part I we found that the relative scores on *dominant* for

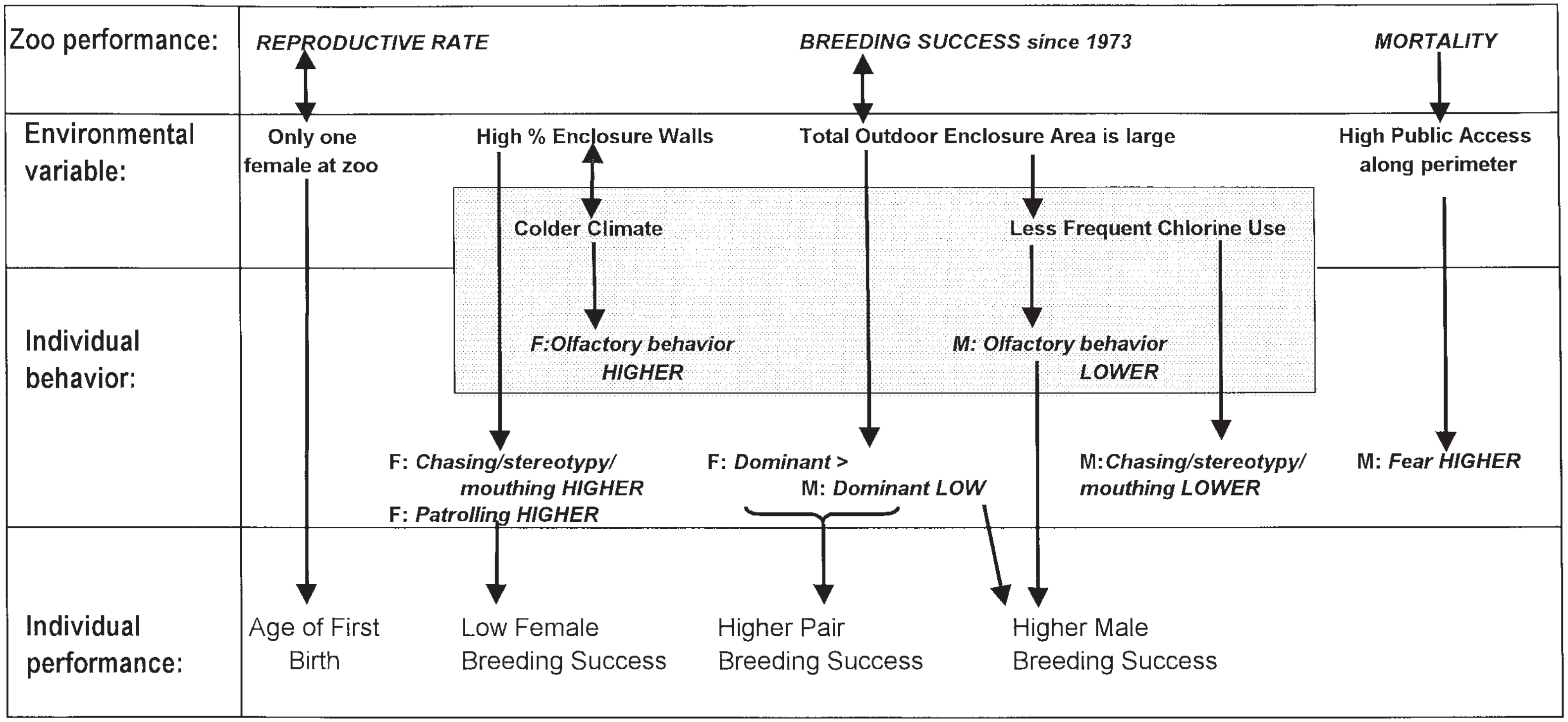

Fig. 6. Table 4. Summary of relationships between environment, behavior and performance of black rhinoceros in North American zoos. Arrows = significant correlation.

the male and female of a pair are important indicators of their breeding success as a pair. We also found in Part I that a female's score on *dominant* tends to increase with her age. In this part of the analysis we found that scores on *dominant* for males are influenced by enclosure size. Therefore, we hypothesize that a zoo's breeding success for black rhinoceros is partially dependent on having large enclosure areas that help reduce dominant, assertive, and aggressive behaviors in the male. This promotes compatibility and breeding success of the pair. b) From this overview, we also hypothesize that females are sensitive to a different aspect of zoo environments than enclosure area. Females residing in walled enclosures tend to be rated higher on active patrolling behavior and behaviors indicative of arousal and frustration; the latter in turn is associated with lower breeding success. c) The two environmental variables most directly related to breeding success of a pair are enclosure area and percentage of walls, but both of these variables may be marker variables for other, confounded environmental variables (i.e., chlorine use and climate) that mediate individual breeding success via their influence on olfactory behaviors (denoted by the shaded box in Fig. 6). d) Zoo visitors around a large portion of the perimeter of black rhinoceros enclosures is associated with higher scores for males on *fear* and higher mortality at a zoo. This behavior may be indicative of stress, and these three variables in combination allow us to hypothesize that public access is a source of stress for black rhinoceros, at least for males.

Prediction of Reproductive Success in Pairs Surveyed in 1996–1997

To test the predictive power of this hypothesis for a pair's breeding success, we conducted a multiple regression analysis for 29 black rhinoceros pairs surveyed 2 years later in 1996–1997. Three independent, or predictor, variables are included in the analysis: enclosure area, percentage of walls, and the difference between the female's and the male's *dominant* score. Collinearity diagnostics indicate that these variables are not linear combinations of each other, because there is no component with a high condition index that contributes strongly to the variance of more than one variable (Table 4). These three variables explain a significant portion of the variance in pair breeding success, 67.9% (R^2, Table 4). Enclosure area is a significant positive predictor ($b = 0.00004$) and walls are a significant negative predictor ($b = –0.002$). Difference in *dominant* score (female-male) is also a significant positive predictor ($b = 0.04$), indicating the higher the female's *dominant* score relative to the male's, the greater is their breeding success.

We conclude, therefore, that the results of our original survey behavior pertaining to behavior and breeding success were repeatable in the second survey 2 years later. We also conclude that behavioral characteristics of individuals, as well as specific aspects of captive environments, have an impact on black rhinoceros breeding success.

DISCUSSION

Smith and Read [1992] identified two management-related problems with captive black rhinoceros reproduction: delayed age of first reproduction and long interbirth interval. The average age of first parturition for females in the wild is estimated to be 4.75–5.25 years. [Schenkel and Schenkel-Hulliger, 1969], although it varies up to 12 years in some populations [Hitchens and Anderson, 1983]. The captive North

TABLE 4. From the 1996–1997 re-survey, results of a multiple regression analysis of pair breeding success (births/years together) with three independent variables

Dependent variable: births/years together

Analysis of variance

Source	DF	F Value	Probability
Model	3	17.6	0.0001
Error	25		
Total	28		

R^2 = 0.679   Adjusted R^2 = 0.641

Parameter estimates

Variable	Unstandardized regression coefficient (b)	Standard error	Probability
Intercept	0.24	0.05	0.0001
F: Dominant–M: Dominant	0.04	0.01	0.0008*
Enclosure area (m^2)	0.000045	0.00001	0.0017*
% Walls	–0.002	0.0007	0.01*

Collinearity diagnostics (intercept adjusted)

Number	Eigenvalue	Condition index	Dominant (M-F)	Enclosure area	% Wall
1	1.39	1.00	.10	.31	.19
2	1.04	1.15	.54	.00	.31
3	0.56	1.57	.35	.68	.49

American population has an average age of first birth of 8.8 years [Smith and Read, 1992]. Interbirth interval in the wild is reported to be about 27 months [Goddard, 1967; Joubert and Eloff, 1971], but in captivity the average is 40.4 months [Smith and Read, 1992]. The latter may be due to delayed reintroduction of a female to a mate postpartum. Our analyses point to the density of female black rhinoceros at a zoo as one potential factor contributing to lowered reproductive rates and delayed age of first reproduction; females who were not the only female at their zoo prior to their first parturition had an average age of first birth almost 3 years later than sole females. In other ungulate species, delayed onset of sexual maturation also occurs among individuals living at high population densities [African elephants: Laws, 1969; wildebeest: Watson, 1969]. In two subpopulations of black rhinoceros in South African protected areas, Umfolozi and the Corridor where rhinoceros densities are 0.1/km^2, females attain sexual maturity at a younger age than in a third subpopulation, Hluhluwe, with a density of 0.7/km^2 [Hitchens and Anderson, 1983]. To test the hypothesis that female density has a negative impact on female black rhinoceros reproductive function, future research should compare reproductive cycles of females at zoos with single and multiple females using physiological indicators of estrous cycling and long-term behavioral monitoring.

Zoo enclosures for black rhinoceros are considerably smaller than their home ranges in the wild, which have been reported to range from 0.5 to 133 km^2 [for a review, see Adcock, 1994]. The largest zoo enclosure in our study is 12,000 m^2. We found that the size of a zoo's outdoor yards for black rhinoceros, where courtship and breeding behavior take place, is one of the factors associated with institutional breeding success. Large enclosure area is anecdotally known to be important for black rhinoceros pre-copulatory behavior, which can be quite aggressive. Large areas allow males and females to separate themselves more effectively than in small enclosures. A potentially important management consideration is whether topographical variation in enclosures, such as visual barriers, hills, and moats, can compensate for lack of large area. In our study, we were unable to determine whether this is the case due to an insufficient sample size of zoos.

It is well known among black rhinoceros managers that pair compatibility is a primary requirement for successful breeding of black rhinoceros. We believe that our methodology has produced a quantitative assessment of pair compatibility that is comparable across zoos. In Parts I and II, we found that a high *dominant* score for the female relative to the male's score is a positive predictor of a pair's breeding success. A "compatible" pair, therefore, is one in which the female is relatively more aggressive and assertive, and the male more submissive and adaptable (see Discussion, Part I).

Male "submissiveness" appears to be facilitated by large enclosure area, for we found that *dominant* scores for males are lower when enclosure area is large and does not force close proximity to a female partner. *Dominant*, however, also appears to be a temperament trait of individuals. When enclosure area was held constant in the multiple regression analysis, the difference between male and female *dominant* scores were still a significant predictor of pair breeding success. Thus temperament, as well as environment, appears to have an impact on reproductive results.

Our analyses pinpoint some compelling relationships between black rhinoceros behavior and the environmental conditions under which they are housed in zoos. Concrete walls have a negative impact on female breeding success that is signified by increased chasing, stereotypy, and mouthing behaviors (Part I). We suggested previously that these behaviors are indicative of heightened arousal or agitation. Walls were also associated with higher levels of active locomotory behavior (*patrolling*). A possible cause of agitated behavior and high levels of activity is the presence of fences and barriers that prevent an animal's contact with, or escape from, conspecifics [see Part I for a discussion]. Walls could deprive animals of physical or visual access (or escape) to or from conspecifics with whom they still have olfactory and auditory contact. Indeed, olfactory investigation and urination were found to be higher in females living in colder climates, where enclosures are more likely to be highly walled. Auditory contact may be particularly important since rhinoceros are thought to emit infrasonic vocalizations [Muggenthaler et al., 1993] that would penetrate the walls. Also, it could be that noise levels are higher in some types of walled enclosures than in others. Hard surfaces generally increase reflected sound and we noticed that noise levels in exhibits with 50–80% upright walls in a U-shaped configuration with respect to the public viewing level tended to have higher noise levels than exhibits with 80–100% walls that were sunken with respect to the viewing level. However, our sample size was too small and our noise measurements too general to confirm this. Higher noise levels in some types of walled enclosures could also interfere in some way with rhinoceros auditory communication. We strongly recommend that research on auditory and olfactory communication, and the acoustical effects of constructed captive environments, be carried out for this species.

For males, on the other hand, olfactory behaviors and chasing, stereotypy, and mouthing behaviors are related to the frequency of chlorine use. Thus, behavioral agitation or heightened arousal in males could be the result of a disturbed olfactory environment. Wild male and female black rhinoceros mark their territories with feces and urine, defecate in piles and scrape the dung with their hind legs, and, at least in the wild, scrape tree stumps and bushes with their horn or head [Schenkel and Schenkel-Hulliger, 1969]. The function of this scent-marking is thought to be information exchange about the movements and presence of rhinoceros inhabiting overlapping home ranges and for identifying conspecifics and their reproductive status [Goddard, 1967]. In the enclosures of captive black rhinoceros, chlorine could mask conspecific odors or remove them entirely, chemically alter conspecific odors, or directly impair mucous membranes in nasal passages and/or other scent organs. Liquid bleaches generally contain sodium hypochlorite, which has a corrosive action on skin and mucous membranes [Coppock et al., 1988]. Pending the results of further research on the effects of chlorine-based disinfectants on black rhinoceros behavior, we recommend reducing the use of bleach, an easily changed husbandry procedure.

Thus, captive environments appear to affect male and female black rhinoceros in different ways. Males are responsive to space limitations and the olfactory environment, and females are sensitive to acoustic and/or visual limitations inherent in some types of concrete wall exhibit construction. The sex differences we have found could be related to natural differences in tolerance to other rhinoceros, as have been reported among wild black rhinoceros [Goddard, 1967; Joubert and Eloff, 1971; Adcock, 1994]. Black rhinoceros are mostly solitary in the wild and maintain overlapping home ranges. Sex-specific behavioral adaptations related to reproductive strategies, such as, in males, defense of breeding territories and detection of estrus females, and, in females, defense of feeding territories and calves, may ultimately explain different sensitivity to environmental factors in zoos that mediate communication with conspecifics.

It is well known that stress may cause changes in immune function and disease status [Selye, 1956; Engel, 1967; Riley and Spackman, 1977]. The positive association between black rhinoceros mortality, percentage of public access, and *fear* scores for males suggest that a high degree of exposure to the public is a stressor for black rhinoceros. Why this effect was found for males and not females is uncertain, but it could be related to a relatively stronger tendency to exhibit territoriality among males compared with females. At about 10 years of age, wild males establish a territory that they demarcate with dung and sprayed urine, and they do not tolerate unfamiliar males within that area. Females also maintain ranges but are more tolerant of the presence of conspecifics [Adcock, 1994]. Males may perceive the public as intrusive or in some way feel constrained in their movements or marking behavior by exhibit construction that allows public access on a large percentage of the perimeter. In zoos, visitors have been found to have effects on vigilance behavior and social spacing, locomotory behavior, affiliative behavior, and/or social aggression [in primates: Glatston et al., 1984; Mitchell et al., 1987; Hosey and Druck, 1987; Chamove et al., 1988; in ungulates: Thompson, 1989]. Our results are encouraging evidence that scales for fear behavior can eventually be developed for cross-institutional assessment of stress in relation to disease incidence and physiological measures of stress. Behavioral measurements are often the best indicator of long-term welfare problems for animals [Broom and Johnson, 1993], and comparative behavioral indices are increasingly being used for this purpose [Huntingford and Giles, 1987; Lawrence et al., 1991; Mendl et al., 1992; Boissy and Bouissou, 1995].

Implications for Black Rhino Management

Because this is a correlational study, relationships between variables we found in our analyses do not demonstrate cause and effect. Additionally, there are doubtless many environmental factors that promote or impede reproduction and stress, factors that cancel out each other's effects or are so complexly interrelated that their separate contributions cannot be determined with the small sample sizes in cross-institutional zoo studies. The results of our study can only pinpoint some general trends across the captive U.S. black rhinoceros population that are possible explanatory factors for poor reproduction and mortality.

Nevertheless, some management implications are readily apparent from our data. Clearly, a high density of females at a zoo, meaning more than one adult female, appears to slow the rate of reproduction. The husbandry guidelines for black rhinoceros in U.S. zoos recommends keeping two pairs if a zoo has the space, based on the desire of the Species Survival Plan to maximize the numbers of rhinoceros held in U.S. zoos. However, the enclosure size and separation distance from conspecifics that might compensate for any effects of population density on reproduction are not known. Thus, multiple pairs of black rhinoceros should only be maintained at those zoos with very large, and probably widely separated, enclosures. Our data also indicate that optimal enclosures for black rhinoceros in zoos are large in area, mostly open around the perimeter, have limited public access along the perimeter, and are not cleaned with chlorine bleach. Although enclosure area cannot be easily altered, exposure to the public and cleaning with chlorine can; managers of black rhinoceros can evaluate the costs and potential benefits of invoking any changes in rhinoceros management at their institution. Our data should also be considered when designing future black rhinoceros enclosures.

Certainly, our data suggest that basic research needs to be carried out on black rhinoceros auditory and olfactory communication. We recommend that zoos experimentally manipulate environmental variables on a subset of black rhinoceros in U.S. zoos and do systematic behavior observations. Also, we highly recommend that more detailed investigation be conducted into the acoustical characteristics of enclosures in relation to rhinoceros behavior and space usage.

CONCLUSIONS

1. We found that zoos with more than one female black rhinoceros have a lower reproductive rate and a later age of first reproduction. We conclude that there may be a density-dependent suppressing effect on reproductive function among females in zoo environments.

2. Captive black rhinoceros facilities influence the behavior and breeding success of each sex differently, probably by interfering with social communication. Males appear to be more affected by limited enclosure area and the olfactory environment as it is altered by chlorine disinfectant. Female black rhinoceros are sensitive to some aspect of concrete enclosure walls, perhaps their acoustical properties or the visual separation from conspecifics.

3. *Dominant* scores for males are negatively associated with enclosure size. However, *dominant* is also a temperament characteristic of individuals.

4. An individual's score on *dominant* relative to that of its partner is the most important behavioral predictor of the breeding success of a pair. More submissive males and more dominant, assertive females are the optimal combination for a compatible pair.

5. A potential stressor for black rhinoceros, especially males, is a high degree of public accessibility along the perimeter of their enclosures.

6. Basic research is needed on auditory and olfactory communication of black rhinoceros for us to understand fully the mechanisms of the compromising effects of captive environments on this species.

7. Behavioral assessments derived from keeper ratings of animal behavior are a useful tool for analyzing, cross-institutionally, the impact of captive environments on black rhinoceros.

8. The results of this and our previous analyses are correlational and cannot determine cause and effect. Results are limited by sample size but can nevertheless pinpoint general trends in the captive population of black rhinoceros that deserve closer evaluation and in some cases, investigation through experimental manipulation.

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