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Black Rhinoceros (*Diceros bicornis*) in U.S. Zoos: I. Individual Behavior Profiles and Their Relationship to Breeding Success

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This is the first part of a multi-zoo study to analyze the effects of captive environments on black rhinoceros *(Diceros bicornis)* behavior, breeding success, and well-being. We estimated the reliability and validity of a standardized method of cross-institutional assessment of the behavior of individual rhinoceros. In 1994 and 1995, we asked zookeepers at 19 zoos to rate their black rhinoceros (a total of 60 animals) on 52 behavior elements using a questionnaire. At 14 zoos, at least two keepers rated all the black rhinoceros at their zoo. We used average differences in their ratings of the 52 behavior elements to determine the most reliably rated behavior elements. Fourteen elements were retained for further analysis. Based on their inter-correlations, we grouped these 14 behaviors into six behavior traits: *olfactory behaviors*, *chasing/stereotypy/mouthing*, *friendly to keeper*, *fearful*, *patrolling and dominant* (*to conspecifics*). A behavior profile of each animal consisted of scores on these six traits that were the sum of the primary keeper's ratings for each element in the group. To test the validity of these profiles, we compared scores on the six traits to the behavior of each rhinoceros during a standardized test of reactivity to a novel object and a novel conspecific scent. Tests were videotaped and analyzed by one researcher. Frequencies and durations of behaviors observed during the tests were correlated with scores on all six rated behavior traits. Scores on *friendly to keeper*, *dominant*, and *olfactory behaviors* described differences between black rhinoceros of captive/wild caught origin, age,and sex, respectively. Among successfully breeding males, scores on *dominant* and *olfactory behaviors* were negatively correlated with reproductive success, as was *chasing/stereotypy/mouthing* for females. To test the repeatability of these results, during 1996–1997, we used a modified questionnaire to re-survey 70 black rhinoceros at 24 zoos. Results of the second survey were also similar to those of the first with respect to the behaviors that distinguish rhinoceros of different origin, age, sex, and reproductive success. We conclude that ratings by keepers of behavior and temperament attributes can be used as reliable and valid cross-institutional descriptions of individual differences between black rhinoceros. Zoo Biol 18:17–34, 1999. © 1999 Wiley-Liss, Inc.

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INTRODUCTION

For any species in captive situations where environmental characteristics may in some way challenge animals, individual differences in responsiveness to the environment may have an impact on reproduction and well-being. How an animal copes with stress and whether it develops and maintains normal, species-specific behavior in captivity is strongly influenced by individual characteristics such as temperament and rearing experience [e.g., Suomi, 1987; Benus et al., 1987]. Pronounced individual differences in behavior and temperament are well-known for black rhinoceros (*Diceros bicornis michaeli* and *D. b. minor*), both wild and captive [e.g., Ritchie, 1968]. In captivity, black rhinoceros exhibit high mortality and inconsistent reproductive rates. Indeed, the captive population has not been able to sustain itself without recruitment from the wild [Smith and Read, 1992]. Therefore, those factors in the captive environment (including facilities design, husbandry procedures, and social densities) that have an impact on the breeding success and health of individual black rhinoceros need to be isolated and investigated.

To evaluate which aspects of captive environments have a significant impact on black rhinoceros, we must empirically examine the behavior of individuals in relation to environmental variation. However, this requires large samples of institutions and individuals, and standardized methods for comparing the behavior of individuals housed in different zoos. Traditionally accepted methods for animal behavior comparisons between zoos involve direct observations carried out by one observer or by various observers that have been trained and tested for inter-observer reliability. However, these methods can be time-consuming, costly, logistically complicated, and difficult to standardize. One solution is to rely on the observations of zoo personnel who, on a daily basis, work with and observe how an animal behaves and reacts under multiple conditions and situations.

Zookeepers, over the course of time, integrate and interpret observations of how their charges interact with the environment. To use their knowledge for comparing animals between zoos requires that we assess different categories of behavior than we would obtain from a researcher doing direct observations. Animal behavior researchers typically make direct observations using a standardized ethogram to quantify behavior into static categories of behavioral states, physical movements, and postures. However, individual animals can be thought of as differing in behavior on two different levels: 1) in terms of quantifiable frequencies, durations, and/or patterning of behavior or 2) in terms of temperament or “behavioral style” [Manteca and Deag, 1993]. Temperament can be defined as “the external manifestations, characteristic of an individual, in which the different behaviors interact temporally and are modulated in intensity “ [Feaver et al., 1986; Mendl and Harcourt, 1988]. Wemelsfelder [1997] suggests that categories of animal temperament or behavioral “style,” such as timid, bored, curious, or dominant, really capture the dynamic and expressive nature of processes of attention, the “flow” of behavior that cannot be described in a standard ethogram. However, to quantify behavioral style requires observation of behavior over a period of time and demands a more active interpretative role of the observer [Wemelsfelder, 1997]. Because zookeepers observe their animals over time they may be better at assessing the dynamic qualities of "style" than a short-term, direct observer.

The goal of this study was to verify that behavior profiles of individual black rhinoceros, derived from zookeepers' assessments of their behavior and temperament, are reliable, valid, and useful for behaviorally distinguishing between black rhinoceros in different institutions.

METHODS

General Summary

We asked keepers at 19 zoos to rate the behavior of their black rhinoceros. The questionnaire we developed asked for ratings of 52 separate behavior elements, mostly on a 1–5 scale of frequency of performance or applicability of an attribute. The 52 elements were a comprehensive list describing possible ways a rhinoceros could respond to its environment or interact with conspecifics and humans. Our intention was to reduce this list post hoc based on the relative reliability of ratings for each element and to group or lump correlated elements into a fewer number of more comprehensive behavior "traits."

To verify that keeper ratings of behavior can be used as cross-institutional assessments of individual differences, we then determined the reliability and validity of these ratings. Since two or more keepers (or observers) rated the same rhinoceros at 14 of the zoos, we could determine the reliability of ratings with respect to repeatability and consistency. We then determined the validity of keeper ratings (i.e., whether they are relative measures of the "behavioral style" of different individuals) by comparing them with quantitative scores obtained by behavioral tests on the same rhinoceros [e.g., Stevenson-Hinde et al., 1980; Lyons, 1989; Bolig et al., 1992; Wielebknowski, submitted]. For each black rhinoceros in our study, we videotaped behavioral reactivity to novel objects in a standardized format. Only one researcher reviewed and transcribed the videotapes. We predicted that positive correlations between keeper-rated and investigator-quantified behaviors would verify that keepers' impressions of an individual's temperament are most likely based on their observations over time of how the animal reacts to its social and physical environment.

If keeper ratings of black rhinoceros behavior are valid descriptions of intra- and inter-institutional differences between individuals, then their ratings should be able to distinguish statistically between behaviorally distinct groups or types of rhinoceros. We, therefore, predicted that keeper ratings of behavior would differ significantly between rhinoceros of different age, sex, origin, and breeding success. We re-surveyed the captive black rhinoceros population 2 years after the original study to determine the repeatability of the results from the original study.

Animals

Our sample of 60 (29.31) black rhinoceros at 19 zoos, ranging in age from 1.5 to 29 years, represents 70% of the U.S. population of captive black rhinoceros at the end of 1995. The age, origin, and reproductive history of each rhinoceros was obtained from the North American Black Rhinoceros Studbook [Foose, 1995, 1996, 1997]. Most of the rhinoceros in this survey were born at one zoo and had been transferred as sub-adults to another zoo. We calculated an individual's breeding success as the number of births (live or stillborn) per year in which it had a partner(s) at its current institution (*Births/Yrs. w/ Partners*). For males with more than one partner concurrently, *Yrs. w/ Partners* was the sum of the years it had access to each female. We only calculated breeding success for individuals that had produced a calf before the end of 1995 (20.23). We excluded rhinoceros that had not yet bred because there is great variability in reported ages of first reproduction in the wild and in captivity [Smith and Read, 1992]; it was therefore difficult to know at what age we could define a young animal as "failing" to breed. For statistical analysis, the variable *Births/Yrs w/ Partners* was transformed using the common logarithm (log10) because its distribution was skewed toward the low end and non-normally distributed according to a Shapiro-Wilk W statistic.

Questionnaires

We mailed questionnaires to keepers at zoos participating in the Methods of Behavioral Assessment Project (MBA). At all 19 zoos we considered the keeper who spent most time with the rhinoceros as the "primary" rater and used his/her responses in all data analyses. At 14 of the zoos, one, two or three additional people also rated the black rhinoceros (40 animals in total); these people were either other rhinoceros keepers, or people familiar with the individual rhinoceros such as curators or behavior observers.

The questionnaire asked for ratings of 44 separate behavior elements. In developing the questionnaire we took a "shotgun" approach and included all behavior elements we thought that keepers could possibly observe during their working day with the animals. These 44 elements pertained to rhinoceros social and sexual behaviors, temperament attributes, interactions with the environment and animal/human interactions. We presented a short description of each behavior in the questionnaire and instructed keepers as follows: "for each behavior in the following list, would you please give your impression, on a 1 to 5 scale, of how often you have seen this animal perform or be engaged in each of these behaviors when it is at its most active and/or interactive."

We developed an assessment of "fear" using methodology taken from the Emotions Profile Index [Plutchik, 1980], originally developed for humans but previously applied to several animal species [chimpanzee, baboons, dolphins; see Buirski et al., 1978; Martau et al., 1985]. Eight attributes (*curious, depressed, aggressive, assertive, timid/shy, sociable, vigilant, anxious*) were presented in pairs and raters were instructed to "circle the word in each pair that better describes how this animal behaves around other animals of the same species." Scores for the emotion 'fearful' were the sum of choices for *depressed, timid/shy,* and *anxious*.

Reducing the Number of Behavior Elements

When the questionnaire was developed we did not know which behavior elements would be the most relevant for describing differences between black rhinoceros. We queried keepers about many more elements than we could analyze statistically, and we wished to use only the most reliably rated behaviors and/or attributes to describe individual differences between rhinoceros. Therefore, we used the following procedures to reduce the number of behavior elements prior to any statistical analyses. 1) To determine the relative reliability of each element, we used the data for 40 rhinoceros at the 14 zoos that were rated by two to four people familiar with their behavior. For each behavior element, the absolute difference between the ratings (1–5) of each pair of raters for each rhinoceros was averaged for all 40 rhinoceros. This produced average difference scores for each element ranging from 0.27 to 1.34, with a mean of 0.84. Choosing the mean as an arbitrary cutoff point, we eliminated 14 behavior elements from further consideration. 2) We examined the frequency distribution of the remaining elements and discarded those that were rated as being rarely performed by black rhinoceros (e.g., hindleg drag), or performed predominantly by one sex (e.g., males: mount, chinrest; females: vulvar winking); this eliminated an additional nine elements. 3) Eight additional behaviors were discarded because they were, in retrospect, determined to be ambiguous and difficult to interpret (e.g., adaptable, dominant to keepers, even-tempered). In Table 1, we list the remaining 13 behavior elements and the "fear" score, their descriptions from the questionnaire, and their descriptive statistics based on ratings by the primary keeper. We used only these elements in further analyses.

Statistical Analyses

To estimate inter-rater reliability for each rhinoceros rated by three to five zoo personnel (21 rhinoceros at seven zoos), we calculated a Kendall's coefficient of concordance *(W)* using only these 14 behavior elements. We used an adaptation of Kendall's *W* for ordinal behavioral data [Lehner, 1979] in which the ratings for each element were regarded as frequencies. Kendall's *W* expresses the degree of association (agreement) between several observers based on rankings of their observed frequencies (in our case, behavior ratings) for these 14 elements.

To develop behavior profiles of individual rhinoceros we only used the ratings of the primary zookeeper for each rhinoceros. Our database for statistical analyses, therefore, is based on 25 keepers rating 60 black rhinoceros at 19 zoos. By using this method of rating animals, we knowingly violate the assumption of independence of sampling units (rhinoceros) in our statistical analyses. However, for practical purposes we considered each "sample" of a rhinoceros by a particular keeper at a particular zoo as an independent "description," and we take this into account when interpreting the results of statistical analyses.

Using primary keeper ratings of rhinoceros on the 14 behavior elements, we calculated a matrix of Pearson correlation coefficients. Based on this matrix, we were able to reduce the 14 elements to six groups of correlated behaviors. We calculated a score for each rhinoceros on each of these final six behavior groups as the sum of the ratings the keeper gave them for each element in the group. *T*-tests were used to compare behavior profiles of males and females, and wild and captive born individuals. Pearson correlations were used for further analysis of behavior profiles. However, non-parametric Spearman correlation coefficients were calculated for comparisons with observed frequencies and durations during the behavior tests because these were not normally distributed. An *alpha* of 0.05 was accepted throughout the analyses. Because many tests were conducted on the same data set, it is likely that a significant comparison could occur based on chance alone. However, we did not adjust our *alpha* level because of the descriptive and exploratory nature of our data analyses. We used *alpha* = 0.05 to identify relationships of particular interest in our data.

We carried out all analyses using SAS for PC [SAS Institute, 1989] version 6.10.

TABLE 1. Descriptions of behaviors and temperament traits presented to keepers on questionnaires.

Behavior Element	Description in questionnaire	Mean[a] (SD)	Min–Max
	(rated on a 1-5 scale: never to often)		
Allows touching	How much the animal allows rater to touch it	4.05 (1.21)	1 – 5
Patrolling	Time the animal spends exploring and patrolling its main enclosure	3.31 (0.83)	2 – 5
Dominant (to conspecifics)	Rate on a 1–5 scale, where 1 = submissive and 5 = dominant to conspecifics	3.51 (1.06)	1 – 5
Sleep	Amount of time per day animal spends sleeping	3.01 (0.70)	1 – 5
Mouthing	Animal makes repeated chewing or gumming motion with open mouth, not associated with eating	1.91 (1.03)	1 – 4
Approaches when called	How consistently animal approaches rater when called	3.83 (1.18)	1 – 5
Anogenital investigation	Animal sniffs anogenital region of other animal	2.35 (0.97)	1 – 5
Stereotypy	Repetitive behavior performed with no apparent purpose	2.10 (1.02)	1 – 5
Urine spray	Bursts of urine (not eliminative urination)	3.6 (1.21)	1 - 5
Chase/charge	Chases or charges other rhinoceros with snorting sound	2.9 (0.83)	1 – 5
Pacing	Repetitive locomotion in a specific area	2.76 (1.14)	1 – 5
Following	Animal walks 1.5 body lengths behind other animal, or parallel within a body length	2.76 (1.14)	1 – 5
Urine/feces investigation	Animal sniffs urine or feces of another animal	3.61 (1.01)	1 – 5
Fearful	Reluctance to approach other animals, novel objects, or new situations (*timid/shy*); Interested but fearful and uneasy, vacillates between approach and withdrawal (*anxious*); Failure to seek out or respond to social interactions, inactive, unresponsive, asocial (*depressed*)	6.93 (2.81)	3 – 14

[a]Descriptive statistics are based on ratings by one primary zookeeper for each animal.

Standardized Behavior Tests

A total of 14 specially trained MBA researchers visited the zoos of 53 of the 60 rhinoceros and conducted standardized behavior tests that were videotaped. Tests consisted of three sequential phases: a 15-min baseline period in a slightly novel situation, a 20-min period in which a novel object was introduced by the keeper into the animal's enclosure at the beginning of the period, and a 20-min period in which a novel scent was introduced at the beginning of the period while the novel object remained in the enclosure. Novel situations were of three types depending on the available facilities. The rhinoceros was filmed: 1) in its usual enclosure but shifted at an unconventional time and separated from conspecifics, 2) in an empty enclosure normally occupied by another conspecific, 3) in an unfamiliar enclosure (the animal has rarely or never been there before) separated from conspecifics. The novel object was a traffic cone (71 cm tall), chosen as a safe and inexpensive object, and the novel scent was a brick wrapped in a paper towel on which we placed 2 cc of urine (irradiated to kill potential pathogens) from a female rhinoceros who was not in the study. All animals were tested alone in a holding enclosure, if possible; otherwise, tests occurred in the outdoor exhibit. The time of testing and the novel situation varied from zoo to zoo. From the videotapes of behavior tests, a single researcher transcribed the frequencies and duration of behaviors and latencies to approach the introduced objects using an event recorder program [developed by Jim Ha, University of Washington] on a laptop computer.

Re-survey of Black Rhinoceros in 1996–1997

We distributed a modified behavior questionnaire 2 years later to keepers at each of 23 U.S. zoos and one Australian zoo asking them to rate a total of 70 adult black rhinoceros on 54 behavior elements. For some behaviors, queries were not identical in both surveys. Forty-four of the rhinoceros in the original survey were included in the second survey (eight of the original animals had died, five had been moved to other zoos, and three were not re-surveyed). For 13 behavior elements used in the original analysis, we calculated correlations between ratings of primary keepers in both surveys to gauge the repeatability of keeper assessments of rhinoceros behavior. We made no attempt to ensure that the animals were rated by the same two raters in both surveys. We also tested whether the relationships between sex, age, breeding success, and behavior from the original survey were repeated in the second survey.

RESULTS

Inter-rater Reliability of Behavior Ratings

Kendall’s concordance coefficients (W) varied from 0.31 to 0.88, with a mean of 0.62. These were significant ($P < 0.05$) for 15 of the 21 rhinoceros that had been rated by 3, 4, or 5 people at their zoo. The six individuals for which there was not significant agreement were housed at four different zoos, indicating that disagreement between keepers was not consistent within any one zoo.

Development of Individual Behavior Profiles

We examined the relationships among the 14 behavior elements retained from the questionnaires (Table 1) using a matrix of correlation coefficients (Table 2). The behaviors are arranged according to their patterns of correlation, which fall into six groups: 1) *Urine spray*, *anogenital investigation*, and *urine/feces investigation* are all significantly positively correlated. All these behaviors appear predominantly to be related to olfaction. Therefore, we named these behaviors as a group *Olfactory Behaviors* and gave each rhinoceros a score that is the sum of the ratings for these three elements. 2) *Chase/charge*, *stereotypy*, and *mouthing* are all significantly correlated. These three behavior elements seem to share the characteristics of arousal as expressed by threat, agitation, and/or frustration (in particular, *stereotypy* and *mouthing*). However, we termed this correlated group *Chasing/Stereotypy/Mouthing* to avoid a misinterpretation of the underlying causes of these behaviors. 3) *Allows touching* and *approaches when called* are positively correlated; we termed these collectively *Friendly to Keeper.* 4) *Sleep* is almost significantly positively correlated with *Fear-*

TABLE 2. Correlation coefficients between the 14 behavior elements retained for analysis

Urine spray													
Anogenital investig.	**0.35**												
Urine/feces investig.	**0.51**	**0.31**											
Chase/charge	–0.14	0.19	0.21										
Stereotypy	–0.11	0.03	0.12	**0.31**									
Mouthing	–0.03	0.04	0.08	**0.34**	**0.25**								
Allows touching	0.17	–0.11	0.30	–0.09	–0.03	0.08							
Approaches when called	0.04	–0.01	0.29	0.09	0.09	0.28	**0.52**						
Fearful	0.15	–0.18	–0.21	–0.24	0.02	–0.03	–0.05	–0.18					
Sleep	–0.05	–0.13	–0.04	0.00	0.07	0.02	0.06	0.04	**0.27**				
Dominant	–0.10	0.12	–0.08	0.09	0.09	0.02	–0.12	0.06	–0.12	–0.10			
Patrolling	0.11	–0.14	0.22	–0.02	–0.08	–0.15	0.00	–0.11	–0.17	0.02	0.08		
Following	0.17	**0.49**	0.23	0.22	0.01	0.08	0.00	0.05	–0.05	–0.14	–0.13	0.18	
Pacing	0.15	0.17	**0.36**	0.25	**0.59**	0.24	0.12	0.15	–0.10	–0.23	0.03	–0.01	0.09

Bold type indicates $P < 0.05$ for n = 60 rhinoceros.

ful (P = 0.06). Because excessive sleeping is sometimes a characteristic of an animal in a chronically aversive situation [e.g., Barnett et al., 1984], as a group we termed these two elements *Fear.* 5) *Dominant (to conspecifics)* is not significantly correlated with any of the other behaviors, and we, therefore, treated it as a single-element group. 6) We did the same with *Patrolling.* We removed *Following* from the behavior profile since it was significantly correlated with only one of the three behaviors in the olfactory group. We also removed *pacing* because it had an irregular pattern of correlation that overlapped the *Olfactory Behaviors* group and the *Chasing/Stereotypy/Mouthing* group.

To summarize, the behavior profile for each rhinoceros consists of scores on six behavior traits, termed *Olfactory Behaviors*, *Chasing/Stereotypy/Mouthing*, *Fear, Friendly to Keeper, Dominant* (to conspecifics), and *Patrolling*.

Comparison of Rated and Observed Black Rhinoceros Behavior

Table 3 describes the eight behaviors we measured from videotapes of tests with the two novel objects and gives correlations with individuals' scores on the six behavior traits. Each trait was significantly correlated with one or more of the observed behavioral reactions. There was a significant positive correlation between O*lfactory Behavior (*which includes *urine spraying* and olfactory investigation behaviors*)* and how often the rhinoceros sniffed the ground and urinated during the test. There was a significant negative correlation between *Chasing/Stereotypy/Mouthing* and the latency to touch the paper towel with the novel conspecific scent. Thus the higher an individual's score on *Chasing/Stereotypy/Mouthing*, the more quickly it touched the towel after it was placed in the enclosure. *Fear* scores were significantly associated with a long latency to approach the paper towel and less frequent interaction with the cone. Individuals with high ratings on *Friendly to Keeper* sniffed the ground significantly more frequently, interacted with the traffic cone significantly more, and approached and touched the traffic cone significantly sooner. There was a significant positive correlation between *Dominant* (to conspecifics) and the amount of time during the entire test spent in a "tail up" posture, and sniffing and snort-charging the towel. "Tail up" is common during agonistic interactions and when a rhinoceros is alert [Schenkel and Schenkel-Hulliger, 1969]. *Patrolling* was significantly positively correlated with the amount of time during the test the rhinoceros spent locomoting and frequency of snort-charging at the novel scent. These correlations indicate that behavior profiles derived from keeper ratings of an animal's behavior correspond to the relative reactivity of the animal to certain types of novelty. As such, keeper ratings are valid descriptions of the behavioral distinctiveness of individual black rhinoceros.

Behavior Profiles in Relation to Sex, Origin, Age, and Breeding Success of Black Rhinoceros

The only behavior trait that differed significantly between male and female rhinoceros was *Olfactory behaviors* (T = 4 .54; n = 29,31; P < 0.001), for which higher scores were found for males (mean score 13.75 ± 2.55 SD compared to 10.5 ± 2.88). *Friendly to Keeper* was the only behavior trait for which captive-born rhinoceros (8.38 ± 1.78) were rated significantly higher (T = 2.96; n = 44,16; P < 0.05) than wild caught rhinoceros (6.68 ± 2.41).

For males and females separately we calculated correlations between age and the six traits of the behavior profile. The only significant correlation we found was

TABLE 3. Spearman correlation coefficients between behavior frequencies and durations observed during novel object tests and behavior traits from keeper ratings

Observed behavior	Freq sniff ground	Freq. urinate	Time to touch towel	Duration interact with cone	Time to touch cone	Freq. tail-up	Freq snort-charge towel	Duration locomote
Mean (SD)	2.14/hr (1.71)	0.20/hr (0.25)	1.45 min (1.01)	23 min/hr (20)	1.46 min (0.86)	0.50/hr (1.16)	0.27/hr (0.24)	30 min/hr (20)
Rated behavior trait								
Olfactory behaviors	**0.39***	**0.32***	–0.22	0.13	0.07	–0.02	0.19	0.06
Chasing/stereotypy/mouthing	0.05	–0.03	**–0.32***	0.15	–0.01	–0.09	0.09	–0.11
Fear	–0.24	0.11	**0.35***	**–0.30***	0.13	–0.01	0.12	–0.01
Friendly to keeper	**0.29***	0.05	–0.18	**0.37***	**–0.36***	–0.19	0.22	–0.01
Dominant	–0.06	–0.09	0.05	–0.09	0.16	**0.26***	**0.26***	0.01
Patrolling	0.14	0.04	–0.08	0.08	0.25	–0.03	**0.29***	**0.26***

*$P < 0.05$.

the score on *Dominant* among females (r = 0 .50, n = 31, $P < 0.05$). Thus keepers tend to describe females as more *Dominant* the older the female.

In Table 4, Breeding Success (*Births/Yrs w/ Partners*) of males and females that had reproduced are compared to their scores on the six traits of the behavior profile. The greater the breeding success of a male, the lower his score on O*lfactory Behaviors* and *Dominant*. These two traits were significantly positively correlated among these males (r = 0 .54, n = 20, $P < 0.05$). The greater the breeding success of females, the lower the score on *Chasing/Stereotypy/Mouthing.* This behavior trait was also negatively correlated to breeding success in males but did not reach statistical significance.

The behavior trait *Dominant* assesses behavior toward conspecifics. In most cases, the conspecific with which a male has direct contact is his female partner(s). The negative relationship between *Dominant* and breeding success of males described above implies that if a male is perceived to be less dominant than his partner, breeding success as a pair is greater. To verify this, we examined our data in another way. We looked at the relative scores on *Dominant* within pairs of black rhinoceros in our population (26 adult males were paired with 29 adult females for a total of 29 pairs). Figure 1 gives the difference between the female's score on *Dominant* and the male's score and its correlation with the pairs' breeding success (number of *Births/Yrs* together). The correlation is highly significant (r = 0.75, n = 29, $P < 0.0001$), indicating that the more successful a pair, the more the female is likely to be rated as more *Dominant* than the male.

The above analyses indicate that behavior profiles for individual black rhinoceros, derived from keeper ratings, describe across institutions black rhinoceros of different sex, origin, age, and breeding success.

Re-survey of Black Rhinoceros in the U.S., 1996–1997

To see if keepers' ratings of rhinoceros are repeatable over long periods of time, we compared ratings of 44 rhinoceros in both our first and second surveys. Of the 14 behavior elements used to develop a rhinoceros behavior profile in the first survey, 13 had been included in the second survey (*mouthing* was omitted because at the time of writing the second survey we thought the description of this behavior might be ambiguous). Table 5 gives the correlation coefficients for these 13 behaviors across surveys. There were significant positive correlations between nine of the elements. Of the four that were not significantly correlated, two are interactive social behaviors (*chase, follow*) that could have changed in frequency during the 2-year

TABLE 4. Correlation coefficients for breeding success (births/year with partners) and behavior profiles for successfully reproducing male and female black rhinoceros

Behavior trait	Males (n = 20)	Females (n = 23)
Olfactory behaviors	–0.65*	–0.10
Chasing/stereotypy/mouthing	–0.23	–0.49*
Fear	0.33	–0.00
Friendly to keeper	0.04	–0.19
Dominant	–0.59*	0.18
Patrolling	–0.12	0.09

*$P < 0.05$.

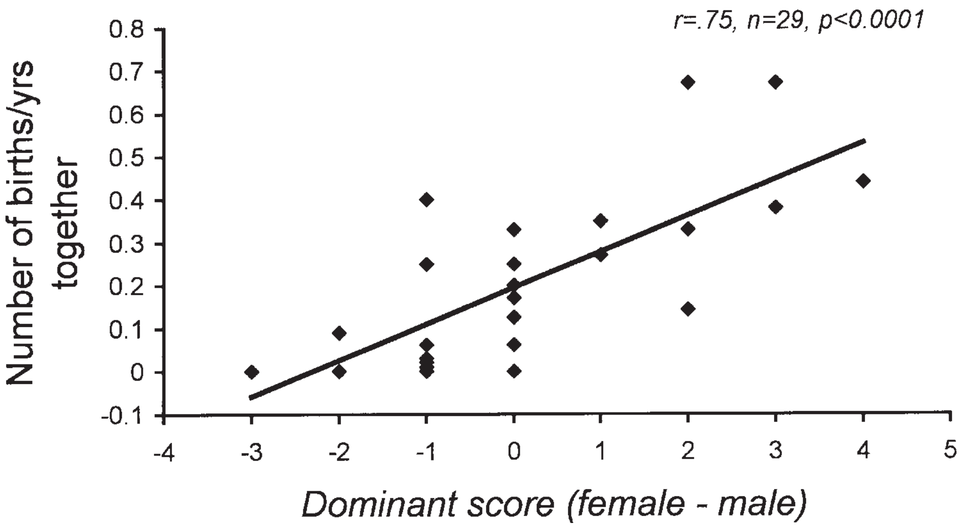

Fig. 1. Correlation between breeding success of black rhinoceros pairs and the relative scores of the male and female on *Dominant* (*r*egression line, y = –1.22 + 6.61).

period between surveys if the rhinoceros's social situation had changed in some way. The two others (*sleep, patrolling time*) were queried differently in each survey.

We analyzed the data from the second survey to see whether the same relationships between behavior and age and sex and breeding success would emerge. As in the first survey, there was a positive correlation between age and *Dominant* among females that was significant (r = 0.30, n = 41, $P = 0.05$). Males' scores on O*lfactory Behaviors* (*urine spray + urine/feces investigation + anogenital investigation*) (14.5 ± 2.25) were again significantly higher than females' scores (10.4 ± 2.17) (T = 7.7; n = 29,41; $P < 0.0001$). The differences between wild-caught and captive-born individuals on *Friendly to Keeper* was almost significant (captive = 8.5 ± 2.11; wild-

TABLE 5. Correlation coefficients for 14 behavior elements rated by keepers in the original survey and a second survey 2 years later for 44 black rhinoceros

Behavior element	Original questionnaire, 1995 (n = 60) and second survey, 1997, n = 44
Urine spray	0.59*
Anogenital investigation	0.32*
Urine/feces investigation	0.36*
Stereotypy	0.51*
Pacing	0.31*
Allows touching	0.29*
Approaches when called	0.41*
Fearful	0.34*
Dominant	0.58*
Chase/charge	0.00
Sleep	0.10
Patrolling	–0.04
Following	0.06

*$P < 0.05$.

caught = 7.6 ± 2.17; T = 1.72; n = 35,35; P = 0.088). Originally, there was a significant negative correlation between breeding success of females and the combination *chase + stereotypy + mouthing.* In the second survey we found a similar but non-significant correlation for *chase + stereotypy* (r = –0.31, n = 27, P = 0.11) *(Mouthing* was not included in the second survey.) There was again a significant negative correlation between male breeding success and *Dominant* (r = –0.39, n = 26, $P < 0.05$) but not *Olfactory behaviors* (r = 0.09, ns).

DISCUSSION

Describing individual differences in the character of wild black rhinoceros in Kenya, one author states "some are moderately even-tempered, and some irritable, some brave and some timid; some volatile and some phlegmatic" [Ritchie, 1968]. Such differences are readily apparent among captive black rhinoceros as well. We based our assessments of individual differences on keepers' impressions of behavior and temperament that describe the "behavioral style" of the rhinoceros with which they work. Keepers observe their animals in many different contexts over long time periods. However, they sometimes appear not to agree with each other on assessments of individual animals because they differ when asked to describe behavior in their own words. In our study, we asked keepers to quantify their opinions within a limited range of possible responses, which resulted in much greater similarity. Only our study and two others [Gold and Maple, 1994; Wielebknowski, submitted] investigated and confirmed that reasonably high levels of agreement between zookeepers can be achieved using this kind of methodology. Wielebknowski's concordance coefficients ranged from 0.57 to 0.98, and Gold and Maple found significant inter-rater correlations for 75% of the temperament traits they studied. Our study is unique because we asked many different people, all at different zoos, to rate different animals. We therefore expected lower inter-observer agreement than in studies in which the same raters rate the same animals and the exact meanings of behavioral terms were agreed upon prior to rating [e.g., Stevenson-Hinde and Zunz, 1978; Stevenson-Hinde et al., 1980; Feaver et al., 1986; Wielebknowski, submitted.] Our methods are similar to those used in psychiatric research to classify different forms of human depression using categories of attentional style [e.g., Tryer et al., 1993]. In such studies, a good level of agreement is considered to be 0.70 [Landis and Koch, 1977]. In our original survey of captive rhinoceros, concordance between keepers was somewhat lower, averaging 0.61, and concordance was significant for 71% of the animals rated.

Our results indicate that behavioral assessments based on keeper ratings can distinguish black rhinoceros on the basis of sex, origin, and age. Males are rated as performing significantly more *Olfactory Behaviors* than females. Captive-born rhinoceros are more likely to be scored highly on *Friendly to Keeper* than wild-caught rhinoceros. The older a female, the higher her rating on *Dominant* to conspecifics. None of these results are unexpected for a population of rhinoceros. The fact that most keepers have knowledge of only a few individuals, rather than an entire population, strongly suggests that our results do not reflect preconceptions among keepers about the characters of different types of rhinoceros.

One goal of our data analyses was to develop assessments of black rhinoceros temperament or behavioral style by grouping correlated behavior elements into more comprehensive behavior traits. A number of studies of animals and humans used groupings of correlated behaviors to describe dimensions of temperament. These studies support the concept that temperament or personality in animals and humans might vary along a few similar dimensions [e.g., Cloninger, 1993]. These studies generally produce three main dimensions: 1) an approach/aggression/boldness factor, 2) an avoidance/escape/anxiety factor, and 3) a factor for either sociality or curiosity/exploration [e.g., bitterling, Wiepkema, 1961; rhesus macaques, Chamove et al., 1972; cichlid fish, Carlstead, 1983; marmots, Armitage, 1986; octopus, Mather and Anderson, 1993; humans, Cloninger et al., 1993; gorillas, Gold and Maple, 1994; piglets, Forkman et al., 1995]. From our analyses, *Dominant, Fear*, and *Olfactory behaviors* and/or *Chasing/Stereotypy/Mouthing* may reflect the black rhinoceros counterparts of these temperament dimensions. The other two traits, *Patrolling* and *Friendly to Keeper* are more likely to be dependent on the rhinoceros' current housing situation and experience with humans.

That our behavior profiles may reflect some aspects of black rhinoceros temperament is supported by the correlations in our study between keeper-rated behavior traits and behavior observed during standardized novel object tests. All six traits in our behavior profile corresponded with the "style" with which individuals reacted to the novel testing situation, the traffic cone and the paper towel with an unfamiliar rhinoceros scent on it. In general, these data suggest that keeper assessments of black rhinoceros temperament and behavioral style are based on their observations of the animals' reactivity to events, objects, and conspecific signals in their environment. Wielebknowski [submitted] obtained results similar to ours for cheetah in zoos. She found that observer/keeper ratings of individual cheetah for *active, aggressive,* and *excitable* all correlated significantly with the number of approaches a cheetah made to a mirror during a standardized behavior test, and to the frequency of growl/hiss. She also found that longer latencies to approach the mirror were significantly correlated with ratings on *fear, tense, less active, less calm,* and *less curious.*

One result from the analysis of the behavior tests was difficult to interpret: there was a significant negative correlation between scores for *Chasing/Stereotypy/Mouthing* and the latency to touch the towel with black rhinoceros urine. The latter could be a measure of a tendency to approach a novel conspecific scent or arousal by social stimuli. We suggested in the results section that C*hasing/charging, stereotypy* and *mouthing* are behaviors sometimes associated with increased arousal or agitation. C*hasing/charging* is an interactive and generally intense, aroused social behavior in black rhinoceros with elements of threat. Opening and closing the mouth has also been described as a threat in black rhinoceros [Schenkel and Schenkel-Hulliger, 1969]. At least in some instances, *stereotypy* and *mouthing* in black rhinoceros may occur at times of intense social interactions, particularly if animals are thwarted by fences or other barriers that separate them or, conversely, prevent them from escaping from each other. Certainly stereotypy occurs in other species when an animal is highly motivated to perform some behavior but is thwarted from doing so by a physical or psychological barrier (such as the aroused pacing that occurs when an animal is denied access to another animal or food) [e.g., Meyer-Holzapfel, 1968]. Therefore, if high scores on *Chasing/Stereotypy/Mouthing* are indicative of arousal or agitation by social stimuli, we can understand the correlation to a quick approach (short latency) to a novel conspecific scent. Interestingly, scores on *Chasing/Stereotypy/Mouthing* in our sample of reproductively successful female black rhinoceros were negatively correlated with birth rates (breeding success). Taken together, all these data suggest that the social interactions of reproductively successful females are less likely to be characterized as "intense" and "aroused." We predict that "behavioral intensity" or highly aroused and agitated behavior in the female of a pair may be an indication of the absence of receptivity to her male partner. This hypothesis should be investigated in individual females by monitoring changes in the frequency of these behaviors in relation to changes in reproductive hormone profiles.

Two other behavior traits were important for describing differences in black rhinoceros reproductive results. The more offspring a male had the lower his score on *Dominant* and also on the correlated trait *Olfactory Behaviors.* The higher the female's score on *Dominant* relative to her male partner, the greater the breeding success of the pair. It would appear, therefore, that with respect to reproduction, *Dominant* is a positive trait for females but a negative trait for males. In our initial survey, "dominant" behavior was not defined; rather keepers were asked to rate an animal on a scale of 1 to 5 from *submissive to dominant to conspecifics.* Keepers' ratings on this scale were positively correlated with *assertive* and *aggressive* and negatively correlated with *hornbutting, jousting, sociable, time spent close to other rhinoceros*, and *adaptable*. From this we can infer that a certain amount of aggressiveness and assertiveness contributes positively to a female's chances of breeding and that a submissive, adaptable and interactive character is advantageous for males. Interestingly, keepers rated older females higher on *Dominant.* This corroborates anecdotal reports of a "key" to black rhinoceros compatibility and breeding success: pair an older female with a younger male. Our results indicate that it is important that a female be paired with a male with a less "dominant" character and that as females get older they are more likely to be more "dominant."

Our results concerning breeding success and behavior perhaps contain no surprises for black rhinoceros managers, for aggressive behavior and chasing/charging are anecdotally well-known to be indicators of potential breeding problems in captivity. However, our results do indicate that we successfully quantified relative differences between rhinoceros individuals in different zoos for some behavioral traits that are important for reproduction. Application of these behavior profiles will allow us to investigate empirically which environmental, social, physiological, or genetic factors modulate "dominant behavior" in males and females, and chasing, stereotypy, and mouthing in females. Our aim is to suggest modifications of husbandry procedures that may optimize these behavioral characteristics and, ultimately, reproductive success.

The most complex aspect of this study was reducing the number of variables. The survey was long and we assessed quite a large number of behavioral variables. There were complex correlations among the variables that we explored using repeated principal components analyses, a multivariate factor analytical technique that groups and reduces variables into a smaller number of components based on their patterns of correlation. However, a very large sample size of animals is required to group so many variables reliably, a sample size that is virtually impossible to obtain for any zoo-housed species. Still, multivariate statistical methods are extremely valuable as exploratory tools. Based on initial explorations of our data, we decided first to reduce our variables to include only behaviors that could be considered characteristic of individuals. We therefore could not use sexual behaviors because they are restricted to only one sex, reducing our sample size by half. Also, the performance of sexual behaviors is highly dependent on the partner's responses rather than an individual's temperament. We also discarded most of the emotional traits we assessed because many were highly inter-correlated. For each variable, we considered how easy it was to interpret in behavioral terms. For example, we kept variables that described human/animal interactions (such as *allows touching* and *approaches when called*) and discarded ones that were subjective judgments (such as *friendly* or *playful*). Finally, and perhaps most important, we only retained variables with high inter-rater reliability. Employment of these criteria led to what we consider a reliable assessment of individual differences in temperament and behavioral style that can be used for further investigation into the environmental factors in zoos that affect black rhinoceros.

CONCLUSIONS

1. We found significant levels of agreement between keepers for 71% of the rhinoceros rated by three or more keepers.

2. Twelve of the most reliably rated rhinoceros behavior elements were grouped according to their inter-correlations to produce a behavior profile comprised of six traits: *Olfactory Behaviors, Chasing/Stereotypy/Mouthing, Fear, Friendly to Keeper, Dominant,* and *Patrolling*.

3. Scores of rhinoceros for these six behavior traits were significantly correlated with behavioral reactions to novel objects in standardized tests. Thus keeper ratings of animal behavior were valid cross-institutional descriptions of individual differences in "behavioral style."

4. The behavior profiles we developed distinguished different types of rhinoceros in the population. Captive-born rhinoceros were rated significantly higher on *Friendly to Keeper* than wild caught rhinoceros. Older females were rated higher on *Dominant* than younger females. Males were rated as more frequently performing *Olfactory Behaviors* than were females.

5. *Dominant* is a negative trait for the reproductive success of males. The most successfully breeding pairs of rhinoceros are those in which the female is rated as more *Dominant* than the male.

6. Females with higher ratings on *Chasing/Stereotypy/Mouthing* have poorer reproductive performance. We suggest that these three behaviors be investigated as indicators of lack of estrus by correlating changes in behavioral frequency with changes in hormone profiles.

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