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Behavioral Differences as Predictors of Breeding Status in Captive Cheetahs

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Individual behavioral variation of 44 adult captive-born cheetahs, *Acinonyx jubatus*, was assessed using observer and keeper ratings on a variety of behavioral attributes. Inter-rater consensus was high for most questionnaire items, several of which were significantly correlated with direct behavioral measures recorded in a mirror-image experiment. Principal component analysis was applied to identify patterns of individual variation as measured by observer and keeper ratings. Three major components, labeled as tense-fearful, excitable-vocal, and aggressive, accounted for 69% of the observed variation. Females showed significantly higher scores on the component tense-fearful than males. Non-breeders of both sexes scored significantly higher on the component tense-fearful than breeders. Assessment of individual behavioral variation through questionnaire ratings may therefore provide a simple and non-invasive tool for predicting an individual's ability to adjust to the constraints of certain husbandry regimens and to reproduce in captivity. Simple measures of behavioral attributes may offer new insights for solving breeding problems and improving conservation management of endangered species in captivity. Zoo Biol 18:335–349, 1999. © 1999 Wiley-Liss, Inc.

Key words: *Acinonyx jubatus*; captive propagation; animal personality; individual behavioral variation

INTRODUCTION

People who spend long hours watching or caring for animals often feel that individuals have distinct personalities [Feaver et al., 1986]. In the past, these differences have not been regarded as particularly useful or even measurable and were merely reported as entertaining anecdotal accounts on the types of behavioral idiosyncrasies found among individuals of a study species [Lawick-Goodall, 1971;

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Yamada, 1971]. Recent studies, however, largely conducted on laboratory and farm animals, examined patterns in individual behavioral variation in relation to measures of productivity, e.g., milk ejection rate in dairy goats [Lyons, 1989], disease resistance [Jones, 1989], and animal welfare [Broom, 1988; Manteca and Deag, 1994]. Such studies have now been used in management decisions and to improve productivity and animal welfare in laboratory and commercial farm settings [Gold and Maple, 1994; Boissy, 1995; Boissy and Bouissou, 1995].

Individual behavioral variation has, however, received little attention in the area of captive propagation of zoo animals. Only very recently have researchers begun to realize the importance of individual differences and their implications for captive management and propagation of zoo-kept species [Mendl et al., 1992; Gold and Maple, 1994; Carlstead et al., 1999a,b]. Captive breeding of endangered species has gained increased importance as a conservation tool due to the rapid decline of populations in the wild [Carpenter, 1983; Olney et al., 1994]. To be effective, however, self-sustaining captive populations need to be established, but so far few captive populations meet this requirement [Magin et al., 1994]. Frequently only some individuals within a captive population breed, whereas others fail to reproduce. In cases in which all individuals appear reproductively sound and healthy, the investigation of individual behavioral differences appears particularly important. Studies on the domestication of wild animals showed that there is inter-individual variation within populations in the ability to cope with and to reproduce in a captive environment [King, 1939; Berry, 1969; Price, 1984]. To facilitate natural breeding in captivity and to preserve the behavioral repertoire of a species, the investigation of potential behavioral factors associated with poor breeding success is of major importance. In the cheetah (*Acinonyx jubatus*), for example, genetic and physiological studies alone have failed to detect differences between breeders and non-breeders [Wildt et al., 1993], and difficulties in captive breeding are now largely ascribed to husbandry and behavioral problems [Caro, 1993; Lindburg et al., 1993; Brown et al., 1996; Wielebnowski, 1996; Wielebnowski and Brown, 1998].

The goal of this study is to provide a method for assessing individual behavioral variation in captive cheetahs. To incorporate the extensive knowledge accumulated by animal keepers at captive facilities, observer/keeper questionnaires were used to obtain ratings on individual behavioral variation for 44 cheetahs housed at four North American breeding facilities [see Stevenson-Hinde et al., 1980a,b; Lyons, 1989; Gold and Maple, 1994]. Then a comparison of observer/keeper ratings was made with direct recordings of behaviors shown in response to mirror-image experiments to examine the validity of the questionnaire. Patterns in behavioral variation obtained from the questionnaire results were identified using principal component analysis. Subsequently, individual cheetah scores on resulting components were examined with regard to breeding status, gender, and rearing history.

METHODS

Study Animals and Facilities

Forty-four adult captive-born cheetahs, 25 females and 19 males, were the subjects of this study. Three females and three males were hand-reared, the remaining individuals were mother-reared. Ages ranged from 3 to 13 years ($\bar{x} \pm SD = 6.6 \pm 2.89$). Individuals had to be at least 3 years old and had to have been introduced to a

member of the opposite sex for at least 1 hr on at least three different occasions before being rated. Breeding success was defined as having sired (breeders: females [n = 13, males n = 12]) or having failed to sire offspring (non-breeders: females [n = 12, males n = 7]).

The cheetahs were distributed over four North American breeding facilities, Fossil Rim Wildlife Center, TX (n = 17), White Oak Conservation Center, FL (n = 14), Wildlife Safari, OR (n = 9), and the Sacramento Zoo, CA (n = 4). Each facility kept individuals in outdoor enclosures ranging from 450 m^2 to 24,400 m^2 in size. Social groups and caging situations were highly variable even within facilities, with cheetahs being frequently switched from one enclosure to another. Feeding occurred once a day at each facility and 1 fast day per week was observed by all facilities. Cheetahs at the Fossil Rim Wildlife Center, White Oak Conservation Center, and the Sacramento Zoo were fed Nebraska Canine Diet (North Platte, NB), supplemented weekly with bones or horse ribs. At Wildlife Safari, cheetah diet consisted solely of carcass meat (horse, cow, deer, chicken, turkey) supplemented with calcium and vitamins. Water was provided ad libitum.

All observations, experiments, and data collection were carried out between April 1992 and July 1994. A total of 6 months, divided into two separate visits, were spent at the Fossil Rim Wildlife Center and the Sacramento Zoo; 5 months at the White Oak Plantation Conservation Center; Wildlife Safari was visited once for 3 months.

Observer/Keeper Questionnaire

Eighteen behavioral adjectives were chosen as items for assessment of individual behavioral variation (Table 1) based on adjectives used in previous studies on domestic cats [Feaver et al., 1986] and rhesus monkeys [Stevenson-Hinde and Zunz, 1978]. However, some changes were made to adapt the items for rating cheetah behavior. Two keepers and the author independently rated individual cheetahs at each

TABLE 1. Behavioral definitions of adjectives used for questionnaire ratings

Active	Moves frequently (e.g., paces, runs, stalks at lot).
Aggressive to conspecifics	Frequently reacts hostile (e.g., attacks, growls) toward other cheetahs.
Aggressive to people	Frequently reacts hostile and threatening toward people.
Calm	Not easily disturbed by changes in the environment.
Curious	Readily approaches and explores changes in the environment.
Eccentric	Shows stereotypic or unusual behaviors.
Excitable	Overreacts to changes in the environment.
Friendly to conspecifics	Social; initiates and seems to seek proximity of other cheetahs.
Friendly to people	Initiates proximity; approaches fence readily and in a friendly manner (e.g., purrs, rubs on fence).
Fearful of conspecifics	Retreats and hides readily from other cheetahs.
Fearful to people	Retreats readily from people.
Insecure	Seems scared easily; ''jumpy'' and fearful in general.
Playful	Initiates and engages in play behavior (seemingly meaningless, but non-aggressive behavior) with objects and/or other cheetahs.
Self-assured	Moves in a seemingly confident, well-coordinated, and relaxed manner.
Smart	Learns quickly to associate certain events and appears to remember for a long time.
Solitary	Spends time alone; avoids company.
Tense	Shows restraint in movement and posture.
Vocal	Frequently and readily vocalizes.

facility. Keepers had worked with cheetahs anywhere from 1 to 23 years ($x \pm SD = 7.13 \pm 6.96$, $n = 8$). Before rating, the keepers and the author only discussed the rating procedure and the definitions of given adjectives. Keepers were advised not to discuss the questionnaire and the ratings of individual cheetahs with each other before scoring. The author rated cheetahs at each facility after a 2–3-month observation period during which she also collected daily behavioral data for a study on estrus and mating behavior.

The rating method was identical to the one presented by Feaver et al. [1986] [see also Martin and Bateson, 1993]. A coding form with a number of calibrated horizontal lines corresponding to the number of individuals per facility was provided for each adjective. Each line was 120 mm long and presented a continuous scale for a particular behavioral item. The minimum score would be placed on the left side of the line (marked by a negative sign) and the maximum score on the right side of the line (marked by a positive sign). Raters then marked each individual's score by placing a cross along the line for each individual and each item (compared to all cheetahs they have ever known). Subsequently, the distance from the left side of the line to the position of the cross was measured in millimeters. This distance then represented the numerical score for a particular individual on a particular item, resulting in scores from 0 to 120. The method used has the advantage over others [Stevenson-Hinde et al., 1980 a,b; Kerr and Wood-Gush, 1987; Gold and Maple, 1994] of not requiring observers to impose their judgment on a discontinuous scale [Martin and Bateson, 1993].

Inter-observer (rater) reliability on all behavioral items was assessed for each facility employing Kendall's coefficient of concordance (W) to test for degree of association among three raters [Siegel and Castellan, 1988]. Items on which inter-rater reliability was below $W = 0.5$, the point at which concordance coefficients failed to reach statistical significance at the level of $p < 0.05$, were subsequently excluded from further analysis. The mean scores on each item calculated over the three raters for each individual formed the input for a principal component analysis (PCA).

PCA is a statistical technique that linearly transforms an original set of variables into a substantially smaller set of uncorrelated (orthogonal) variables (components) that capture most of the variation and information of the original set of variables. This technique has been frequently used for analyzing the type of data collected in this study [Chamove et al., 1972; Stevenson-Hinde et al., 1980a,b; Kline, 1981; Frey and Pimentel, 1978; Mather and Anderson, 1993; Gold and Maple, 1994; Forkman et al., 1995], and the underlying data appear to meet the basic assumptions of PCA. These include that data are drawn from a multivariate normal distribution and variables should be continuous or at least measured on an interval scale [Kim and Mueller, 1978]. Ideally variables should show a linear relationship to each other; however, PCA analysis is assumed to be relatively robust to some deviations [Frey and Pimentel, 1986]. The goal of PCA is to reduce the dimensionality of the original data set. The PCA in this study was carried out on a Pearson product-moment correlation matrix. This method examines the matrix of correlation coefficients between all variables and deduces latent variables (components) that may describe the relationships between data in a more economic way. A certain variable is then defined by its loadings on the new components (which can be interpreted as the correlation between the measured and the latent variable) [Dunteman, 1989]. Components with eigenvalues >1 were retained for interpretation and were labeled according to the two variables

that showed highest positive loadings for this component. Component scores for each individual were calculated by multiplying an individual's standardized rating on an item by the loading of that item divided by the eigenvalue of a component, summed up over all components [Kim and Mueller, 1978; Stevenson-Hinde and Zunz, 1978]. A very high positive score on a component therefore reflects high ratings on positively loaded items and low ratings on negatively loaded items. Conversely, a very low negative score reflects negative standardized ratings on positively loaded items and positive standardized ratings on negatively loaded items [Stevenson-Hinde and Zunz, 1978].

Mirror-Image Stimulation

The exposure of animals to their mirror image, also termed *mirror-image stimulation* (MIS) [Gallup, 1968], has been used to study patterns of aggressive and social behavior in a variety of animals [Svendsen and Armitage, 1973]. Mirrors appear to elicit reliable and repeatable responses for a number of species [Gallup and Capper, 1970], and have been used for assessing some aspects of individual behavioral variation [Armitage, 1986 a,b]. In this study MIS was used to obtain conventionally recorded behavioral data for comparison with, and possible validation of, the observer/keeper ratings. Forty-one of the original 44 cheetahs in this study were exposed to a 36×157-cm mirror before observer/keeper ratings. No keepers or other observers were present during the experiments, and individual cheetahs were always tested without presence of other cage mates. The mirror was placed upright on the outside of the wire-mesh fence of the enclosure and fastened to the fence with a wire hook. To start the experiment a cheetah had to be approximately 20 m distant and either sitting or lying alert. After securing the mirror, I moved at least 10 m away from the fence. Continuous time sampling was used [Martin and Bateson, 1993] to measure approach time and four different types of behavioral events (Table 2) over a 15-minute period. On frontal approach toward the mirror, cheetahs were able to see their full-size image approaching on the other side of the fence. All testing took place between 0600 and 0900 hours and before feeding since cheetahs were generally more active at this time.

To test for reliability of the observed MIS response, the experiment was repeated after 1 year for eight (four males and four females) of the cheetahs. A Spearman rank-order correlation coefficient [Siegel and Castellan, 1988] was used to test for association between the scores obtained from these two tests. Subsequently, scores on behavioral events measured during MIS were compared to the average scores of questionnaire items obtained for each of the 41 cheetahs using Spearman rank-order correlation coefficients.

TABLE 2. Behavioral definitions for mirror responses

Approach	Approaches mirror to within one body length, while looking at mirror.
Sniff	Olfactory examination of mirror.
Stare	Looks straight into the mirror while assuming a rigid body posture.
Growl/hiss	Growl: low-pitched, drawn out ''snarling'' sound; hiss: voiceless expulsion of air, mouth open.
Approach time	Time it takes for the individual to approach the mirror to within one body length starting from the moment the mirror was placed on the fence and the observer had retreated to a 10-m distance.

Comparison of Principal Component Scores with Respect to Breeding Status, Gender, and Rearing Type

Component scores of all individual cheetahs were compared to the variables, breeding status (breeder/non-breeder), gender, and rearing type (hand/mother-reared), using a Mann-Whitney U-test [Siegel and Castellan, 1988]. In addition, the effect of age on breeding status and on component scores and possible facility differences in component scores were examined using the following statistics: Mann-Whitney U-test (age and breeding status), Spearman rank-order correlation coefficient (age and component scores), and Kruskal-Wallis test statistic (facilities and component scores) [Siegel and Castellan, 1988]. Statistical significance was assumed at the level of $P < 0.05$ for all tests. Statistical analysis, except PCA, were carried on the software programs SPSS (Version 6.1 for Macintosh) and StatViewSE&Graphics. PCA was performed using the program SYSTAT (version 5).

RESULTS

Observer/Keeper Questionnaire

For 15 of the 18 items, rater concordance coefficients ranged from W = 0.57 to 0.98 with *P*-values between 0.14 and <0.001 (Table 3). Three items, friendly to people, friendly to conspecifics, and solitary, were excluded from further analysis since rater concordance values on these items ranged from W = 0.16 to 0.48 with *P*-values of >0.2. Due to the small sample size of cheetahs rated at the Sacramento Zoo (n = 4), concordance values for this facility did not always reach statistical significance for the 15 retained items (Table 3). However, concordance values for the Sacramento Zoo were generally high (Table 3), and for the variables on which statistical signifi-

TABLE 3. Kendall coefficients of concordance (W) for three raters (keepers/observers) per facility on 15 questionnaire items measured on cheetahs at four North American zoological facilities

	Facility			
Item	Fossil Rim Wildlife Center (n = 17)	White Oak Conservation Center (n = 14)	Wildlife Safari (n = 9)	Sacramento Zoo (n = 4)
Active	0.67[a]	0.87[b]	0.79[a]	0.98[c]
Aggressive to conspecifics	0.72[a]	0.89[b]	0.85[a]	0.89[c]
Aggressive to people	0.73[a]	0.72[a]	0.86[a]	0.95[c]
Calm	0.64[c]	0.71[a]	0.65[c]	0.79
Curious	0.68[a]	0.60[a]	0.75[a]	0.81[c]
Eccentric	0.57[c]	0.62[c]	0.91[a]	0.98[c]
Excitable	0.67[a]	0.67[a]	0.78[a]	0.70
Fear of food	0.68[a]	0.80[a]	0.77[a]	0.60
Fearful of people	0.70[a]	0.77[a]	0.81[a]	0.90[c]
Insecure	0.72[a]	0.75[a]	0.87[a]	0.82[c]
Playful	0.77[a]	0.58[c]	0.60[c]	0.63
Self-assured	0.80[b]	0.67[c]	0.91[a]	0.70
Smart	0.76[a]	0.60[c]	0.75[a]	0.67
Tense	0.82[b]	0.66[c]	0.75[c]	0.69
Vocal	0.78[a]	0.70[a]	0.65[c]	0.93[c]

[a]$P < 0.01$; [b]$P < 0.001$; [c]$P < 0.05$.

cance was not reached, *P*-values ranged from 0.06 to 0.14. I therefore decided to include these scores in the further analysis.

PCA resulted in three components with eigenvalues >1, accounting for 69% of the observed variance (Table 4). These components were labeled according to the variables showing the highest positive loading: tense-fearful (component 1), vocal-excitable (component 2), aggressive (component 3). Component 1 showed high positive loadings on the following variables: tense, fear of conspecifics, fear of people, and insecure, and high negative loadings for self-assured, curious, and calm (Table 4). Individual cheetahs with high scores for this component were therefore regarded as more tense, fearful, insecure, and less self-assured, curious, and calm than individuals with low scores on this component. Component 2 had high positive loadings on the variables vocal, excitable, playful, active, smart, aggressive to people. The only negative loading shown for this component is the variable tense; however, this loading was very low (Table 4). Component 3 showed high positive loadings for the variables rating aggressiveness (aggressive to conspecifics and aggressive to people). Note that individuals with high scores on this last component had generally lower scores (see negative loadings) on fearfulness, playfulness, vocal behavior, and several other variables (Table 4).

Mirror-Image Stimulation

The repetition of the MIS experiment on eight cheetahs after 1 year showed very high reliability for the five behavioral measures recorded, with Spearman rank-order correlation coefficients ranging between 0.81 and 0.94 (all *P*-values < 0.05).

Several questionnaire items correlated significantly with the direct measures of behavior obtained during MIS (Table 5). Active correlated positively and significantly with

TABLE 4. Three major components of individual behavioral variation in captive cheetahs derived from combined score results of keeper/observer questionnaires on 44 adult cheetahs at four North American facilities obtained through principal component analysis

	Component		
Item	I	II	III
Active	–0.30	0.66[a]	0.47
Aggressive to conspecifics	–0.04	0.33	0.67[a]
Aggressive to people	0.19	0.59	0.60[a]
Calm	–0.59	0.26	–0.40
Curious	–0.60	0.41	–0.11
Eccentric	0.38	0.51	0.33
Excitable	0.51	0.74[a]	0.10
Fearful of conspecifics	0.83[a]	0.15	–0.13
Fearful of people	0.54	0.49	–0.38
Insecure	0.75[a]	0.07	–0.47
Playful	–0.01	0.69[a]	–0.41
Self-assured	–0.83	0.23	–0.15
Smart	–0.40	0.65[a]	–0.30
Tense	0.83[a]	–0.10	0.01
Vocal	0.02	0.82[a]	–0.27
Eigenvalues	4.304	3.838	2.041
Variance proportion	0.29	0.26	0.14

[a]Values, i.e., component loadings, ≥0.6.

all behaviors except approach time, which showed a low negative association (Table 5). This was interpreted to mean that individuals scoring higher on active were slightly faster to approach the mirror and showed higher overall activity during MIS than individuals with low scores on this questionnaire item. Aggressive (with conspecifics and people) showed a significant positive correlation with the number of agonistic vocalizations (growl/hiss) during MIS. The variable calm showed negative associations with all behaviors; however, only three of these correlations were significant: stare, growl/hiss, and approach time, indicating that individuals scoring high on calm approached the mirror faster but showed less overall activity on other behaviors. Curious was associated significantly and negatively only with approach time (i.e., shorter approach time for more curious individuals) and showed positive but low and non-significant relationships to other behavioral events. Excitable showed a low, but significant, positive correlation with the number of approaches and approach time. The items fear (of conspecifics and people), insecure, and tense, showed moderate to substantial, positive and significant correlations with approach time, indicating that animals which scored high on these items were slower to approach the mirror. The item self-assured correlated significantly and negatively with approach time indicating a faster approach when scoring high on self-assured. No correlations could be found between the items eccentric, playful, smart, vocal and any of the recorded behaviors (Table 5).

Comparison of Principal Component Scores with Respect to Breeding Status, Gender, and Rearing Type

Before testing for differences in component scores of breeders/non-breeders, males/females, and hand-reared/mother-reared individuals, possible confounding effects of age and facility were examined.

There was no significant effect of age on breeding status of both sexes with breeders showing an average age of $\bar{x} \pm SD = 7.04 \pm 2.74$ years (n = 25) and non-

TABLE 5. Spearman rank-order correlation coefficients between quantitative behavioral responses of cheetahs to their mirror image and scores obtained from keeper/observer questionnaires

	Responses to mirror				
Item	Number of approaches	Sniff	Stare	Growl/hiss	Approach time
Active	0.55[a]	0.35[b]	0.35[b]	0.61[a]	–0.25[b]
Aggressive to conspecifics	0.17	–0.07	–0.10	0.59[a]	–0.06
Aggressive to people	0.45[c]	0.10	0.32[b]	0.44[c]	0.24
Calm	–0.17	–0.23	–0.38[b]	–0.31[b]	–0.50[c]
Curious	0.22	0.29	0.20	0.08	–0.62[a]
Eccentric	0.18	0.05	<0.01	<0.01	0.13
Excitable	0.35[b]	0.03	0.30	0.23	0.33[b]
Fearful of conspecifics	0.24	0.13	0.24	–0.15	0.52[a]
Fearful of people	0.12	0.06	0.27[b]	–0.17	0.40[c]
Insecure	–0.21	–0.04	0.03	0.25[b]	0.37[b]
Playful	0.03	0.21	0.10	–0.18	–0.06
Self-assured	0.10	0.08	0.04	0.15	–0.50[c]
Smart	–0.01	–0.14	–0.01	–0.11	0.03
Tense	0.09	0.17	0.24	0.15	0.53[a]
Vocal	0.15	–0.15	–0.02	–0.18	0.03

[a]$P < 0.001$; [b]$P < 0.05$; [c]$P < 0.01$, two-tailed.

breeders of $\bar{x} \pm SD = 6.03 \pm 3.05$ years (n = 19) (U = 175.5, $P = 0.14$). No significant correlation was found between age and component scores (component 1: $r_s = 0.008$, n = 44, $P = 0.97$; component 2: $r_s = -0.23$, n = 44, $P = 0.13$; component 3: $r_s = -0.16$, n = 44, $P = 0.29$). When scores were compared across all four facilities, no significant difference could be found (component 1: H = 7.06, df = 3, $P = 0.07$; component 2: H = 6.07, df = 3, $P = 0.12$; component 3: H = 1.85, df = 3, $P = 0.61$), indicating no substantial effect of age or facility on the observed variability of component scores.

Comparison of component scores of breeders versus non-breeders showed significant differences for the first component with non-breeders scoring significantly higher on the component tense-fearful than breeders (Table 6). Furthermore, a significant difference was detected in component scores of males and females for the first component, with females showing generally higher scores on the component tense-fearful than males (Table 6).

The significant difference in component scores of breeders and non-breeders held up even when female (breeders: $\bar{x} \pm SD = -0.09 \pm 0.73$, n = 13; non-breeders: $\bar{x} \pm SD = 0.92 \pm 1.0$, n = 12; U = 34, $P = 0.017$) and male scores (breeders: $\bar{x} \pm SD = -0.85 \pm 0.60$, n = 12; non-breeders: $\bar{x} \pm SD = 0.05 \pm 0.64$; U = 16, $P = 0.028$) were examined separately. However, no significant differences in component scores of breeders/non-breeders and males/females were found for components 2 and 3 (Table 6).

There was also no significant difference in component scores between hand-reared and mother-reared individuals for any of the components; however, the sample size for examining this factor was small (n = 6 for hand-reared individuals) and scores on the components tense-fearful and aggressive were generally lower in hand-reared individuals than in mother-reared ones (Table 6).

DISCUSSION

Observer/keeper ratings of individual cheetahs appear to provide a valid method for assessment of individual distinctiveness in behavior. Inter-rater agreement was high for most items at each facility. Several direct behavioral measures obtained through MIS correlated significantly with appropriate questionnaire items. Although several of these correlations were relatively low, it needs to be noted that the questionnaire was not designed to replicate easily quantifiable behavioral measures but

TABLE 6. Mean and standard deviation of component scores of individual cheetahs grouped by breeding status, gender, and rearing type

	Component		
Item	I	II	III
Breeder (n = 25)	$\bar{x} = -0.46 \pm 0.07$	$\bar{x} = -0.14 \pm 0.99$	$\bar{x} = 0.01 \pm 0.62$
Non-breeder (n = 19)	$\bar{x} = 0.60 \pm 0.97$	$\bar{x} = 0.18 \pm 1.01$	$\bar{x} = -0.02 \pm 1.37$
Mann-Whitney test	U = 93, $P < 0.001$[a]	U = 183, $P = 0.20$	U = 224, $P = 0.75$
Females (n = 25)	$\bar{x} = 0.40 \pm 1.00$	$\bar{x} = 0.07 \pm 1.12$	$\bar{x} = -0.05 \pm 1.08$
Males (n = 19)	$\bar{x} = -0.52 \pm 0.75$	$\bar{x} = -0.09 \pm 0.83$	$\bar{x} = 0.06 \pm 0.91$
Mann-Whitney test	U = 111, $P = 0.003$[b]	U = 204, $P = 0.43$	U = 230, $P = 0.86$
Mother-reared (n = 38)	$\bar{x} = 0.03 \pm 1.30$	$\bar{x} = -0.01 \pm 1.02$	$\bar{x} = 0.06 \pm 0.86$
Hand-reared (n = 6)	$\bar{x} = -0.18 \pm 0.84$	$\bar{x} = 0.08 \pm 0.93$	$\bar{x} = -0.36 \pm 1.71$
Mann-Whitney test	U = 106, $P = 0.78$	U = 103, $P = 0.71$	U = 85, $P = 0.32$

[a]$P < 0.001$; [b]$P < 0.01$, two-tailed.

rather to include a variety of attributes that escape conventional measurement [Stevenson-Hinde et al., 1980a]. Questionnaire ratings and MIS responses are therefore of a different nature, with questionnaire items generally presenting compound measures based on a complex process of filtering and accumulating a variety of information over a relatively long time [Block, 1977], and MIS responses consisting of a much shorter list of specific actions and measures. For these reasons, it is difficult to identify one or two directly measurable behavioral events that could be expected to correlate strongly with the selected questionnaire items. Some of the items were not comparable to any of the behavioral events measured during MIS (e.g., playful, eccentric).

Several studies on a variety of species (e.g., rhesus monkeys, *Macaca mulatta* [Stevenson-Hinde and Zunz 1978; Bolig et al., 1992]; spotted hyenas, *Crocuta crocuta* [Gosling, 1998]; brown bears, *Ursus arctos* [Fagen and Fagen, 1996]; domestic cats, *Felis catus* [Feaver et al., 1986]; dairy goats, *Capra* sp [Lyons, 1989]; and black rhinos, *Diceros bicornis* [Carlstead et al., 1999a,b]) also attest to the validity of observer ratings. Reliability, i.e., consistency, of ratings on individual distinctiveness over time has been shown in some of these studies [Stevenson-Hinde et al., 1980a,b]. Although not directly examined in this study, the high repeatability of MIS results may reflect consistency of individual variation of cheetah behavior over time.

PCA analysis of questionnaire ratings obtained for individual cheetahs yielded three major components: tense-fearful, vocal-excitable, and aggressive. Other studies employing a factor analytic approach to examine individual behavioral variation in different animal species and in humans have frequently resulted in anywhere from two to four major components (or factors), which may be a reflection of underlying patterns within the observed variability [Chamove et al., 1972; Eysenck, 1976, 1978; Stevenson-Hinde and Zunz, 1978; Feaver et al., 1986; Zuckerman et al., 1991; Gold and Maple, 1994; Forkman et al., 1995]. Demonstrated consistency of such patterns in inter-individual behavioral variability over time and environmental changes may indicate the existence of basic individual differences in temperament, reflecting contrasting personal histories and perhaps underlying genetic and physiological differences [Boissy, 1995]. For example, developmental studies on domestic cats revealed that individual behavioral variation can be evident at birth and persist over time [Moelk, 1979; Karsh, 1984; Turner et al., 1986]. Studies on pigs, *Sus scrofa* [Hemsworth et al., 1990; Hessing et al., 1993]; dogs, *Canis familiaris* [Goddard and Beilharz, 1983]; rats, *Rattus* sp [Broadhurst, 1975]; and humans [Kagan, 1976; Sigvardsson et al., 1987; Loehlin, 1989] showed similar results and implied moderate to high heritability for some basic behavioral traits [Plomin, 1990].

The three components derived for cheetahs in this study appear to be equivalent to personality dimensions reported for other species (e.g., humans [Eysenck and Eysenck, 1969; Zuckerman et al., 1991; Cloninger et al., 1993]; gorillas, *Gorilla gorilla* [Gold and Maple, 1994]; rhesus monkeys [Stevenson-Hinde and Zunz, 1978]; spotted hyenas [Gosling, 1998]; domestic cats [Feaver et al., 1986; Meier and Turner, 1985]; dogs [Goddard and Beilharz, 1984]; pigs [Forkman et al., 1995]; and octopus, *Octopus rubescens* [Mather and Anderson, 1993]); in particular, tense-fearful and vocal-excited seem to have clear equivalents in all these studies. The third component aggressive in cheetahs appears similar to components labeled as dominant or social in other species since these components also appear to measure aggressiveness toward conspecifics in other studies [Gold and Maple, 1994; Forkman et al., 1995].

Considerable evidence indicates that individual behavioral characteristics are linked to differential physiological and neuroendocrine responses [Gray, 1971; Eysenck, 1980; Raleigh et al., 1989; Boissy, 1995]. Major dimensions underlying variation in temperament may therefore be associated with identifiable neurophysiological variables [Eysenck, 1980]. In particular, one dimension, or component, of individual behavioral variation has been examined in considerable depth with regard to its physiological correlates: measures of fear and fearfulness have received increasing attention in the study of laboratory and domestic animals [reviewed by Boissy, 1995]. Chronic states of anxiety have been found to correlate negatively with milk production, growth rate, egg production, and disease resistance, and may negatively affect reproductive performance in laboratory and farm animals [Gray, 1971; Hemsworth et al., 1990; Vandenheede and Bouissou, 1993; Boissy, 1995]. The findings on cheetahs in this study are therefore interesting, since non-breeders were found to score significantly higher on tense-fearful than breeders.

Female cheetahs scored higher on tense-fearful than males. Gender differences in fear reactions have been reported for a variety of other species. Although several studies on rodents showed higher rates of fear response in males than females [reviewed by Gray, 1971], studies on dogs [Goddard and Beilharz, 1983] and primates, e.g., chimpanzees, *Pan troglodytes* [Buirski et al., 1978], found females to be more fearful than males. Buirski et al. [1978] maintained that the need for females to protect offspring and show higher levels of watchfulness may account for such differences. Female cheetahs raise their cubs alone and spend about 17 months to get cubs to independence [Laurenson et al., 1992]. Since lion predation has been found to account for 64% of cheetah cub mortality during the first 3 months of life in the Serengeti [Laurenson et al., 1992], high levels of fearfulness for females may be an important adaptive trait, particularly in an open habitat and where lion density is high.

Although early rearing experiences, among other factors, most likely play an important role in shaping an individual's tendencies to be anxious, fearful, or tense, this study did not find a significant difference in scores of tense-fearful for hand-reared versus mother-reared individuals. However, the sample size of hand-reared individuals in this study was small (n = 6), and it is worth noting that scores on the components tense-fearful and aggressive, obtained from hand-reared cheetahs, were generally lower than those of mother-reared individuals. A study on domestic cats found that human-reared females were less likely to copulate successfully and were more aggressive than mother-reared females [Mellen, 1992]. Profound effects of early rearing conditions on subsequent adult behavior were reported for a variety of other species (e.g., rhesus monkeys and chimpanzees [Mason et al., 1968; Rogers and Davenport, 1969; Walsh et al., 1982]; dogs [Fox and Stelzner, 1966]; domestic cats [Guyot et al., 1980]; silver foxes, *Vulpes vulpes* [Pederson, 1993]; rabbits, *Oryctolagus cuniculus* [Kerstner et al., 1989]; and rats [Levine et al., 1967]). It has been suggested that individuals reared in a socially deficient environment may be less able to cope with novel or otherwise stressful situations such as mate introductions and caring for young [Carlstead and Shepherdson, 1994]. Interestingly, another study conducted on several exotic felid species housed at different zoological facilities found a significant and positive relationship between the reproductive success of cats and the time keepers spent interacting with their animals [Mellen, 1991]. Based on these findings,

it was suggested that, since humans, particularly keepers, play an important role in the daily routine of captive-held species, animals should learn to be comfortable with the inevitable presence of their human caretakers. The development of a relaxed and comfortable keeper-animal relationship should, however, not be equated with a hands-on policy or an endorsement for hand-rearing; rather it intends to minimize the stress of captivity by acquainting animals with human presence while at the same time promoting an enriched environment to facilitate normal behavioral development [Mellen, 1991]. The results from the current study on cheetahs also indicate that hand-reared individuals may be more relaxed in their captive environment than mother-reared individuals given their lower scores on the components tense-fearful and aggressive. Although these results are not statistically significant and the sample size is small, the observed trend suggests that a more detailed investigation of differences in early experience and differences in handling and rearing style would be of interest.

This study showed that behavioral assessment may allow us to predict an individual's ability to reproduce in the captive environment. For example, individuals with high scores on the component tense-fearful may have more difficulty coping with the captive environment than individuals with lower scores on this component. Such individuals may therefore require more secluded enclosures and provision of ample hiding places. However, to identify specific recommendations further studies are necessary.

In combination with newly developed, non-invasive steroid monitoring techniques involving fecal, urine, and saliva steroid assays developed to assess ovarian function [for reviews of fecal and urinary steroid monitoring for a variety of species, see Lasley and Kirkpatrick, 1991; Brown and Wildt, 1997; for fecal steroid assays to monitor ovarian function in cheetahs, see Brown et al., 1994, 1996; Czekala et al., 1994; Graham et al., 1995; for salivary steroid evaluation, see Sufi et al., 1985 and stress level, i.e., monitoring urinary cortisol levels in non-domestic felids, see Carlstead et al., 1992; for fecal corticoid monitoring in the domestic cat, see Graham and Brown, 1996; and recently in the cheetah, see Jurke et al., 1997; Terio et al., in press], behavioral assessments can be used to identify stressors associated with husbandry practices and environmental conditions. In short, assessment of individual behavioral variation may offer a new approach to analyzing breeding problems of captive endangered species by focusing on the individual as well as on the species.

CONCLUSIONS

1. Keeper/observer questionnaires appear to provide a valid method for assessing individual behavioral variation in cheetahs.

2. Keeper/observer ratings on several of the chosen adjectives correlated significantly with appropriate direct behavioral measures obtained during MIS.

3. Principal component analysis of the ratings resulted in three major components labeled tense-fearful, excitable-vocal, and aggressive and accounted for 69 % of the observed variation.

4. Females scored significantly higher than males, and non-breeders scored significantly higher than breeders on the component tense-fearful.

5. Keeper/observer questionnaires in combination with direct behavioral obser-

vations can provide a useful tool for investigating breeding problems and behavioral idiosyncrasies in captive-held species.

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