BEHAVIORAL, SPATIAL USE, AND SOCIAL PROXIMITY ANALYSES OF A CAPTIVE GROUP OF MANDRILLS AT THE TULSA ZOO

By

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER II

CHAPTER III

CHAPTER IV

CHAPTER I
INTRODUCTION

This thesis consists of three separate manuscripts written in the format for Zoo Biology. Each of the following chapters is complete in and of itself. Chapter II discusses the behavioral aspect of my research on the mandrills at the Tulsa Zoo. Chapter III is an analysis of the spatial use of the Tulsa Zoo exhibit by the mandrills, and Chapter IV investigates the social proximity of the captive mandrills.

CHAPTER II

BEHAVIORAL ANALYSIS OF THREE DIFFERENT GROUP COMPOSITIONS OF MANDRILLS AT THE TULSA ZOO.

The social behavior of three different group compositions of captive mandrills (Mandrillus sphinx) was assessed at the Tulsa Zoo in Tulsa, Oklahoma. From November 1995 to August 1996, many changes occurred in the mandrill group resulting from the removal of animals and a reintroduction of two females. Group composition 1 was a multi-male group, while group compositions 2 and 3 were uni-male groups, differing only in the number of females. Data were collected using all occurrence and instantaneous sampling on a focal animal. For instantaneous sampling, focals were observed for 10 min intervals with behavioral data being recorded every 30 sec. Behaviors were grouped into the following categories: Agonistic, Sexual, Affiliative, Active Nonsocial, and Inactive Nonsocial. Chi-square tests on the behavior categories indicated that individuals differed in their frequencies of behavior depending on the group composition ($p < 0.001$). Dominance hierarchies were constructed for each group composition using the frequencies of agonistic behaviors between each dyad. Matrilines were ranked in many cases due to the infrequent agonistic behaviors among kin. The all occurrence rates of agonistic and affiliative behavior for the different group compositions were found to be not significantly different using the Kruskal-Wallis test. The multi-male group (group composition 1) did not differ from the uni-male groups (group compositions 2 and 3). The different number of females in group compositions 2 and 3 also had no significant effect on the agonistic or affiliative rate. Group composition changes, resulting from the removal of the dominant male and the reintroduction of the two females, altered the dominance hierarchy significantly.

Key words: agonism, dominance hierarchy, Mandrillus sphinx, primate

INTRODUCTION

The mandrill (Mandrillus sphinx), a member of the Old-World monkeys subfamily Cercopithecinae, is found in the rainforests of equatorial west Africa, with Gabon containing perhaps the largest portion of the remaining mandrills [Feistner et al., 1992]. Since mandrills are elusive and their environment densely forested, it is difficult to study them in the wild [Norris, 1988; Wickings and Dixson, 1992]. Since studies in the wild are so difficult, captive studies of mandrills are of great benefit and supplement the data obtained in the wild [Mellen et al., 1981].

The mandrills at the Tulsa Zoo have been studied previously for their reproductive characteristics, such as age of first swelling and conception, and gestation length [Bettinger et al., 1995], and behavior [Hartley et al., 1996; Terdal, 1996]. Many changes occurred in the composition and size of the mandrill group at the Tulsa Zoo, which resulted in a continuation of the research on this group. Behavior was observed, and comparisons of the behaviors in the different group compositions were made. The effects of changing group composition and group size on the behavior of the mandrills can be valuable information for zoos in determining the best means of housing this species.

King and Mitchell (1987) suggested that the best way to house mandrills in zoos was in a single male, multi-female condition. Multiple males in a group were thought to increase aggression (Crandall, 1964). The ability to house multiple males in a group is important for zoos, since available space is a constant problem. Determining whether increased agonism is the result of the number of males or females is valuable information. A greater understanding of the species may also be gained through such a study.

The small group size (an average of 4) of zoo mandrills limits the value of extending results to wild mandrills. Abnormal behavior is common in most zoos [Feistner, 1990], which also limits the application of results to the management of wild mandrills. The captive mandrills at the Tulsa Zoo, in Tulsa, Oklahoma, are excellent subjects, especially because the group is larger than at most zoos.

METHODS

Group Composition

During the course of the study, group composition changed three times due to removals and reintroductions. Life history data on each mandrill is given in Table 1. Individuals were classified as adult at the age of 5 years, and juvenile when younger. No infants were present in this study. All mandrills belonged to one of three matrilines (Figure 1) and all were born at the Tulsa Zoo, except for the three matriarchs. AFA1 came from Dallas Zoo, TX. AFD1 from Reid Park Zoo, AZ, and AFP1 from Brookfield Zoo, IL. Table 2 includes a description of the events leading to the various changes in group composition.

Individuals were given an id for the purposes of this analysis (see Appendix) which included information on the age, sex, matriline, and the age of the animal within the matriline. Each id consisted of three letters followed by a number, an example was AFD1 for Darla. The A designated an adult animal (J if the animal was a juvenile), the F for female (M for male), D indicated the Darla matriline (other matrilines include Annie-A and

Pearl-P), and the 1 showed that this individual was the oldest of the matriline (Offspring began at 2 with oldest offspring receiving the lowest number).

Exhibit Design

The mandrills were housed in a grotto-style exhibit that faced east, and were locked outside whenever the temperature was above 18.3 °C and locked in when it was less than 4.4 °C. Between 4.4-18.3 °C the animals were given access to the den. Wind chill, moisture, and other weather conditions prompted occasional departure from these guidelines. The exhibit was surrounded by a dry moat on three sides, and logs were placed on the exhibit. The mandrills had free access to the 6.7 m deep moat. The outside exhibit was 50 x 16.6 m with a back wall measuring 6.7 m high. The inside of the grotto consisted of four 3.3 x 6.7 m dens and the off-exhibit, outdoor area was 5 x 4 m. The grotto consisted of various levels some of which were concrete while others had dirt or grass. Most of the levels were 15 cm higher or lower than the others, while the levels in the southwest corner were 2.4 m high at the highest point and were covered by an overhang from the grotto wall.

Method of Observation and Analysis

The mandrills at the Tulsa Zoo, Tulsa, Oklahoma, were observed between November 1995 and August 1996. Instantaneous sampling was used to observe an individual for 10 min., recording the behavior of the focal animal at 30 sec intervals. An ethogram was altered from a previous study designed by T. Bettinger in 1993 at the Tulsa Zoo (see Appendix). Behaviors were also grouped into categories, such as Agonistic.

Affiliative, Sexual, Active Nonsocial, and Inactive Nonsocial. All occurrence agonistic, affiliative, and sexual behaviors were also recorded throughout the 10 min. observation period on a focal animal. The order of observing each mandrill was chosen at random before data collection began. There were differing amounts of observation time for each group composition which were accounted for in the analysis. Group composition 1 was observed for 12.5 hrs., group composition 2 for 46.8 hrs, and group composition 3 for 119.8 hrs. Within a group composition, individuals were observed for an approximately equal amount of time.

Data were entered into PcFile, and Windows SAS was used in the analyses of this study. The frequencies of the different behavior groupings, such as Agonistic, Affiliative, Sexual, Active Nonsocial, and Inactive Nonsocial were calculated. The frequencies of behaviors were compared for all of the individuals across the group compositions using chi-square.

The all occurrence rates of agonistic and affiliative behaviors were calculated for each group composition. The variances of the different group compositions were found to be significant using Levene's test for agonistic but not for affiliative behaviors (affiliative $F=0.44$, $p=0.6471$; agonistic $F=3.43$, $p=0.0472$). Because of the unequal variances between group compositions for agonistic behavior, the Kruskal-Wallis test was used to compare the rates of agonistic and affiliative behavior for the three group compositions.

Dominance hierarchies were constructed by calculating the frequency of wins and losses between each pair of individuals in each group composition. The agonistic behaviors recorded from the instantaneous scan sampling and all occurrence observations were used in this analysis. Due to the infrequent occurrence of these behaviors between mother and offspring and between siblings, the resulting dominance hierarchies only ranked matrilines.

RESULTS

Chi-square Analyses on the Behavior of Individuals Across the Group Compositions

Using the behavior categories, Active Nonsocial, Affiliative, Inactive Nonsocial, and Other, the comparisons of each individual across the different group compositions indicated significant differences in rates of behavior ($p<0.001$). The category "other" included the low frequency behavior categories, sexual and agonistic. Individuals present in only one group composition were not used in this analysis. Depending on the group composition, individuals were found to alter their behavior frequencies.

Dominance Hierarchies

Hierarchies were constructed using agonistic behaviors. Ranking individuals was difficult due to the lack of these behaviors among kin. In these cases, the matrilineal rank order was given by indicating the mother of each group of individuals. The female dominance matrix for group 1 (Figure 2) resulted in the matrilineal hierarchy: D (Darla), A (Annie), P (Pearl). The placement of AFA1 was uncertain in the hierarchy due to the lack of agonistic behaviors between this female and several other females. The male dominance hierarchy for group composition 1 was AMD2, AMP2, AMD4, and JMA4 (Figure 3). The female dominance matrix for group composition 2 resulted in the following matrilineal order: A (Annie), P (Pearl), and D (Darla) (Figure 4). Group composition 3 females were ranked in the overall matrilineal order of A (Annie), P (Pearl), and D (Darla) (AFD3 was omitted from the matrix) (Figure 5). Numerous reversals were found in the overall dominance matrix which indicates that the dominance hierarchy was not stable over time. For this reason, the hierarchy was determined on a weekly basis (AFD3 was present during weeks 1 and 2) (Table 3). Most of the hierarchy changes were among the lower-ranking females, with the alpha and beta female (JFA3 and AFA2) remaining fairly consistent.

Observations on All Occurrence Agonistic Behavior Across the Different Group Compositions

The average, all occurrence, agonistic rate for the three group compositions were 16.2, 13.3, and 15.1 respectively. In group composition 1 (Figure 6), the highest rates of agonistic behavior were displayed by the related dominant male and female, AMD2 and AFD1, and a related subordinate male AMD4. AMD4, a relative of the dominant male, received the highest rate of agonistic behavior, unlike AMP2, an older male, who initiated the aggressive behavior the majority of the time. JFA3 and JFP3, two subordinate females, only received agonistic behavior. In group composition 2, the dominant male and female, AMP2 and JFA3, showed the highest rates of agonistic behavior (Figure 7). Subordinate females, AFD5, AFD1 and JFP3 received high rates of agonistic behaviors. In group composition 3, the highest agonistic rate was displayed by the dominant female, JFA3. Subordinate females, JFP3, AFD5, JFD6, and AFD1 received the most aggression of any group members. Due to the removal of AFD3, a reintroduced female, early during the observation time for this group composition, her agonistic rate may not be accurate (Figure 8).

Observations on Affiliative Behavior Across the Different Group Compositions

The average, all occurrence, affiliative rates for the three group compositions were 13.8, 15.5, and 16.5 respectively. Group composition 1 individuals AMD4 and JFA3, a subordinate male and female, displayed the highest affiliative rates. The dominant female, AFD1, and JFA3 received the highest amount of affiliative behavior. JMA4 and AMD4, a sub-adult and adult male, frequently were observed playing. Older males, AMD2 and AMP2, spent less time engaging in affiliative behavior than females, and the males were found to display rather than receive this behavior (Figure 9). Dominant individuals JFA3 and AMP2 had the highest affiliative rates in group composition 2. JFA3, AFA2 (Beta female), and AFD1 (low-ranking female) received the highest rates of affiliative behavior (Figure 10). JFD6, a reintroduced female, had the highest affiliative rate given and received in group composition 3. Due to the removal of AFD3, another reintroduced female, early during the observation time for this group composition, her affiliative rate may not be representative (Figure 11).

Sexual Behavior Rates For Each Group Composition

The average, all occurrence rates for sexual behavior for each group composition were 0.6, 1.0, and 0.8, respectively.

Comparison of the Different Group Compositions for their Rates of Agonistic and Affiliative Behavior

The all occurrence rates for each individual were calculated and the different group compositions were compared using the Kruskal-Wallis test. The affiliative and agonistic rates were found to be not significant across all group compositions (affiliative p=0.6337; agonistic p=0.6665). The different group compositions did not differ in their affiliative and agonistic rates.

Effects of Reintroduction of Two Females on Affiliative and Agonistic Behaviors

The changes on a weekly basis in the agonistic and affiliative rates after the reintroduction of the two females were presented in Figure 12. Week 1 was part of the "Howdy" period, when the alpha male was reintroduced to the two females, AFD3 and JFD6, after the two females had been "Howdied" to the group by allowing visual, olfactory, and auditory access to the two females in the den. During weeks 2 and 3, group composition 3 individuals were present, including AFD3 and JFD6. Weeks 4-11 one of the reintroduced females, AFD3, was removed from the group. The agonistic rate increased after all individuals were placed together, until the removal of AFD3 in week 4. After this time, agonism slowly decreased as the dominance hierarchy was reestablished. The affiliative rate fluctuated as the dominance hierarchy stabilized.

DISCUSSION

Dominance Hierarchies

Dominance, or social rank of an animal, determines the resources the animal can attain, including mates, food, and grooming partners. Dominance hierarchies become increasingly unstable as the groups become larger [Dunbar, 1988]. For some baboon females, status is at least partially inherited, while males must win their status [Hausfater, 1975; Altmann, 1980]. A female mandrill's rank changes during estrus as the female gains the attention of the alpha male. The social stability of a group may fluctuate due to changes in group size, age of individuals, or by death of important individuals [Colmenares and Gomendio, 1988; Mason, 1993]. The death of the old alpha male at Tulsa Zoo resulted in high agonistic levels for two years, with changes in both the male and female hierarchies [Hartley, 1996].

The ranking of kin was difficult due to the lack of agonistic behaviors between related individuals. For this reason, matrilines were ranked instead. In primates, mothers may rank above daughters or daughters may rank above mothers depending on the species. In Japanese macaques, it was found that offspring ranked in reverse order of their ages at least till adolescence, and mothers usually outranked their offspring [Kawamura, 1958; Kawai, 1965; Koyama, 1967; Sade, 1967; Missakian, 1972]. Adult daughters, with the youngest being highest ranked, could outrank their mothers in langurs, geladas, baboons, and howler monkeys [Hrdy and Hrdy, 1976; Dunbar, 1980; Jones, 1980; Sigg, 1980; Hausfater et al., 1982]. No literature was found to indicate which occurs in mandrills, but presents an interesting future study.

Matrilines may be ranked in large groupings of macaques [Kawamura, 1958; Kawai, 1965; Koyama, 1967]. Females, especially, have been found to come to the aid of their relatives, forming alliances so that grouping individuals in matrilines is appropriate [Marsden, 1968; Kaplan, 1977; Massey, 1977; Kaplan, 1978]. Matriline rank in macaques was found to be dependent upon the power of the dominant member in small groups, with the matriline size being unimportant [Dunbar, 1980; Fa, 1986]. In large groups of macaques, matriline size was found to influence matriline rank [Mori, 1975; Sade et al., 1976]. Larger matrilines in general have been found to be dominant over smaller matrilines [Silk and Boyd, 1983].

Altering the group composition affected the dominance hierarchy. The removal of the dominant male was the main cause of the differing hierarchies between group composition 1 and 2. With the removal of the dominant male AMD2, the D (Darla) matriline did not remain dominant under the new alpha male, AMP2. Perhaps surprising is the fact that the P (Pearl) matriline, to which the new alpha male belonged, did not rise to the alpha position. Instead, the A (Annie) matriline, the largest matriline, gained the alpha female position. The reintroduction of the two females in group composition 3 also destabilized the female hierarchy. AFD3 attempted to gain the alpha position which resulted in her serious injury. With the removal of AFD3, the other reintroduced female, JFD6, settled into a low-ranking position with her matriline.

Linear hierarchies are rare in wild populations of primates, but triangular relationships, reversals and "central hierarchies" are common [Gartlan, 1968]. Forest-living primates have less well-defined dominance hierarchies and rare dominance interactions compared to primates living in open areas [Jouventin, 1975]. Gartlan (1968) stated that the presence of more pronounced and rigid hierarchies and higher levels of aggression in captivity, negates the belief that dominance hierarchies reduce aggression. Captivity increased the social interactions of the primates and the level of stress, leaving the individuals little means of escape from social interactions. Comparing a captive and wild baboon group, it was found that the captive baboons had a straight-line hierarchy [Rowell, 1966], while wild baboons had no obvious hierarchy.

Observations on Agonistic Behavior

The surprising difference in the agonistic frequency between the two males in group composition 1 may be the result of AMD4 remaining within the group to give and receive agonistic behavior, while AMP2, on the other hand, remained in the periphery of the group thus reducing the opportunity for aggressive interactions.

Since the agonistic rates for the group compositions were not significantly different, it cannot be said that the number of males in the group caused increased rates of aggression. The number of females in the uni-male groups also did not cause a significant difference in the rates of aggression. Future studies are needed to prove that the number of males or females does not affect the rate of agonistic behavior.

Aggression is more frequent in captive mandrills than wild mandrills [Rowell, 1967; Gartlan, 1968]. Females and matriline composition were found to play an important role in a group's agonistic interactions in a previous captive study at the Tulsa Zoo. Twelve years of daily keeper reports were analyzed to evaluate determine any causes of aggression. It was determined that the number of adults present in the group best accounted for any changes in aggression. Both males and females were found to participate equally in agonistic interactions. All matrilines were also found to have roughly equal, overall rates of agonistic behavior, although the DL matriline, with twice as many members, initiated 2-3 more aggressive bouts, and received twice as many submissive behaviors [Hartley et al., 1996].

Reintroducing the two females was found to increase the amount of contact aggression, leading to the serious injury of one of the reintroduced females as she quarreled with the existing alpha female. Feistner et al. (1992) advised that the males of each captive group should be replaced every 3 years to prevent inbreeding. This suggestion may be warranted but must be balanced against the risk that introducing new individuals to the group may result in increased aggression, altered hierarchies, and serious injuries.

Observations on Affiliative Behavior

Affiliative behavior was displayed by the males more often than it was received. This higher rate of displayed behavior was not due to the amount of grooming since males were not found to groom other males or any females. All grooming was directed toward the males from females.

The different group compositions did not differ in their rates of affiliative behavior. The number of males or females in the group did not significantly alter the rate of affiliative behavior.

Observations on Sexual Behavior

The highest average, all occurrence rate of sexual behavior was for group composition 2, when AMP2 became alpha male for the first time. The high rate may be the result of the new alpha male asserting his dominance over the females to strengthen his position. It could also be the result of his novel ability to copulate with females without the threat of a another more dominant male. The females may have developed genital swellings as a result of the novel alpha male. The presence of multiple males in a group may also reduce the ability of an alpha male to display this behavior. The alpha male in group composition 1 may have been too busy chasing the other males and maintaining his dominance to copulate with females. The lower rate of sexual behavior in group composition 1 was surprising due to the number of males who might engage in this behavior.

Differences in Behavior Depending on the Group Compositions

Individuals differed between group compositions in their frequencies of behavior, indicating that group composition changes may have an influence on the behavior of mandrills. These changes in the behavior displayed may be the result of individuals changing positions in the dominance hierarchies. Other possible causes of these differences may be group size, season or age of the individual.

CONCLUSIONS

1. Changing the group composition either by removing or reintroducing individuals was found to have a profound effect on the female dominance hierarchy. Altering the male hierarchy was found to alter the female hierarchy.

2. The number of adult males in a group composition did not have a significant effect on the rate of agonistic behavior.

3. Increasing the number of females also did not cause a significant increase in the rate of agonism.

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Table 1: Life History Data on Mandrills at the Tulsa Zoo.

ID	HOUSE NAME	SEX	BIRTH-DATE	AGE AT START STUDY (YRS.)	STUD BOOK #
AMD2	BOOMER	M	5/21/87	8	486
AMP2	SABRE	M	9/09/88	7	522
AMD4	L.C.	M	9/10/89	6	549
JMA4	LBM	M	7/09/93	2	828
AFA1	ANNIE	F	8/18/75	20	212
AFD1	DARLA	F	6/20/79	16	286
AFP1	PEARL	F	1/05/85	11	421
AFD3	IVY	F	7/19/88	6	518
AFD5	DARCY	F	10/05/90	5	585
AFA2	ANGIE	F	10/17/90	5	586
JFD6	PATIENCE	F	10/12/91	4	690
JFA3	PANDORA	F	2/10/92	4	691
JFP3	TAMMIE	F	4/28/92	4	692

Information taken from Tulsa Zoo records.

Table 2: Sequence of Events Leading to Group Composition Changes and the Individuals Comprising Each Group Composition.

Group Composition #	Dates	Group Members	Comments
1	11/19/95-12/19/95 12/18/95	3 adult males, 1 subadult male, 5 adult females, 2 subadult females	 Adult male, AMD4, removed after injuries
DATA NOT USED	12/20/95-4/9/96 2/23/96	1 adult male, 1 subadult male, 2 adult females, 1 subadult female	Split mandrills into 2 groups. Alpha male, AMD2, removed.
2	4/10/96-5/20/96	1 adult male, 1 subadult male, 5 adult females, 2 subadult females	2 groups reunited under a new alpha male, AMP2.
DATA NOT USED	5/21/96-5/28/96	1 adult male, 1 adult female, 1 subadult female	2 previously removed females, AFD3 and JFD6, reintroduced to alpha male
3	5/29/96-6/5/96 6/6/96-8/24/96	1 adult male, 1 subadult male, 6 adult females, 3 subadult females 1 adult male, 1 subadult male, 5 adult females, 3 subadult females	2 females reintroduced to the group. Reintroduced female, AFD3, suffered injuries and was removed from the group

Table 3: Weekly Changes in the Female Dominance Hierarchy for Group Composition 3.

RANK	WEEK 1	WEEK 2	WEEK 3	WEEK 4	WEEK 5	WEEK 6	WEEK 7	WEEK 8	WEEK 9	OVER-ALL
1	JFA3	JFA3	JFA3	JFA3	JFA3	JFA3	JFA3	JFA3/ AFA2	JFA3/ AFA2	JFA3
2	AFD3	AFA1/ AFA2	AFA2	AFA2	AFA2	AFA2	AFA2	JFA3/ AFA2	JFA3/ AFA2	AFA2
3	JFD6	AFA1/ AGA2	AFA1	AFA1	AFA1	AFA1	AFA1	AFA1/ AFP1	AFA1	AFA1
4	AFA2	AFP1/ JFP3	AFP1	AFP1	AFP1/ JFP3	AFP1	AFP1/ JFP3	AFA1/ AFP1	AFP1/ JFP3	AFP1
5	AFA1	AFP1/ JFP3	JFP3	AFD1	AFP1/ JFP3	JFP3/ JFD6	AFP1/ JFP3	JFP3/ AFP1	AFP1/ JFP3	JFP3
6	AFP1/ JFP3	AFD1/ AFD3/ AFD5/ JFD6	AFD1/ AFD5/ JFD6	JFP3	AFD1/ AFD5/ JFD6	JFP3/ JFD6/ AFD1/ AFD5	AFD1/ JFD6	AFD1/ AFD5/ JFD6	AFD5/ JFD6	AFD1/ AFD5/ JFD6
7	AFP1/ JFP3/ AFD5	AFD1/ AFD3/ AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD1/ JFD6	AFD1/ AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD1/ AFD5/ JFD6
8	AFD1/ AFD5/ AFP1	AFD1/ AFD3/ AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD1/ AFD5/ JFD6	AFD5	AFD1/ AFD5/ JFD6	AFD1/ AFD5	AFD1/ AFD5/ JFD6
9	AFD1/ AFD5	AFD1/ AFD3/ AFD5/ JFD6								

Figure 1: Three Matrilines of the Tulsa Zoo Mandrills Listed by Age (Mothers at the top) Along With the ID Used During the Study for Each Animal.

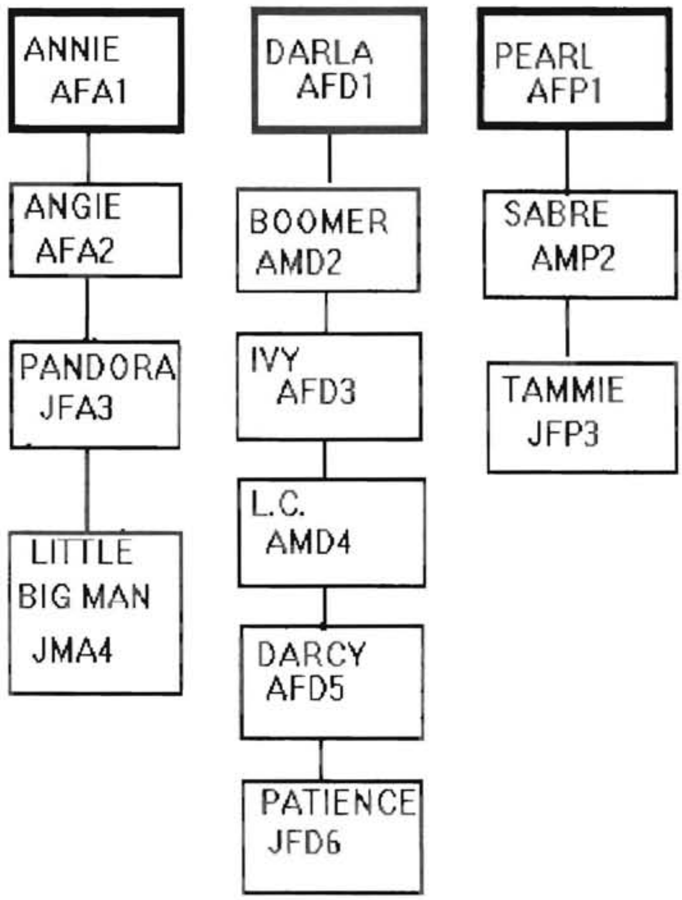

ANNIE AFA1
ANGIE AFA2
PANDORA JFA3
LITTLE BIG MAN JMA4
DARLA AFD1
BOOMER AMD2
IVY AFD3
L.C. AMD4
DARCY AFD5
PATIENCE JFD6
PEARL AFP1
SABRE AMP2
TAMMIE JFP3

Figure 2: Dominance Matrix for the Females in Group Composition 1.

WINNER

LOSER	AFD1	AFD5	JFA3	AFA2	AFA1	AFP1	JFP3
AFD1	-----------	0	0	0	0	0	0
AFD5	0	-----------	0	0	0	0	0
JFA3	4	4	-----------	0	0	0	0
AFA2	11	1	1	-----------	0	0	0
AFA1	2	3	0	0	-----------	0	0
AFP1	8	8	1	7	0	-----------	0
JFP3	2	1	0	2	6	1	-----------

Figure 3: Dominance Matrix for the Males in Group Composition 1.

WINNER

LOSER	AMD2	AMP2	AMD4	JMA4
AMD2	-------------------	0	0	0
AMP2	5	-------------------	2	0
AMD4	35	7	-------------------	0
JMA4	1	0	2	-------------------

Figure 4: Dominance Matrix for the Females in Group Composition 2.

WINNER

LOSER	JFA3	AFA2	AFA1	AFP1	JFP3	AFD1	AFD5
JFA3	-----------	0	0	0	0	0	0
AFA2	13	-----------	0	2	0	0	0
AFA1	11	22	-----------	0	0	0	0
AFP1	9	27	12	-----------	1	0	0
JFP3	12	33	34	2	-----------	0	0
AFD1	18	9	17	5	17	-----------	0
AFD5	16	18	28	13	24	1	-----------

Figure 5: Dominance Matrix for the Females in Group Composition 3.

WINNER

LOSER	JFA3	AFA2	AFA1	AFP1	JFP3	JFD6	AFD1	AFD5
JFA3	---------	0	0	0	0	1	0	0
AFA2	46	---------	0	9	4	1	1	1
AFA1	21	58	---------	6	0	0	0	0
AFP1	16	37	48	---------	0	0	0	1
JFP3	96	67	42	2	---------	1	0	0
JFD6	58	22	60	51	49	---------	0	0
AFD1	40	14	14	45	15	6	---------	0
AFD5	14	31	16	44	31	2	1	---------

Figure 6: All Occurrence Rates of Agonistic Behavior Given and Received for the Individuals in Group Composition 1.

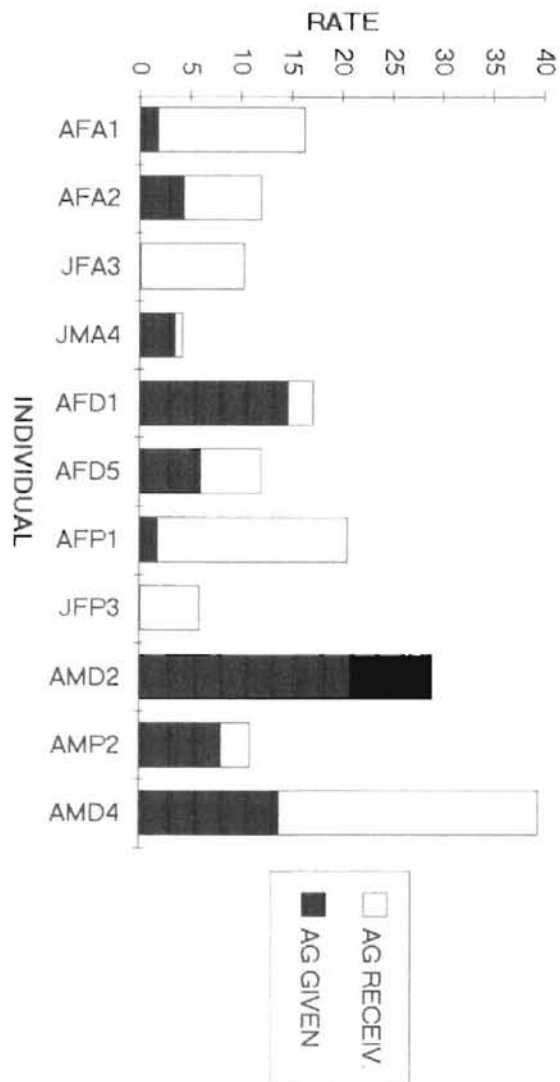
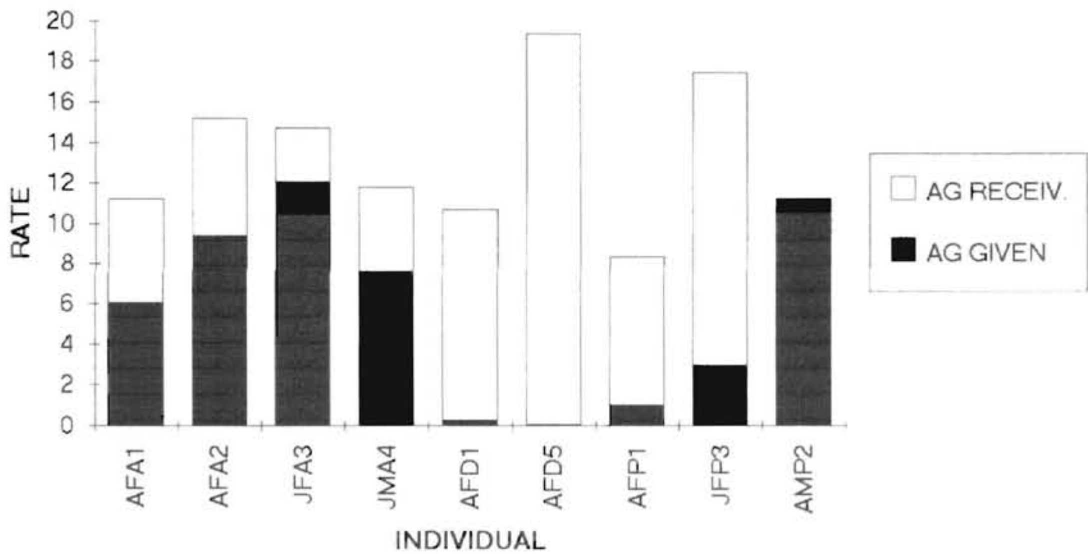

RATE
0
5
10
15
20
25
30
35
40
INDIVIDUAL
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMD2
AMP2
AMD4
AG RECEIV.
AG GIVEN

Figure 7: All Occurrence Rates of Agonistic Behavior Given and Received for the Individuals in Group Composition 2.



RATE
20
18
16
14
12
10
8
6
4
2
0
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMP2
INDIVIDUAL
AG RECEIV.
AG GIVEN

Figure 8: All Occurrence Rates of Agonistic Behavior Given and Received for the Individuals in Group Composition 3.

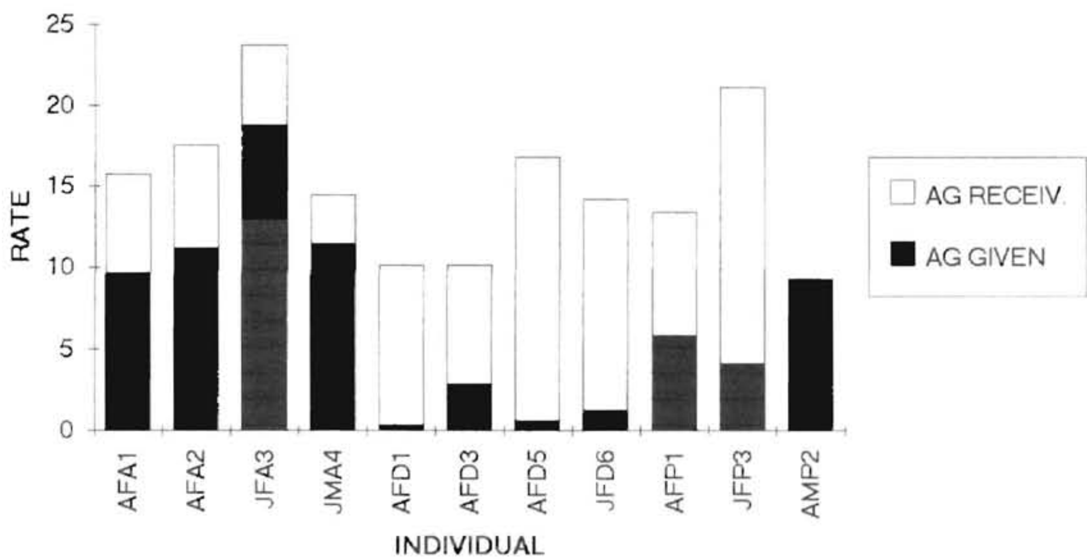

25
20
15
10
5
0
RATE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD3
AFD5
JFD6
AFP1
JFP3
AMP2
INDIVIDUAL
AG RECEIV.
AG GIVEN

Figure 9: All Occurrence Rates of Affiliative Behavior Given and Received for the Individuals in Group Composition 1.

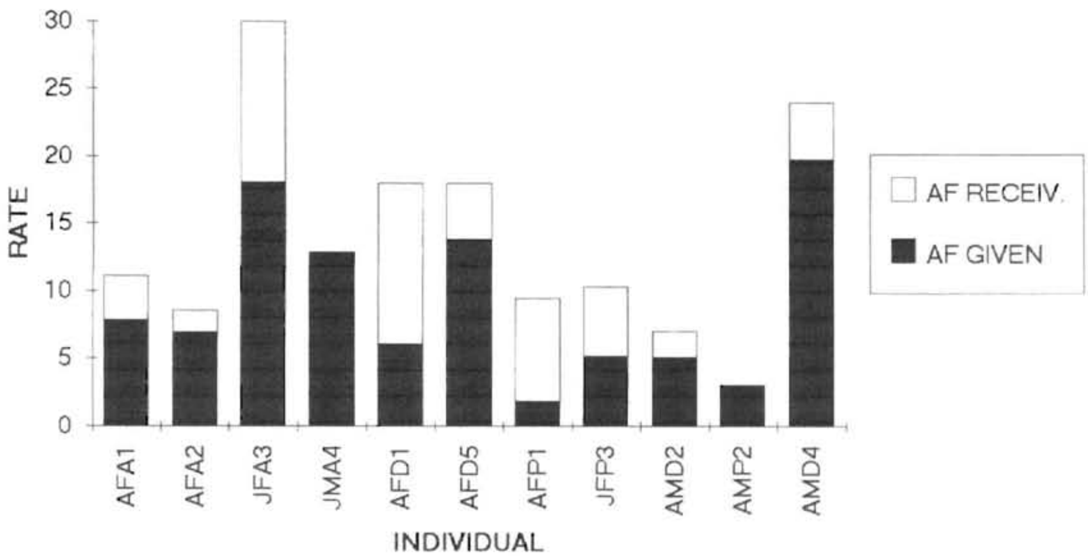

30
25
20
15
10
5
0
RATE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMD2
AMP2
AMD4
INDIVIDUAL
AF RECEIV.
AF GIVEN

Figure 10: All Occurrence Rates of Affiliative Behavior Given and Received for the Individuals in Group Composition 2.

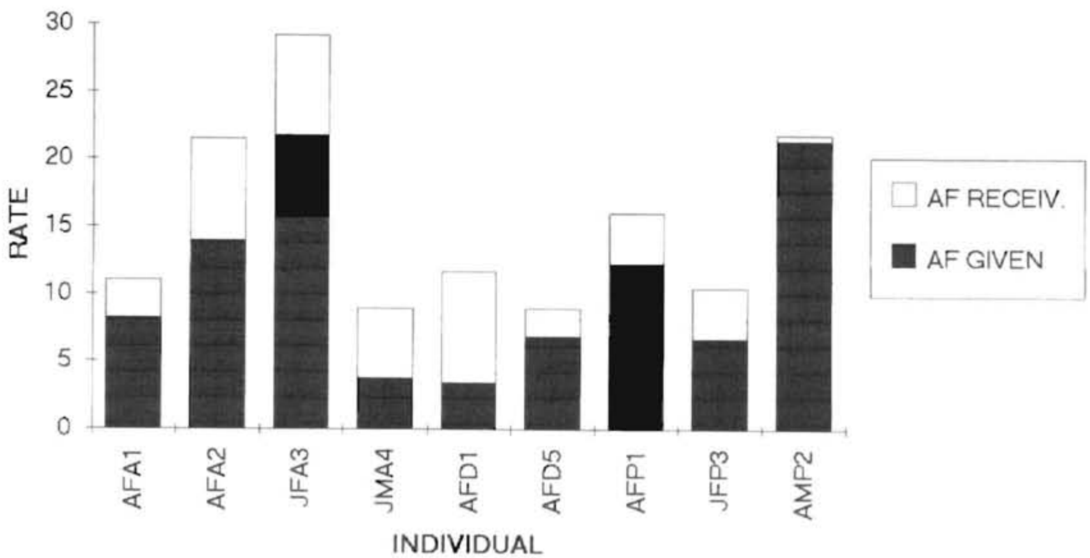

30
25
20
15
10
5
0
RATE
AF RECEIV.
AF GIVEN
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMP2
INDIVIDUAL

Figure 11: All Occurrence Rates of Affiliative Behavior Given and Received for the Individuals in Group Composition 3.

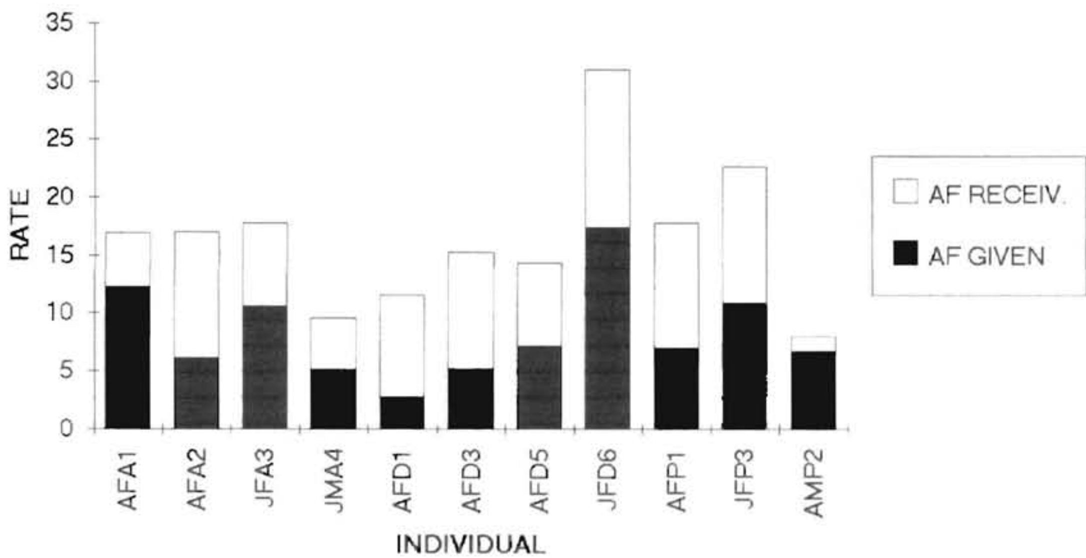
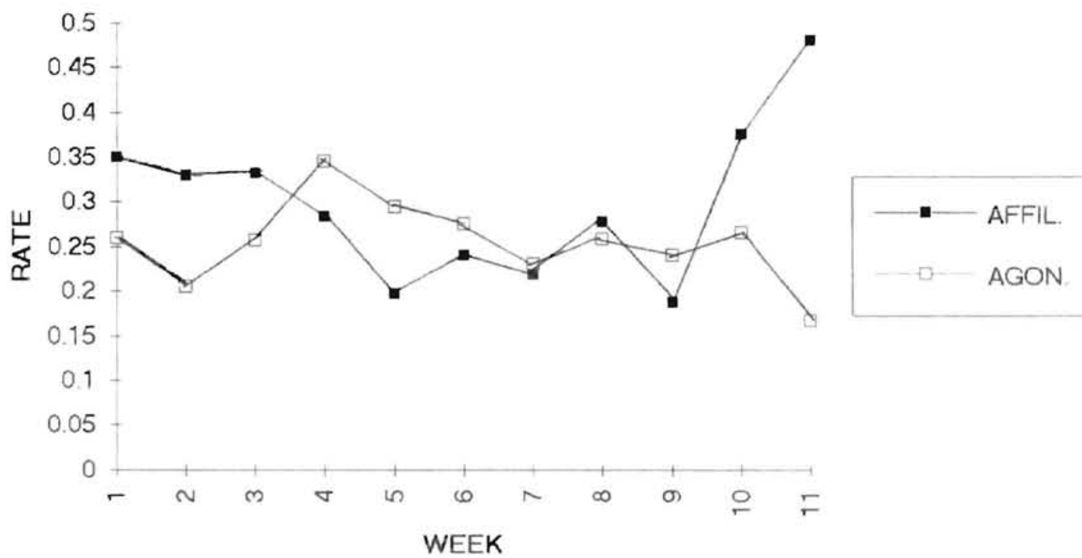

35
30
25
20
15
10
5
0
RATE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD3
AFD5
JFD6
AFP1
JFP3
AMP2
INDIVIDUAL
AF RECEIV.
AF GIVEN

Figure 12: Change in the Rates of Agonistic and Affiliative Behavior Over Time Following the Reintroduction of the Two Females, AFD3 and JFD6. (Week 1 alpha male with two females; Weeks 2 and 3 AFD3 present; Weeks 4-11 AFD3 removed)



0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
RATE
1
2
3
4
5
6
7
8
9
10
11
WEEK
AFFIL.
AGON.

CHAPTER III

SPATIAL USE ANALYSIS OF THREE DIFFERENT GROUP COMPOSITIONS OF MANDRILLS AT THE TULSA ZOO

The spatial use of the exhibit by mandrills, (Mandrillus sphinx), at the Tulsa Zoo, Tulsa, Oklahoma, was analyzed to determine if there were significant differences between individuals or for individuals across the three different group compositions (group composition 1--multi-male group, group compositions 2 and 3--uni-male groups), which resulted from removals and reintroductions. Instantaneous sampling was used to record spatial use data on three group compositions from November 1995 to August 1996. The exhibit was divided into levels (1, 2, 3, 4, moat) and quadrants (South to North--A, B, C, D, E, F), and for each observation, a level and quadrant was recorded. The frequencies were then analyzed using chi-square to determine any differences in spatial use by the mandrills. Individuals were found to differ from one another within a group composition in their spatial use and the mandrills were also found to alter their use of the exhibit depending on the group composition ($p < 0.001$). Dominance, age, and weather conditions affected exhibit use. Individuals tended to congregate in the southwest corner of the exhibit, especially during the summer. The dominant male used area A1 extensively; the location functioning as a "throne". The moat may have provided an escape route for individuals to avoid other more dominant individuals, reducing social tension. The improvement of zoo exhibits, creating more natural areas, may aid in decreasing aggression and increasing activity levels of captive mandrills.

Key words: Mandrillus sphinx, primate, location

INTRODUCTION

Mandrills (Mandrillus sphinx) inhabit the rainforests of equatorial west Africa, with Gabon containing perhaps the largest portion of remaining wild mandrills [Feistner et al., 1992]. In the wild, 80% of the day is spent foraging [Hall, 1965; Crook and Aldrich-Blake, 1968; Altmann and Altmann, 1970]. Foraging occurs throughout the day with 66.8% of the foraging occurring within 5 m of the ground despite the fact that half of their preferred food items were found greater than 5 m above the ground [Hoshino, 1985].

In a semi-free ranging group of mandrills in Gabon, it was determined that 67% of all behaviors were feeding, with 77% of all feedings (72% eating and 83% foraging) taking place on the ground. Feeding off the ground (23%) was divided into 10% in trees, 7% in vines, and 6% in saplings. Juveniles tended to remain in the understory while the adults foraged on the ground [Norris, 1988]. Females and young frequently used the canopy to feed, while the males spent most of their time on the ground [Napier and Napier, 1985]. To sleep or to escape, wild mandrills climb into the forest canopy [Hill, 1970].

Since mandrills are elusive and their environment so dense, it is difficult to study them in the wild [Norris, 1988; Wickings and Dixson, 1992]. However, mandrills have been studied in captivity, which is a great benefit and supplement to the data obtained in the wild [Mellen et al., 1981]. The mandrills at the Tulsa Zoo have been studied previously for their reproductive characteristics, such as age of first swelling and conception, and gestation length [Bettinger et al., 1995] and behavior [Hartley et al., 1996; Terdal, 1996]. Few spatial use studies have been done on captive mandrills. The captive mandrills at Tulsa Zoo, Tulsa, Oklahoma, are excellent subjects, because the group is unusually large and more closely approximates the natural group size [Terdal, 1996].

METHODS

Group Composition

During the course of the study, many changes occurred within the mandrill group. Group composition was altered three times due to removals and reintroductions. Life history data on each mandrill is given in Table 1. Individuals were classified as adult at the age of 5 years, and juvenile when younger. No infants were present in this study. All mandrills belonged to one of three matrilines (Figure 1). All mandrills were born at the Tulsa Zoo, except for the three matriarchs. AFA1 came from Dallas Zoo, TX, AFD1 from Reid Park Zoo, AZ, and AFP1 from Brookfield Zoo, IL. Table 2 includes a description of the events leading to the various group composition changes.

Individuals were given an id for the purposes of this analysis (see Appendix) which included information on the age, sex, matriline, and the age of the animal within the matriline. Each code consisted of three letters followed by a number, an example was AFD1 for Darla. The A designated an adult animal (J if the animal was a juvenile), the F for female(M for male), D indicated the Darla matriline (other matrilines include Annie-A and Pearl-P), and the 1 showed that this individual was the oldest of the matriline (Offspring began at 2 with oldest offspring receiving the lowest number).

Exhibit Design

The mandrills were housed in a grotto-style exhibit that faced east (Figure 2), and were locked outside whenever the temperature was above 18.3 °C and locked in when it was less than 4.4 °C. Between 4.4-18.3 °C the animals were given access to the den. Wind chill, moisture, and other weather conditions prompted occasional departure from these guidelines. The exhibit was surrounded by a dry moat on three sides, and logs were placed on the exhibit. The mandrills had free access to the 6.7 m deep moat. The outside exhibit was 50 x 16.6 m with a back wall measuring 6.7 m high. The inside of the grotto consisted of four 3.3 x 6.7 m dens and the off exhibit, outdoor area was 5 x 4 m. The grotto consisted of various levels some of which were concrete while others had dirt or grass. Most of the levels were 15 cm higher or lower than the others, while the levels in the southwest corner were 2.4 m high at the highest point and were covered by an overhang from the grotto wall.

Method of Data Collection and Analysis

The mandrills at the Tulsa Zoo, Tulsa, Oklahoma, were observed between November 1995 and August 1996. Instantaneous sampling was used to record the location of a focal animal at 30 sec intervals for 10 min. The exhibit was divided into quadrants and levels to record the exhibit use by the focal (Figure 2). Quadrants were from South to North (A, B, C, D, E, F), while the levels were from the highest to lowest points (1, 2, 3, 4, moat). For each observation, a quadrant and level was recorded. The order of the observing each mandrill was chosen at random before data collection began. There were differing amounts of observation time for each group composition which were accounted for in the analysis. Group composition 1 was observed for 12.5 hrs., group composition 2 for 46.8 hrs., and group composition 3 for 119.8 hrs. Within a group composition, individuals were observed for approximately equal amounts of time.

Data were entered into PcFile, and Windows SAS was used in the analyses of this study. From the instantaneous sampling data, the frequency for each individual at each location was calculated. The locations used in the statistical analyses included 1, 2, 3, 4, moat, and A, B, C, D, E, and F. The spatial use of the exhibit was compared among individuals in each group composition and for each individual across the group compositions using chi-square. The percentages use of the exhibit were calculated for each individual and the individuals were then compared for their use of the exhibit within a group composition and across the group compositions. The seasonal influence on exhibit use was analyzed for locations A, B, and C.

RESULTS

Chi-square analyses

Within a group composition, individuals were compared for their use of the exhibit. The use of locations 1, 2, 3, 4, and moat, as well as locations A, B, C, D, E, and F, was analyzed using chi-square. At least some individuals within each group composition were found to differ in their use of these locations ($p<0.001$ for all group compositions).

Individuals were also compared across group compositions for their use of the levels and quadrants. All individuals were found to differ in their use of the exhibit depending on the group composition ($p<0.001$).

Trends and Observations on the Use of the Exhibit by the Mandrills

The percentages of time individuals were recorded in the levels and quadrants were compared within group compositions and across the different group compositions (Figures 3-8). Individuals were arranged according to relation and decreasing age with adult males positioned on the right side of the graph. Females within a matriline differed from one another in their use of various locations. Because of the differences in spatial use between relatives, comparisons could only be made at the individual level.

The most extensively used level was 2, which had the largest area containing grassy areas for foraging (Figures 3-5). Level 1, in the southwest corner of the exhibit, was frequently occupied by dominant animals, especially the dominant male (Note AMP2 in group composition 2 and 3). AMD2, alpha male in group composition 1, did not use area 1 as extensively as the alpha male in group compositions 2 and 3. More individuals occupied level 1 in group compositions 2 and 3 (Figures 4-5) which were uni-male groups. The moat was used for foraging and to escape the aggression of more dominant animals. Younger individuals were more often observed in the moat.

The use of the quadrants was also compared within a group composition and across the group compositions (Figures 6-8). Dominant individuals tended to occupy quadrant A more than any other individuals. For group composition 1 (Figure 6), the dominant male AMD2 and female AFD1 had the highest uses of area A. AMP2 rarely occupied area A, but tended to remain in the periphery of the group. In group composition 2 (Figure 7), AMP2, now the alpha male, increased his use of area A. The highest use of area A by a female was AFP1, the mother of AMP2. However, this female was not alpha; the alpha position was occupied by JFA3. AFD1, now a low-ranking female, had one of the lowest percentages of use for this area. In group composition 3 (Figure 8), AFD1 and her relatives, all low-ranking females, used area A the least of all individuals.

The percentage use of location A increased across the group compositions for most individuals. Area A was used more than any other areas in group composition 3. This increased use of area A may have been due to changing weather conditions. Location A was the only area that provided sufficient shade at all times of the day. The more heavily used quadrants A, B, and C were graphed across the different seasons (Figure 9). Winter and spring each were represented by one month of data, but summer was represented by three different months. Only area A was found to differ significantly across the seasons, with June and July having the highest percentages of use.

DISCUSSION

Dominance, temperature, and age may influence the use of the exhibit by the mandrills. There was a tendency for individuals to prefer the areas near 1 and A. The preference for higher ground seemed to be apparent in the individuals' selection of locations. The dominant male occupied area A1, displacing and even chasing any individuals who tried to remain there.

The occupation of the southwest corner of the exhibit may be a sign of dominance for the mandrills. Location A1 resembled a "throne" for the dominant male. The moat was often used as an escape route by subordinate individuals. As the dominance hierarchy changed with removals and reintroductions, the use of the different areas of the exhibit also changed. The resulting shift in the use of the exhibit with a change in dominance could be seen in AFD1, who lowered her dominance status, and AMP2, who became alpha male in group composition 2.

The use of the moat as an escape route from aggression and other social tensions notes the artificiality of the zoo exhibit. In the wild, the mandrills escape notice of other individuals in the thick forest or by climbing a tree. A more naturalistic zoo exhibit with complex vertical and horizontal structure may decrease the agonistic behaviors seen in this group of mandrills.

Weather was an important influence on the percentage of time an animal spent at a certain location. The use of area A, the only location providing sufficient shading, increased across the group compositions due to the increasing temperatures.

Individuals used the exhibit differently from their relatives which was surprising. While observing the mandrills, it appeared that relatives tended to congregate together. The differences in age between mother and offspring may account for the differing percentages of exhibit use. Older individuals tended to be more inactive and remained at a certain location for long periods of time.

Other Studies

Dominance, weather, and age seem to have an influence on the locations chosen by the different individuals. Traylor-Holzer and Fritz (1985) working with captive chimpanzees (Pan troglodytes), found that dominance, affiliative, and antagonistic relationships along with the position of certain focal individuals such as estrous females and infants, may influence the spatial relationships in the group. Other primate studies also indicate that dominance has an influence on the locations chosen by individuals. In a captive group of lowland gorillas (Gorilla g. gorilla), a larger dominant individual occupied a certain area, leaving the remainder of the exhibit to the subordinates. A positive relationship was found between dominance rank and the frequent use of certain areas [Fischer and Nadler, 1977; 1978].

In general, captive primates were found to locate themselves near walls, perimeter edges and corners, and vertical objects. Resting took place more frequently on elevated structures than at ground level [Bernstein and Mason, 1963; Rosenblum et al., 1964; Menzel, 1967, 1969; Wilson, 1972; Hughes and Menzel, 1973]. The use of certain locations in free-ranging and captive primates may be related to better vantage points, escape routes, food and water resources, or sleeping sites [Wilson, 1972]. Peripheral areas may provide security or maximize distance between individuals [Traylor-Holzer and Fritz, 1985]. Escape areas, such as platforms or other visual barriers, reduce aggression and social stress [Kortlandt, 1966; van Hooff, 1967; Wilson and Wilson, 1969; van Hooff, 1973; Maple, 1978; Maple and Stine, 1982; Fritz and Nash, 1983].

CONCLUSIONS

1. Dominance appeared to influence exhibit use with the dominant male claiming an area or "throne", and chasing any individuals attempting to use the area. A change in dominance for an individual resulted in changes in exhibit use.

2. Weather had an influence in the spatial use of the exhibit with summer increasing the amount of time individuals spent in the shade (area A).

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Table 1: Life History Data on Mandrills at the Tulsa Zoo.

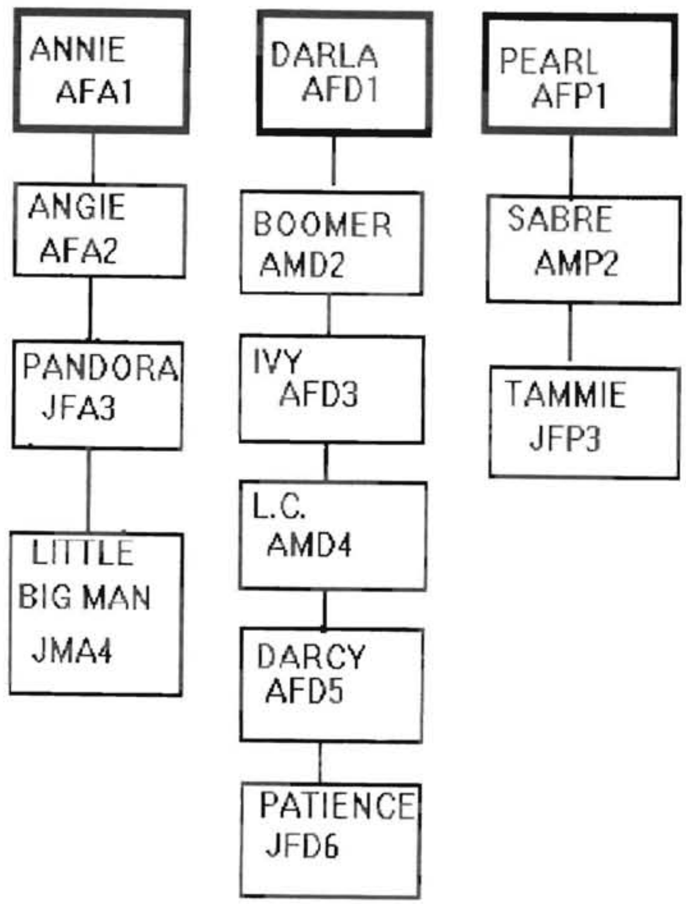
ID	HOUSE NAME	SEX	BIRTH-DATE	AGE AT START STUDY (YRS.)	STUD BOOK #
AMD2	BOOMER	M	5/21/87	8	486
AMP2	SABRE	M	9/09/88	7	522
AMD4	L.C.	M	9/10/89	6	549
JMA4	LBM	M	7/09/93	2	828
AFA1	ANNIE	F	8/18/75	20	212
AFD1	DARLA	F	6/20/79	16	286
AFP1	PEARL	F	1/05/85	11	421
AFD3	IVY	F	7/19/88	6	518
AFD5	DARCY	F	10/05/90	5	585
AFA2	ANGIE	F	10/17/90	5	586
JFD6	PATIENCE	F	10/12/91	4	690
JFA3	PANDORA	F	2/10/92	4	691
JFP3	TAMMIE	F	4/28/92	4	692

Information taken from Tulsa Zoo records.

Table 2: Sequence of Events Leading to Group Composition Changes and the Individuals Comprising Each Group Composition.

Group Composition #	Dates	Group Members	Comments
1	11/19/95-12/19/95 12/18/95	3 adult males, 1 subadult male, 5 adult females, 2 subadult females	 Adult male, AMD4, removed after injuries
DATA NOT USED	12/20/95-4/9/96 2/23/96	1 adult male, 1 subadult male, 2 adult females, 1 subadult female	Split mandrills into 2 groups. Alpha male, AMD2, removed.
2	4/10/96-5/20/96	1 adult male, 1 subadult male, 5 adult females, 2 subadult females	2 groups reunited under a new alpha male, AMP2.
DATA NOT USED	5/21/96-5/28/96	1 adult male, 1 adult female, 1 subadult female	2 previously removed females, AFD3 and JFD6, reintroduced to alpha male
3	5/29/96-6/5/96 6/6/96-8/24/96	1 adult male, 1 subadult male, 6 adult females, 3 subadult females 1 adult male, 1 subadult male, 5 adult females, 3 subadult females	2 females reintroduced to the group. Reintroduced female, AFD3, suffered injuries and was removed from the group

Figure 1: Three Matrilines of the Tulsa zoo Mandrills Listed by Age (Mothers at the top) Along With the ID Used During the Study for Each Animal.



ANNIE AFA1
ANGIE AFA2
PANDORA JFA3
LITTLE BIG MAN JMA4
DARLA AFD1
BOOMER AMD2
IVY AFD3
L.C. AMD4
DARCY AFD5
PATIENCE JFD6
PEARL AFP1
SABRE AMP2
TAMMIE JFP3

Figure 2: Exhibit Layout and Artificial Divisions Used in Analysis.

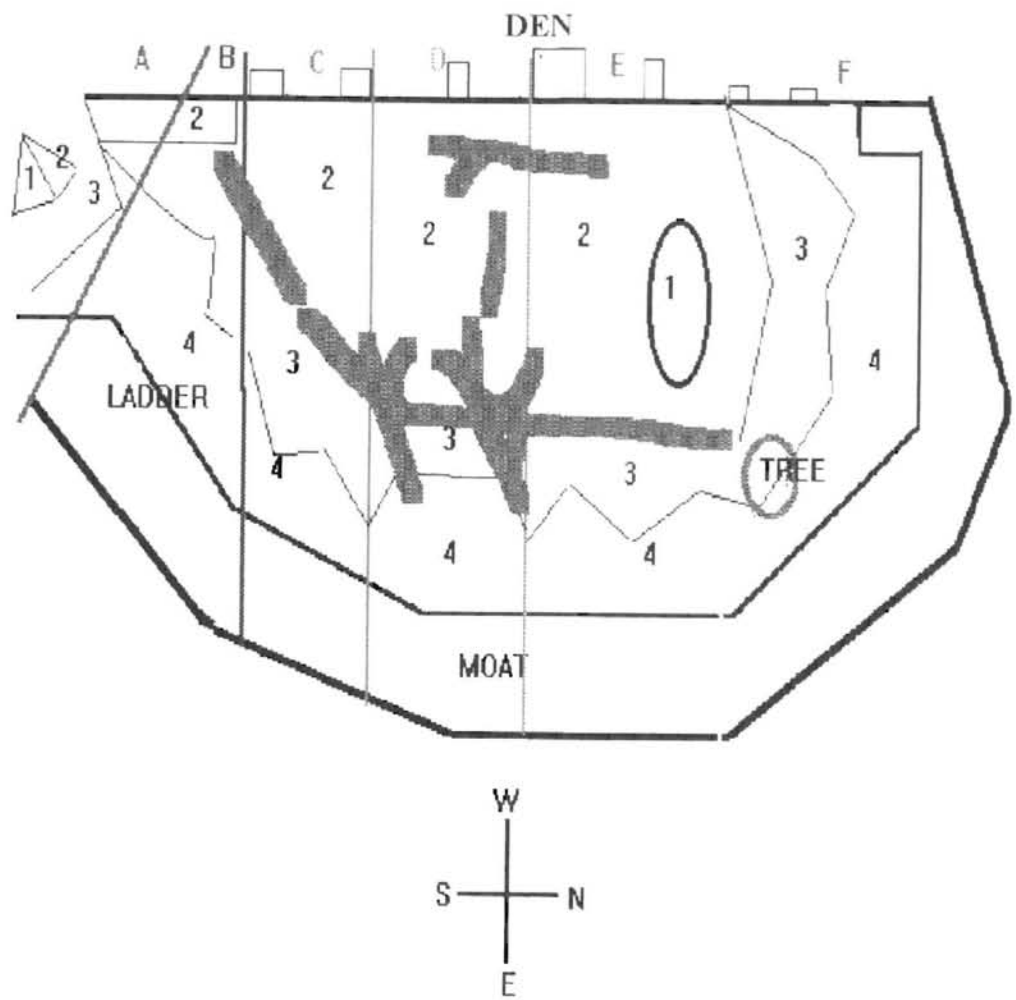

DEN
A
B
C
D
E
F
LADDER
MOAT
TREE
W
S
N
E

Figure 3: Group Composition 1 Percentages of Use for Locations 1, 2, 3, 4 and Moat.

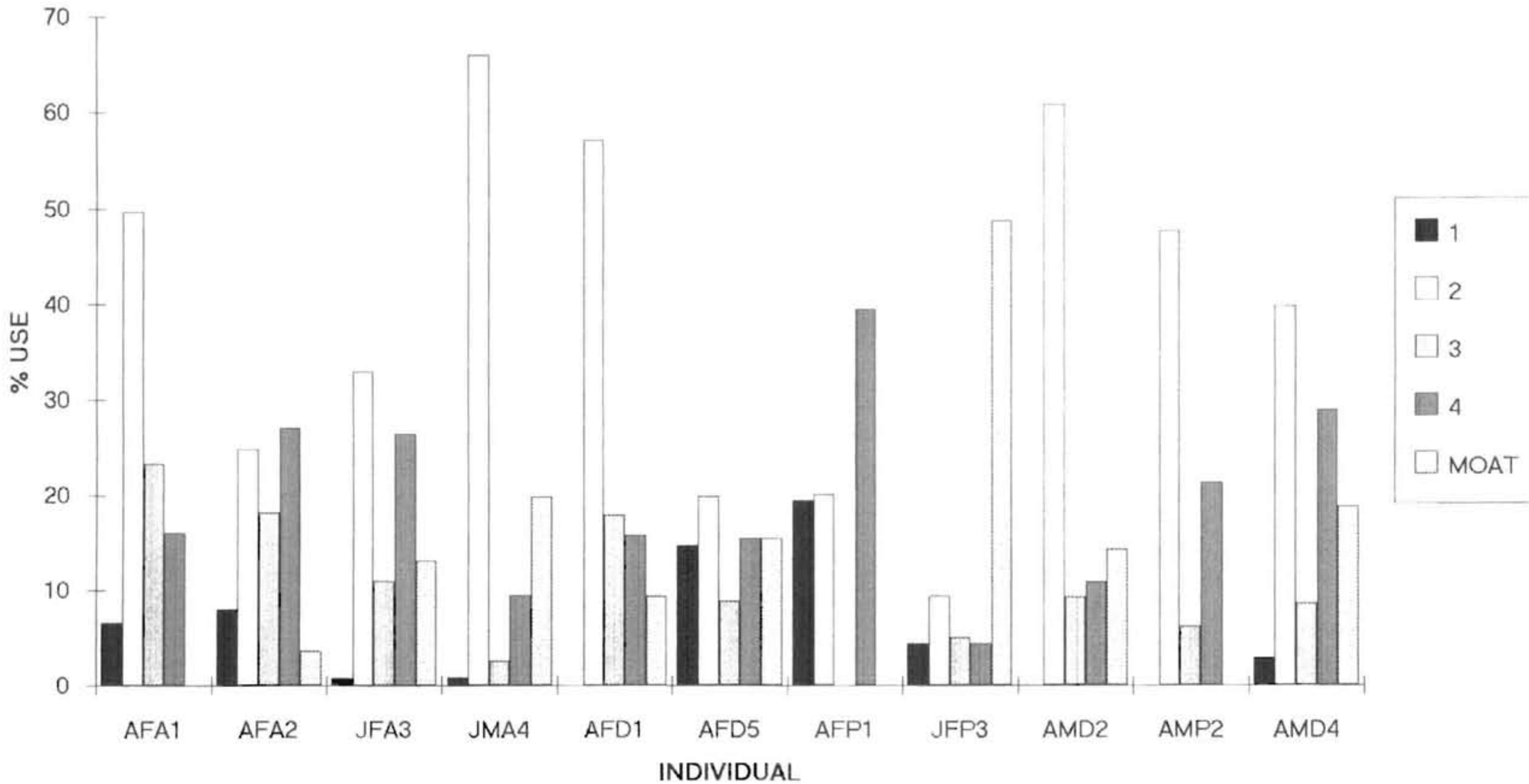
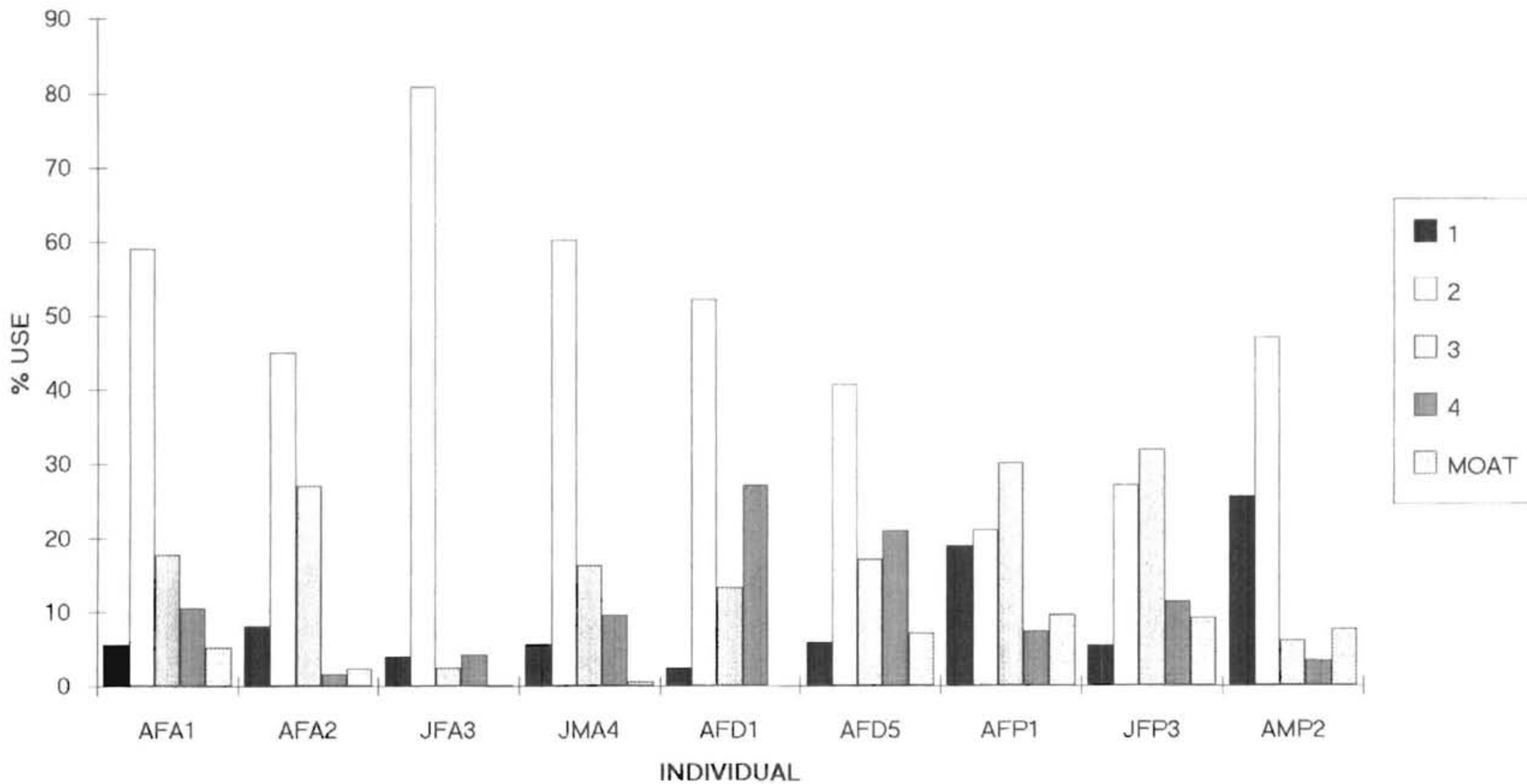
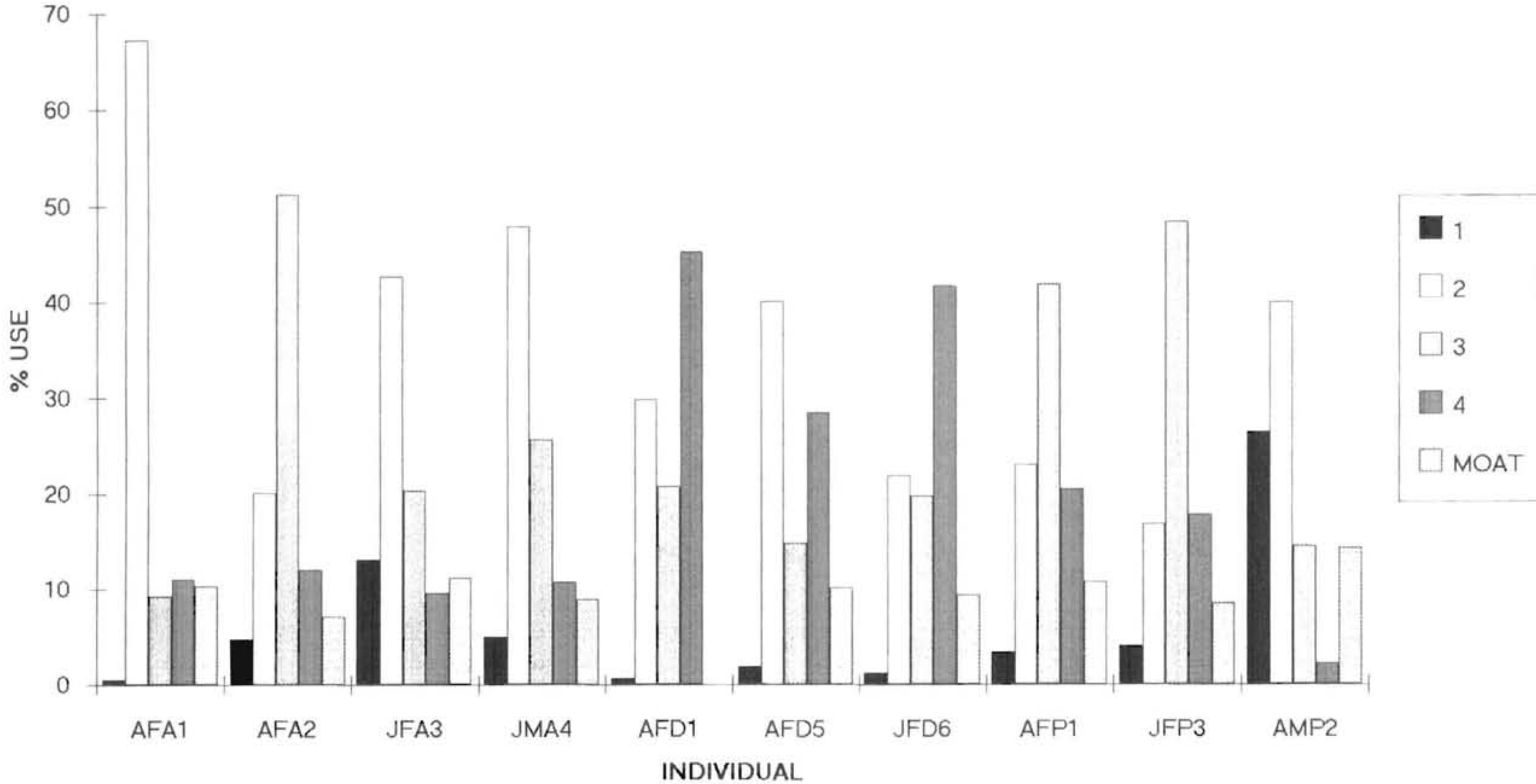

70
60
50
40
30
20
10
0
% USE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMD2
AMP2
AMD4
INDIVIDUAL
1
2
3
4
MOAT

Figure 4: Group Composition 2 Percentages of Use for Locations 1, 2, 3, 4 and Moat.



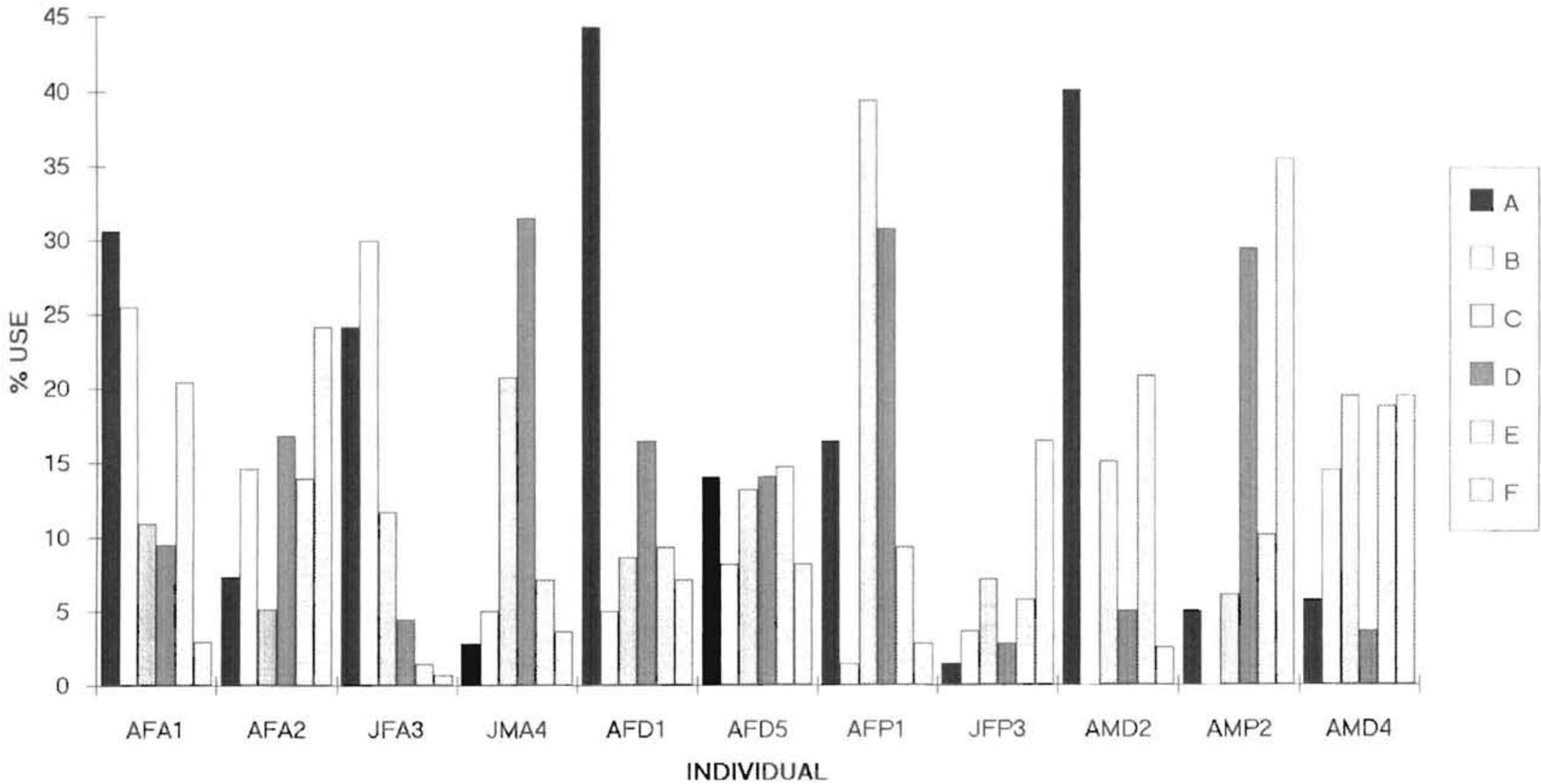
90
80
70
60
50
40
30
20
10
0
% USE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMP2
INDIVIDUAL
1
2
3
4
MOAT

Figure 5: Group Composition 3 Percentages of Use for Locations 1, 2, 3, 4 and Moat.



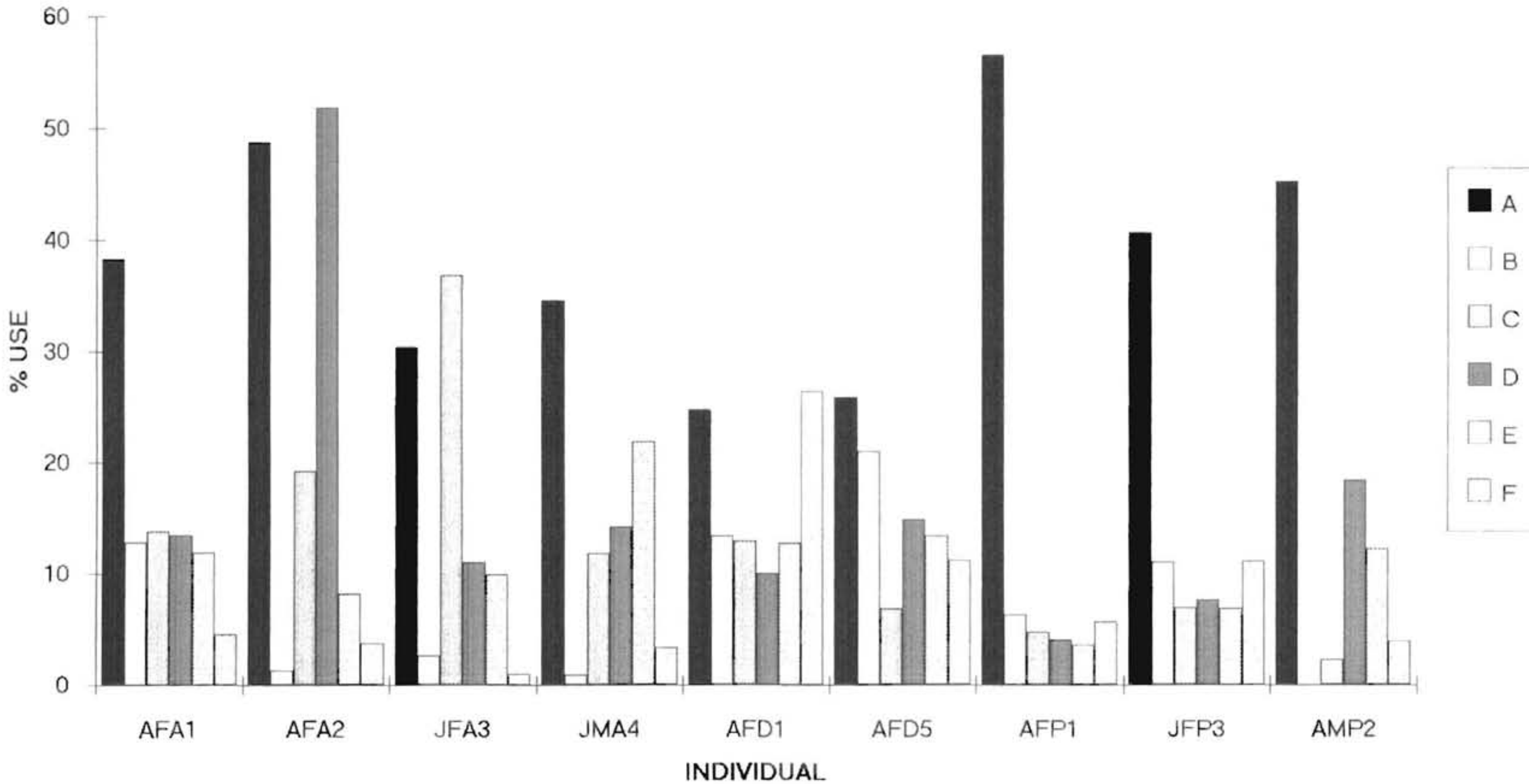
70
60
50
40
30
20
10
0
% USE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
JFD6
AFP1
JFP3
AMP2
INDIVIDUAL
1
2
3
4
MOAT

Figure 6: Group Composition 1 Percentages of Use for Locations A, B, C, D, E and F.



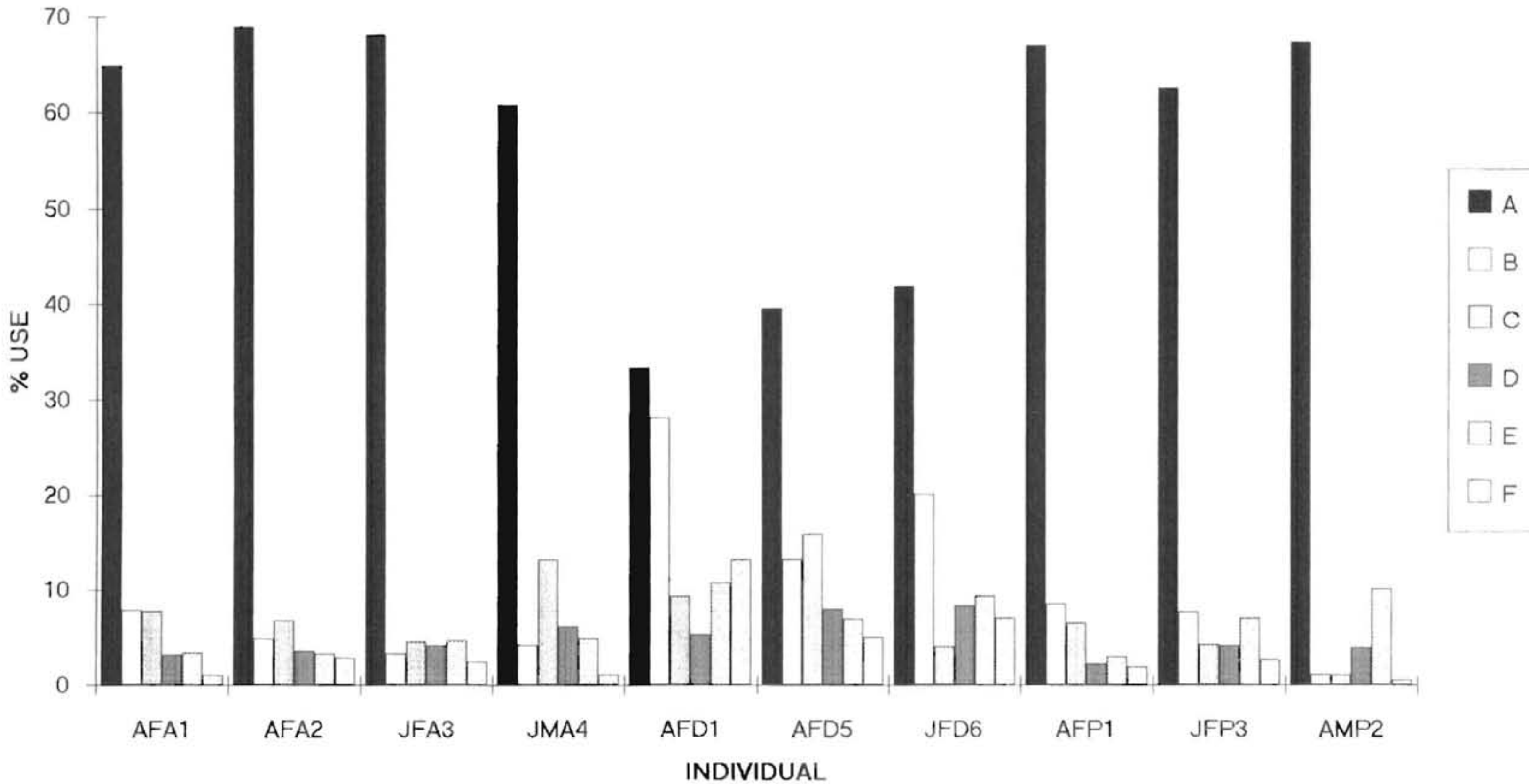
45
40
35
30
25
20
15
10
5
0
% USE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMD2
AMP2
AMD4
INDIVIDUAL
A
B
C
D
E
F

Figure 7: Group Composition 2 Percentages of Use for Locations A, B, C, D, E and F.



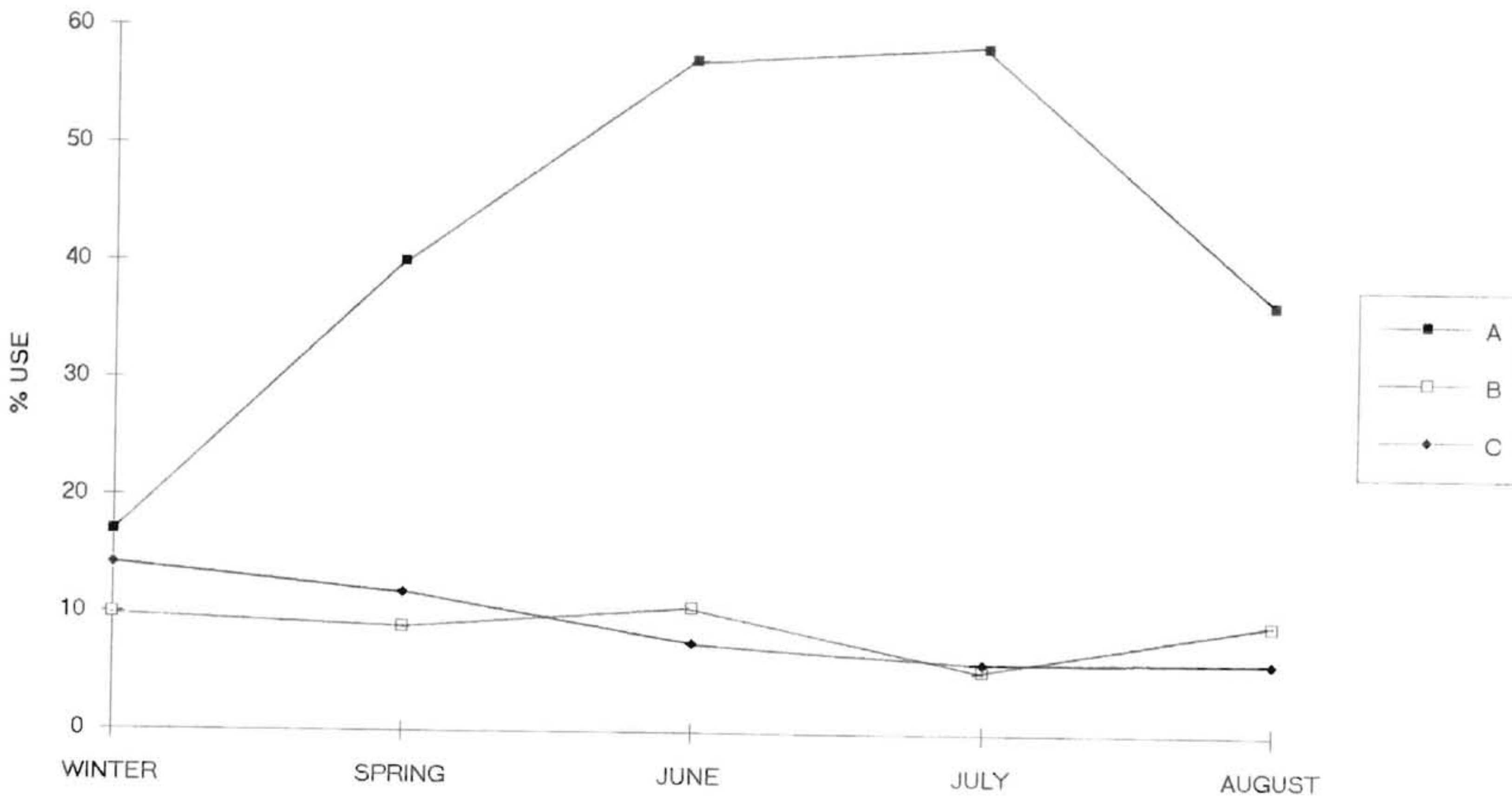
60
50
40
30
20
10
0
% USE
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMP2
INDIVIDUAL
A
B
C
D
E
F

Figure 8: Group Composition 3 Percentages of Use for Locations A, B, C, D, E and F.



70
60
50
40
30
20
10
0
% USE
A
B
C
D
E
F
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
JFD6
AFP1
JFP3
AMP2
INDIVIDUAL

Figure 9: Seasonal Changes in the Percentages of Use for Locations A, B and C.


60
50
40
30
20
10
0
% USE
WINTER
SPRING
JUNE
JULY
AUGUST
A
B
C

CHAPTER IV

SOCIAL PROXIMITY IN A CAPTIVE GROUP OF MANDRILLS AT THE TULSA ZOO

Mandrills were studied at the Tulsa Zoo in Tulsa, Oklahoma, for their social proximity using instantaneous sampling from November 1995 to August 1996. The nearest neighbor(s) of the focal animal at each 30 sec interval was recorded for 10 min. The nearest neighbors were defined as the individuals within 1 m of the focal animal. One or two individuals could be recorded as neighbors, and if more than two individuals were present, the category "group" was recorded. Three different group compositions (group composition 1--multi-male group, group compositions 2 and 3--uni-male groups) were observed. Chi-square was used to compare the frequencies of one neighbor, two neighbors, group and nonsocial for individuals within a group composition and individuals across the different group compositions. Individuals spent high percentages of time farther than 1 m from other mandrills. When with a neighbor, it was most often one other individual. Individuals tended to be in close proximity to relatives, except in group composition 3 when the reintroduction of two females disrupted the dominance hierarchy. The percentage of time in social proximity increased across the group compositions with the removal of the dominant male and reintroduction of two females. Another possible cause may be the change in weather; individuals increasingly congregated in the shade as temperatures increased. Males had a greater tendency to be nonsocial than females, and males had no clear preference to be near relatives or nonrelatives.

Key words: Mandrillus sphinx, neighbor, primates, sociality

INTRODUCTION

The mandrill (Mandrillus sphinx), a member of the Old-World monkeys subfamily Cercopithecinae, is found in the rainforests of equatorial west Africa, with Gabon containing perhaps the largest portion of the remaining mandrills [Feistner et al., 1992]. Since mandrills are elusive and their environment so densely forested, it is difficult to study them in the wild [Norris, 1988; Wickings and Dixson, 1992]. Since studies in the wild are so difficult, captive studies of mandrills are of great benefit and supplement the data obtained in the wild [Mellen et al., 1981].

Not much is known about wild mandrills, especially in their preference for neighbors. Mandrills in the wild are found as solitary males and in groups of 20 up to 300 or more [Stuhsaker, 1969; Gartlan, 1970; Sabater Pi, 1972; Jouventin, 1975; Hoshino et al., 1984; Lahm, 1985; Harrison, 1988]. In a group of 20 individuals, only one male was present [Gartlan, 1970]. It is not known whether the females in the small groups were related.

The mandrills at the Tulsa Zoo have been studied previously for their reproductive characteristics, such as age of first swelling and conception, and gestation length [Bettinger et al., 1995], and behavior [Hartley et al., 1996; Terdal, 1996]. Most captive mandrill studies focus on reproduction and behavior, but few discuss their preference for neighbors, or social proximity. Social interactions are closely tied to the preference for neighbors. Mandrills may have a comfort zone, or distance they prefer to be away from more dominant or aggressive animals. Also, closely related individuals or allies may tend to remain fairly close together. This study explores the preference for neighbors, including whether the animal prefers to be nonsocial, with one, two, or a group of individuals more frequently, and also looks at which individuals seem to more closely associate or keep fairly distant.

METHODS

Group Composition

During the course of the study, group composition was altered on three occasions through removals and reintroductions. Life history data on each mandrill is given in Table 1. Individuals were classified as adult at the age of 5 years, and juvenile when younger. No infants were present in this study. All mandrills belong to one of three matrilines (Figure 1). All mandrills were born at the Tulsa Zoo, except for the three matriarchs. AFA1 came from Dallas Zoo, TX, AFD1 from Reid Park Zoo, AZ, and AFP1 from Brookfield Zoo, IL. The sequence of events leading to the group composition changes are listed in Table 2.

Individuals were given a code for the purposes of this analysis (see Appendix) which included information on the age, sex, matriline, and the age of the animal within the matriline. Each code consisted of three letters followed by a number, an example was AFD1 for Darla. The A designated an adult animal (J if the animal was a juvenile), the F for female (M for male), D indicated the Darla matriline (other matrilines included Annie-A and Pearl-P), and the 1 showed that this individual was the oldest of the matriline (Offspring began at 2 with the oldest offspring receiving the lowest number).

Exhibit Design

The mandrills were housed in a grotto-style exhibit that faced east, and were locked outside whenever the temperature was above 18.3 °C and locked in when it was less than

4.4 °C. Between 4.4-18.3 °C the animals were given access to the den. Wind chill, moisture, and other weather conditions prompted occasional departure from these guidelines. The mandrill exhibit was surrounded by a dry moat on three sides, and logs were placed on the exhibit. The mandrills had free access to the 6.7 m deep moat. The outside exhibit was 50 x 16.6 m with a back wall measuring 6.7 m high. The inside of the grotto consisted of four 3.3 x 6.7 m dens and the off-exhibit, outdoor area was 5 x 4 m. The grotto consisted of various levels some of which were concrete while others had dirt or grass. Most of the levels were 15 cm higher or lower than the others, while the levels in the southwest corner were 2.4 m high at the highest point and were covered by an overhang from the grotto wall.

Methods of Observation and Analysis

The mandrills at the Tulsa Zoo, Tulsa, Oklahoma, were observed between November 1995 and August 1996. Instantaneous sampling was used to observe an individual for 10 min, recording the nearest neighbor(s) of the focal animal at 30 sec intervals. Nearest neighbors were defined as the individuals within 1 m (approximate touching distance) of the focal animal, with one or two individuals being recorded as neighbors. If more than two individuals were within 1 m of the focal, then "group" was recorded as a neighbor.

Since the exhibit was of varying elevations, the vertical distance between individuals was also taken into account when deciding if an individual was within 1 m of the focal. The horizontal and vertical distances were considered equally important, with more than 1 m vertical distance signifying the individual was out of the vicinity of the focal.

The order of observing each mandrill was chosen at random before data collection began. There were differing amounts of observation time for each group composition which were accounted for in the analysis. Group composition 1 was observed for 12.5 hrs., group composition 2 for 46.8 hrs., and group composition 3 for 119.8 hrs. Within a group composition, individuals were observed for approximately equal amounts of time.

Data were entered into PcFile, and Windows SAS was used in the analyses of this study. Frequencies of neighbors were obtained for each individual in each group composition. The individuals within a group composition were compared using chi-square for their neighbor preference--one neighbor, two neighbors, group (more than two individuals), or nonsocial. The individuals were also compared across the different group compositions for their neighbor preference using chi-square. The percentages of time a focal spent with the different types of neighbors were calculated, as well as the percentages of time with relatives and nonrelatives.

RESULTS

Neighbor Preferences Compared Using Chi-square

A chi-square comparison of the individuals in each group composition for their social preferences, including the categories one neighbor, two neighbors, group, and nonsocial, indicated a significant difference in all group compositions ($p=0.001$). Due to low frequency counts, two neighbors and group were combined for group compositions 1 and 2. At least some individuals within each group composition differed in the amount of time spent in the different neighbor situations.

Chi-square analyses for each individual across the group compositions indicated that individuals differed in their choice of neighbors depending on the group composition ($p<0.001$ for all except AMP2-0.091). The categories two neighbors and group were removed from the analysis for AMP2 due to low frequency counts. AMP2 spent most of his time nonsocial in each group composition, causing the insignificant chi-square result.

Comparing Individuals for Neighbor Preference

In group composition 1 (Figure 2), individuals were mostly nonsocial, but all animals spent at least some time with one other individual. Percentages for more than one neighbor were present only for the subordinate A matriline, the largest matriline, and for AFP1. Adult males were found to be primarily nonsocial animals. AMD2, the dominant male, was more social than the other adult males.

The percentages of time spent nonsocial was lower for group composition 2 (Figure 3) individuals, except for the alpha male AMP2. In group composition 2, percentages with two neighbors were present for all individuals except the alpha male. The percentage of time spent socially for AMP2 in group composition 2 was similar to his percentage in group composition 1. The high percentage of social behavior for the alpha male in group composition 1 compared to the dominant male in group composition 2 may be due to personality differences between the two males, AMD2 and AMP2.

Group composition 3 individuals (Figure 4) spent higher percentages of time socially than group composition 2 individuals. The amount of time spent with two or more neighbors was higher than in group composition 2. Members of the D and P matrilines spent more time with more than one neighbor than the A matriline, the dominant females.

The alpha male was mostly nonsocial and was only observed in the vicinity of one other individual.

Observations on Percentages of Time Spent with Relatives and Nonrelatives

The percentage of time with nonrelatives included one, two or more neighbors which were nonrelatives but also may have included relatives and nonrelatives together as two or more neighbors. The percentage for relatives included one, two or a group of neighbors all of which were related to the focal.

For many individuals there was a trend to spend a substantial part of their social time with relatives (Table 3). Mother-offspring pairs were often seen together in this study. JMA4 consistently spent a higher percentage of time with relatives than nonrelatives. No trend could be found for adult males; they did not consistently spend more time with relatives or nonrelatives. The only adult male present in all group compositions shifted in his preference for relatives and nonrelatives across the group compositions. In two out of the three group compositions he preferred nonrelatives, although his percentages for both neighbor types were low. The alpha male in group composition 1, AMD2, was very social, but his percentages for relatives and nonrelatives were similar. AMD4, a subordinate male, preferred nonrelatives, but was not very social.

Group compositions 1 and 2 females consistently remained with relatives rather than nonrelatives. The amount of time in a social situation increased from group composition 1 to 2 and from 2 to 3. The amount of time spent with nonrelatives was higher in group composition 3, with 50% of the females spending significantly more time with nonrelatives than relatives. For two individuals, the percentages of time spent with relatives and nonrelatives were similar.

DISCUSSION

Patterns and Observations

There was a tendency in the mandrills to occupy an area near relatives. The amount of time spent with relatives for each individual was influenced by the number of relatives present in each group composition for that animal. The most common social situation was one neighbor. A group of individuals within the vicinity of a focal was not a frequent occurrence. Mothers and offspring were most consistently observed together.

Adult males had low percentages of all types of social situations, except for AMD2, and could not be said to spend more time with relatives or nonrelatives. The alpha males AMD2 and AMP2 differed in the percentages of times spent socially. This may be attributable to personality differences or perhaps the differing number of males in the group compositions. Perhaps a multi-male situation required the alpha male to be more social. The juvenile male, JMA4, consistently spent more time with relatives. Group composition 1 males were never seen in the vicinity of one another, except for the juvenile male's play behavior with the low-ranking adult male AMD4.

The amount of time spent socially increased across the different group compositions. A possible cause for this increased social focus could be the changing dominance hierarchy. The removal of the dominant male in forming group composition 2 and the reintroduction of two females, AFD3 and JFD6, to form group composition 3 altered the dominance hierarchies. The increased social orientation may correspond to periods of social tension when relatives congregate together or may be the result of individuals gaining allies as in group composition 3 when nonrelatives remained in close vicinity. In group composition 3, one of the reintroduced females vied for the alpha position, conflicting with one of the resident females. The disruption of the dominance hierarchy may have been the cause of the higher rates of social orientation, especially with nonrelatives. Another possible cause for increased rates of social proximity may be changes in weather. Group composition 3 individuals may have congregated together because of the suitability of the location for shading.

Altering the area or structure of a zoo exhibit may decrease the amount of time individuals spend in a social situation, or at least give the mandrills the opportunity to voluntarily remain in a social situation. A larger or more complex exhibit, with vertical structure and vegetation, may allow an animal to escape the tension caused by being in close vicinity to dominant individuals. Perhaps the only reason the mandrills in this study spent a considerable amount of time with relatives was for protection from the dominant individuals and to relieve tension. Future exhibit designs may focus on creating a naturalistic environment for the mandrills with both vertical and horizontal complexity. Such complexity may relieve the tension in many mandrill groups that leads to increased aggression and death of individuals.

Applying the findings to wild mandrills is difficult. Mothers and infants can be found in close proximity even in the wild, but the relationships of mothers and older offspring are not known. Perhaps they do remain in close proximity. Unrelated individuals, especially males, probably do not remain in close association.

One possible reason for remaining close together could be predator avoidance. Mandrills are preyed upon by crowned hawk-eagles (Stephanoaetus coronatus), leopards (Panthera pardus), and perhaps chimpanzees (Pan troglodytes) and some larger snakes (Bitis, Python), in addition to humans [Lahm, 1985; Harrison, 1988]. Humans may be the main incentive for any close associations of wild mandrills.

It is probable that the social proximity found in captive studies is a result of the mandrills being in an artificial environment. The tendency to remain with relatives, especially for females, may not be found in the wild. Social proximity and the reliance on relatives in the wild would be a valuable future study.

Other Studies

Whitehouse and Fried (1992) observed a group of seven mandrills at the Dallas Zoo and Aquarium and found that the mother and infant had the highest frequency of social proximity (within 3 ft). The adult male tended to associate with the dominant female(32.8%) and her infant male (25%). Social proximity was found to be associated with kinship ties, although there was only one unrelated individual in the group. Greater distances between non-kin have also been reported in rhesus monkeys [Quiatt, 1966].

Altering the size of the exhibit may influence the amount of time spent with other individuals in the group. Chang (1991) found that the mean amount of time the adult male and female mandrill spent together more than doubled when the exhibit at Zoo Atlanta was increased by a factor of 10. The adult female and her offspring, and the juvenile female and the sub-adult female spent less time together in the new exhibit. The unrelated sub-adult female spent more time with the adult male in the new exhibit. The number of social interactions decreased in the new exhibit as nonsocial activities such as foraging increased. Fried and Whitehouse (1992) did not find a similar increase in social proximity between the adult male and female mandrill when the exhibit at the Dallas Zoo was enlarged.

Terdal (1993) found that low-ranking animals, especially the sub-adult male, occupied whichever room the adult male was absent from in the two-room enclosure at the Milwaukee County Zoo. In captive lowland gorillas (Gorilla gorilla gorilla), a less dominant animal avoided the area around a more dominant one [Fischer and Nadler, 1977; 1978].

CONCLUSIONS

1. The highest percentages for any type of neighbor situation were nonsocial throughout all group compositions, males tending to be more nonsocial than females.

2. Captive mandrills tended to spend a higher percentage of time with related rather than unrelated individuals.

3. Changing group composition or weather conditions influenced the amount of time spent with relatives and nonrelatives. The amount of time spent socially increased after the removal of the dominant male and the reintroduction of the two females.

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AMD4	L.C.	M	9/10/89	6	549
JMA4	LBM	M	7/09/93	2	828
AFA1	ANNIE	F	8/18/75	20	212
AFD1	DARLA	F	6/20/79	16	286
AFP1	PEARL	F	1/05/85	11	421
AFD3	IVY	F	7/19/88	6	518
AFD5	DARCY	F	10/05/90	5	585
AFA2	ANGIE	F	10/17/90	5	586
JFD6	PATIENCE	F	10/12/91	4	690
JFA3	PANDORA	F	2/10/92	4	691
JFP3	TAMMIE	F	4/28/92	4	692

Information taken from Tulsa Zoo records.

Table 2: Sequence of Events Leading to Group Composition Changes and the Individuals Comprising Each Group Composition.

Group Composition #	Dates	Group Members	Comments
1	11/19/95-12/19/95	3 adult males, 1 subadult male, 5 adult females, 2 subadult females	
	12/18/95		Adult male, AMD4, removed after injuries
DATA NOT USED	12/20/95-4/9/96	1 adult male, 1 subadult male, 2 adult females, 1 subadult female	Split mandrills into 2 groups.
	2/23/96		Alpha male, AMD2, removed.
2	4/10/96-5/20/96	1 adult male, 1 subadult male, 5 adult females, 2 subadult females	2 groups reunited under a new alpha male, AMP2.
DATA NOT USED	5/21/96-5/28/96	1 adult male, 1 adult female, 1 subadult female	2 previously removed females, AFD3 and JFD6, reintroduced to alpha male
3	5/29/96-6/5/96	1 adult male, 1 subadult male, 6 adult females, 3 subadult females	2 females reintroduced to the group.
	6/6/96-8/24/96	1 adult male, 1 subadult male, 5 adult females, 3 subadult females	Reintroduced female, AFD3, suffered injuries and was removed from the group

Table 3: Percentage of Time Spent with Relatives and Nonrelatives for Each Individual in each Group Composition. (Males are listed above females and individuals are listed with decreasing age within each matriline.)

INDIV.	GROUP 1		GROUP 2		GROUP 3	
	WITH RELAT.	WITH NON-RELAT.	WITH RELAT.	WITH NON-RELAT.	WITH RELAT.	WITH NON-RELAT.
AMD2	16.7	15.8	-----------	-----------	-----------	-----------
AMP2	0	3.3	4.3	0.6	1.5	5.7
AMD4	0.7	3.6	-----------	-----------	-----------	-----------
JMA4	15.7	1.4	29.8	10.8	28.2	11.8
AFA1	16.4	0.7	39.7	6.1	24.7	26.1
AFA2	13.6	1.4	27.2	11.7	13.5	29.7
JFA3	22.8	10.7	39.5	7.9	22.2	22.7
AFD1	27.8	0	35.2	3.7	26.1	26.1
AFD5	12.8	2.2	31.7	4.3	30.7	24.8
JFD6	------------	------------	------------	------------	27.0	30.2
AFP1	27.8	16.4	36.9	7.6	33.6	25.0
JFP3	5.0	2.8	31.6	13.8	21.7	31.7

Figure 1: Three Matrilines of the Tulsa Zoo Mandrills Listed by Age (Mothers at the top) Along With the ID Used During the Study for Each Animal.

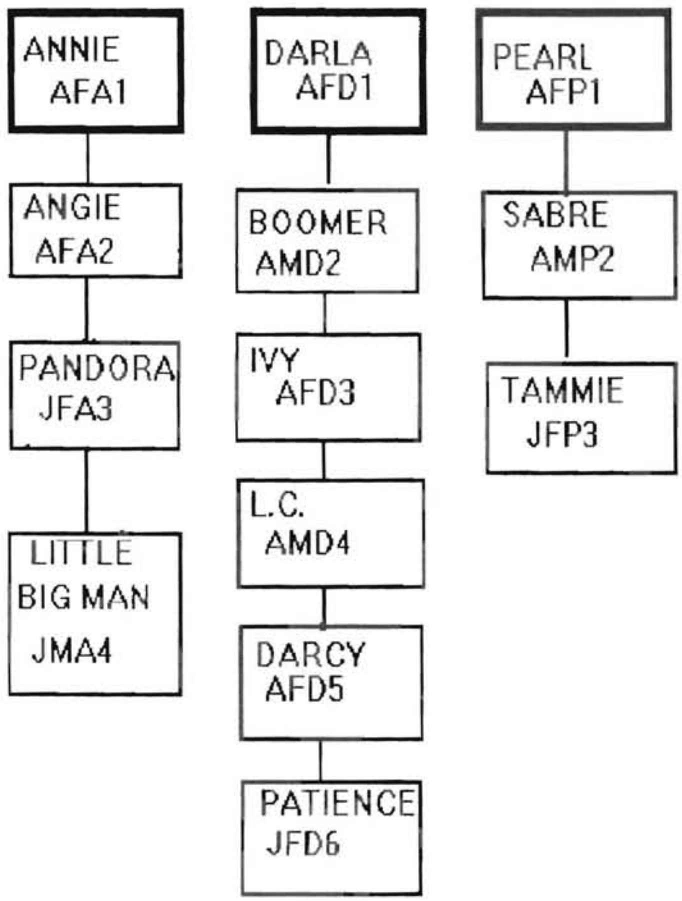

ANNIE
AFA1
ANGIE
AFA2
PANDORA
JFA3
LITTLE
BIG MAN
JMA4
DARLA
AFD1
BOOMER
AMD2
IVY
AFD3
L.C.
AMD4
DARCY
AFD5
PATIENCE
JFD6
PEARL
AFP1
SABRE
AMP2
TAMMIE
JFP3

Figure 2: Percentage of Time Spent in the Different Types of Neighbor Situations for Group Composition 1 Individuals.

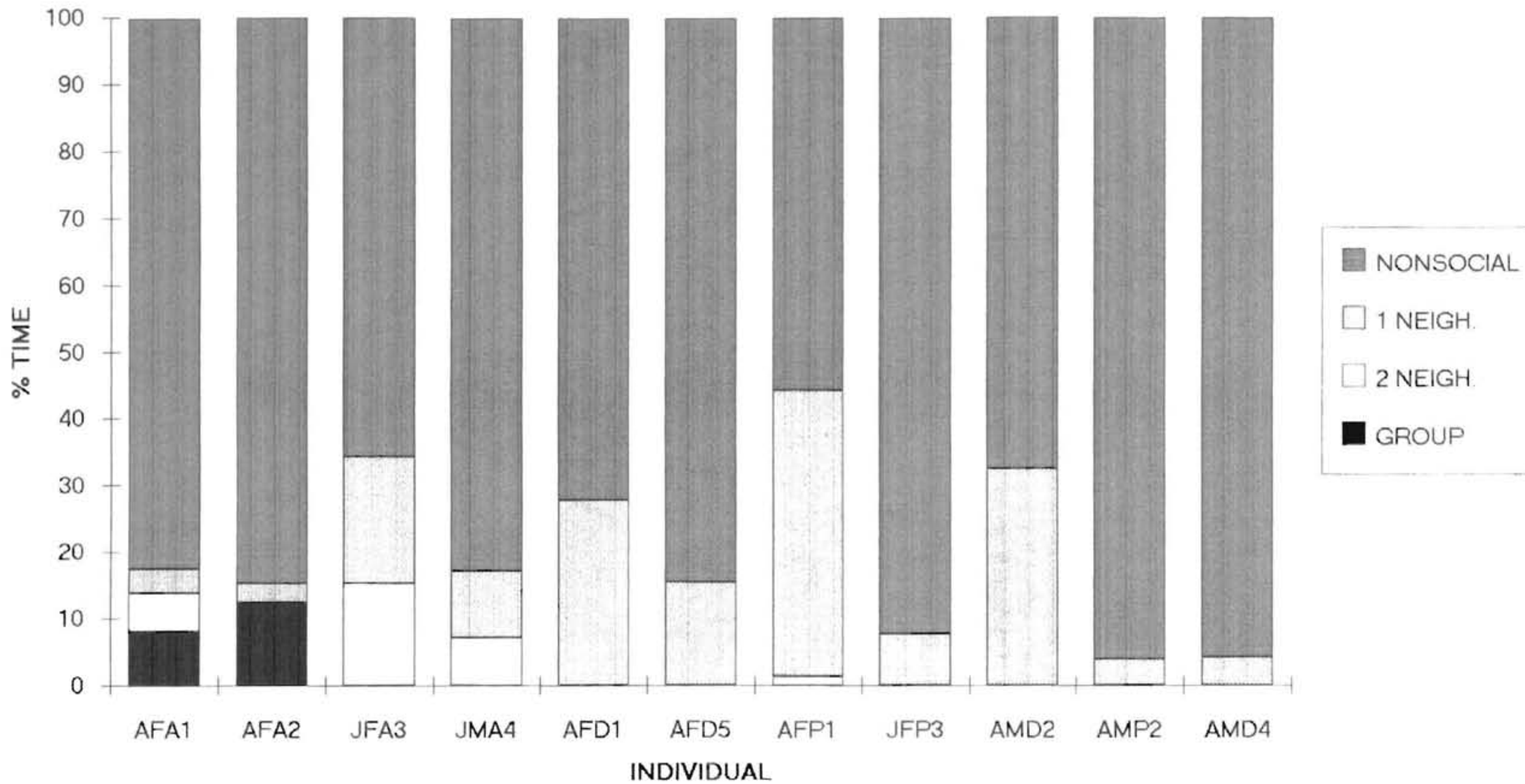
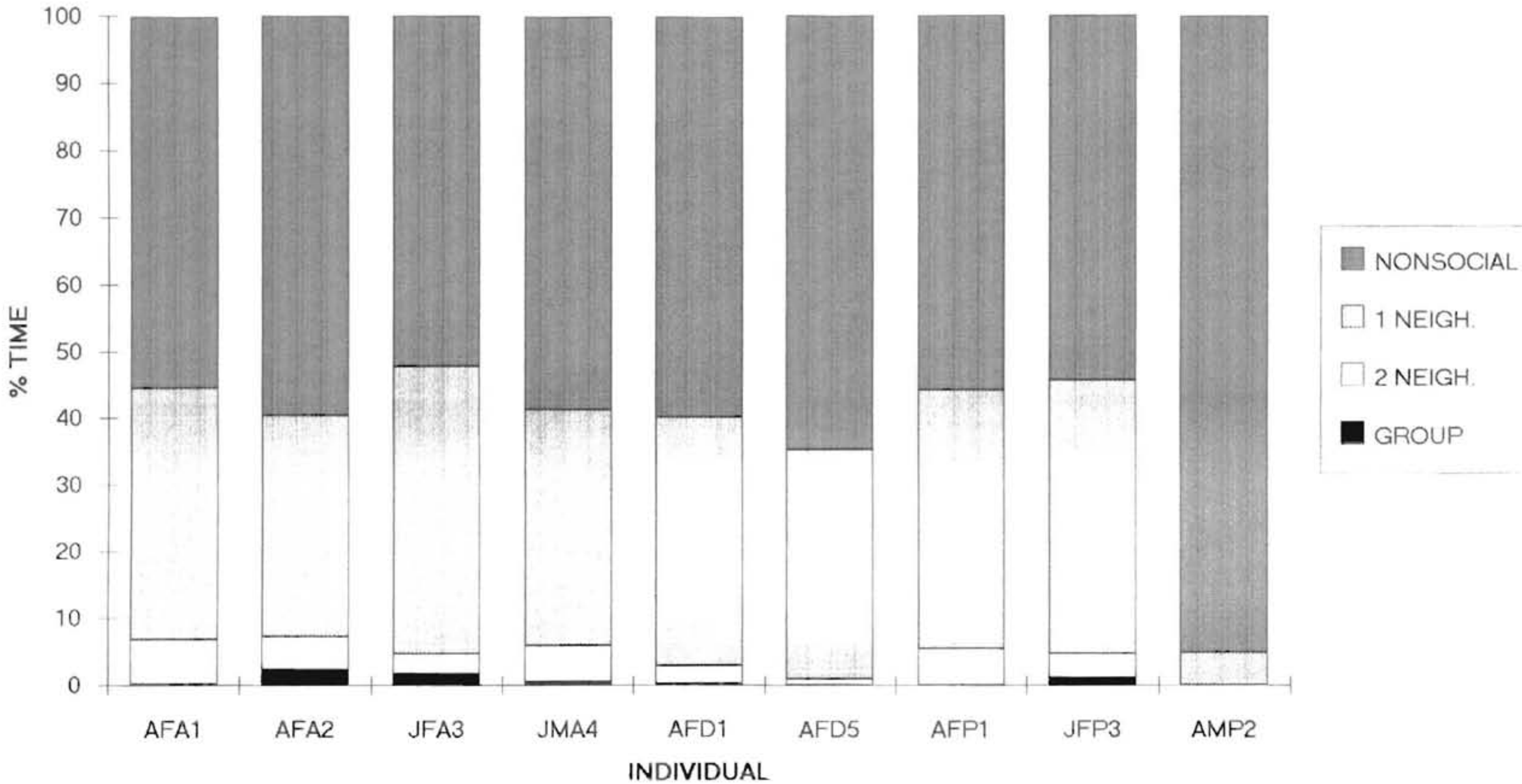
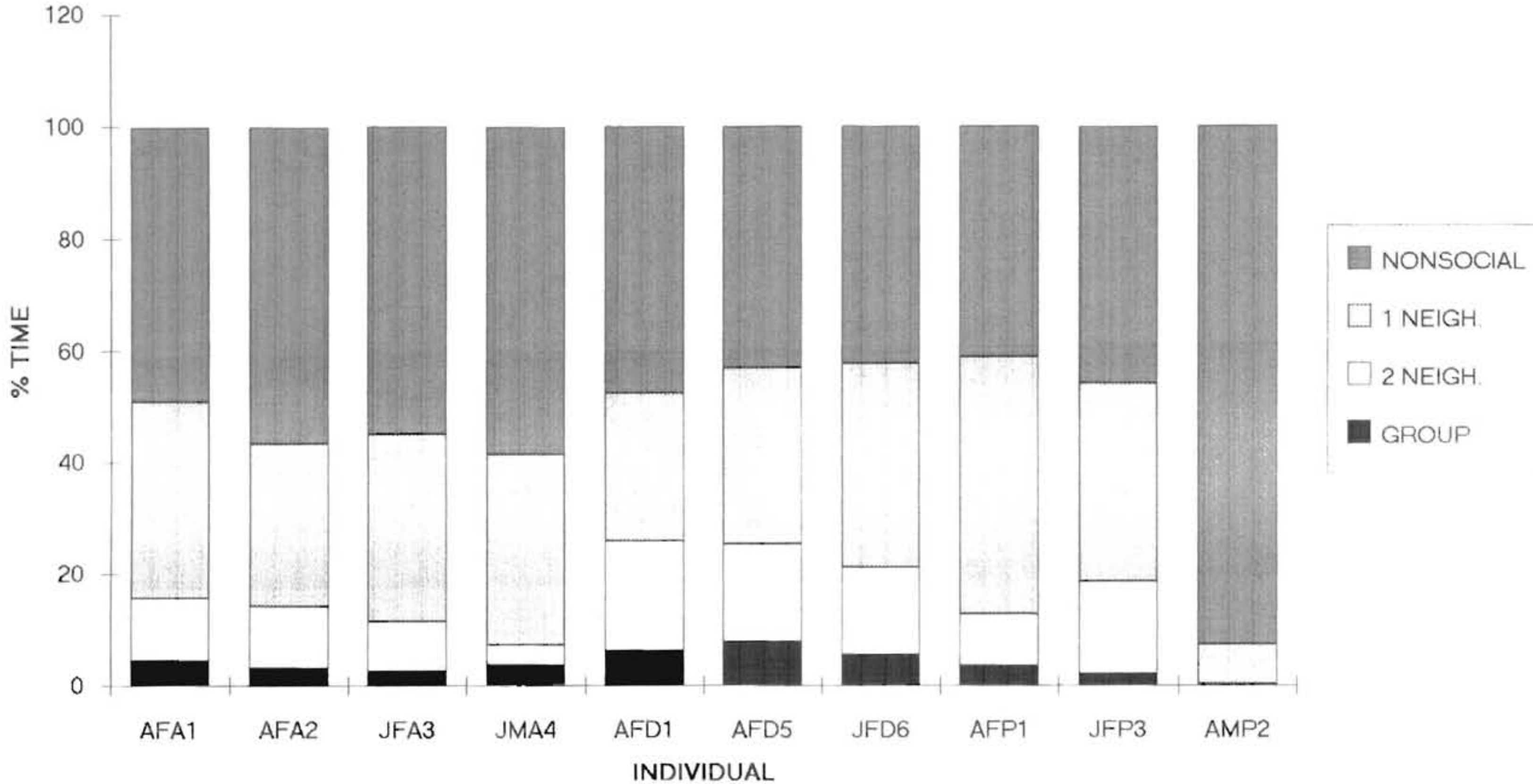

100
90
80
70
60
50
40
30
20
10
0
% TIME
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMD2
AMP2
AMD4
INDIVIDUAL
NONSOCIAL
1 NEIGH.
2 NEIGH.
GROUP

Figure 3: Percentage of Time Spent in the Different Types of Neighbor Situations for Group Composition 2 Individuals.



100
90
80
70
60
50
40
30
20
10
0
% TIME
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
AFP1
JFP3
AMP2
INDIVIDUAL
NONSOCIAL
1 NEIGH.
2 NEIGH.
GROUP

Figure 4: Percentage of Time Spent in the Different Types of Neighbor Situations for Group Composition 3 Individuals.


120
100
80
60
40
20
0
% TIME
AFA1
AFA2
JFA3
JMA4
AFD1
AFD5
JFD6
AFP1
JFP3
AMP2
INDIVIDUAL
NONSOCIAL
1 NEIGH.
2 NEIGH.
GROUP

APPENDIX

Name Designations for Each Focal Animal. (Designations include Adult/Juvenile; Male/Female; Matriline-Annie, Darla, or Pearl; Rank of age-matriarch=1, oldest offspring=2, etc.)

ANNIE=AFA1	DARLA=AFD1	PEARL=AFP1
ANGIE=AFA2	BOOMER=AMD2	SABRE=AMP2
PANDORA=JFA3	IVY=AFD3	TAMMIE=JFP3
LITTLE BIG MAN=JMA4	L.C.=AMD4	
	DARCY=AFD5	
	PATIENCE=JFD6	

Ethogram of Behaviors Used in Studying the Mandrills at the Tulsa Zoo. (Altered from a Previous Ethogram Designed by T. Bettinger at the Tulsa Zoo in 1993). (Agonistic-AG, Affiliative-AFF, Sexual-SE, Active Nonsocial-ACT, Inactive Nonsocial-INA)

BEHAVIOR CATEGORY	ABBREVIATION DIRECTED BY/TO FOCAL	DEFINITION
AG	AG/AC	Aggressive contact including hitting, biting, grabbing.
AG	AM/AT	Arm threat-extending forearm at another individual.
AG	AV/AD	Avoid-one animal walks or runs away from an approaching individual.
AG	CH/CE	Chase-when one animal lunges toward another, actively pursuing.
AG	HB/HD	Head bob-up and down motions of the head at another individual.
AG	PN/PR	Present-animal crouches with genitalia directed towards another or approaches and orients genitalia in another's line of vision.
AG	YA/YN	Yawn-display canines to another in an open mouth gesture-mostly seen in the alpha male.
AFF	AP/AH	Approach-One individual deliberately walks toward another individual.
AFF	FL/FW	Follow an individual.
AFF	GR/GM	Groom-picking through hair or at skin, removing debris with hand or mouth-groom self, groom other, or being groomed.
AFF	GT/GE	Greet-includes "Figure 8" face, smile.
AFF	GW	Three-way groom-three individuals involved in a grooming bout.
AFF	MU	Mutual grooming-two individuals groom each other at the same time.
AFF	PL/PY	Social Play

AFF	WA/WT	Watch-one individual actively watches another.
SE	CP/CO	Copulate-male mounts and thrusts female.
SE	IN/IS	Inspect-individual sniffs or probes genitalia of another individual.
SE	MN/MT	Mount, non-copulatory-one animal mounts another but thrusting does not occur, recorded mostly for female/female mountings.
ACT	EX	Examine/explore object-examine or manipulate object.
ACT	FO	Forage-consuming or searching for food.
ACT	SC	Scratch
ACT	DR	Drink
ACT	GO	Groom self.
ACT	TR	Travel-walking from one area to another.
INA	ID	Idle-no active behavior-sit, lay, or stand.

VITA

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Master of Science

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