SPATIAL SELECTION, ASSOCIATION PATTERNS AND BEHAVIOR OF CAPTIVE CHIMPANZEES (*Pan troglodytes*) AT THE TULSA ZOOLOGICAL PARK

By

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CHAPTER I

INTRODUCTION

This thesis is composed of 3 manuscripts formatted for submission to the American Journal of Primatology. This chapter introduces the rest of the thesis. Each of the following chapters is complete as written and needs no additional support material.

A study was conducted on the chimpanzee, *Pan troglodytes*, population at the Tulsa Zoo. The study was divided into 3 components. These components comprise the remaining 3 chapters of this thesis. Chapter II, Spatial selection in captive adult chimpanzees, addresses habitat utilization. Chapter III, Association patterns in captive adult chimpanzees, analyzes time spent in solitary and social interactions and interactive partners. Chapter IV, Behavior exhibited by captive adult chimpanzees, reviews the behavioral activities of the chimpanzees.

CHAPTER II

SPATIAL SELECTION IN CAPTIVE ADULT CHIMPANZEES

SPATIAL SELECTION IN CAPTIVE ADULT CHIMPANZEES

Spacing behavior in the chimpanzees at the Tulsa Zoo was studied to determine if they were selecting certain areas of their island habitat for heavier use. Data were collected by instantaneous sampling on a focal animal. High-ranking female chimpanzees used the island differently than did other group members. The 2 subordinate females showed an overlap in their usage of the island, but their usage differed from that of the high-ranking females. Each female's most frequently used area was different. Subordinate females were seldom present in areas most heavily used by higher-ranking females. High-ranking females used the areas heavily used by subordinate females. The male used the island differently from the females. He most frequently occupied the areas the 2 multiparous cycling females used. The spacing behavior exhibited by these captive chimpanzees is similar to the spacing behavior used by wild chimpanzees.

Key Words: core area, spacing behavior, spatial selection

INTRODUCTION

Chimpanzees (Pan troglodytes) exhibit a social organization unusual among animals. A group of chimpanzees shares a common home range but individuals may travel within the range either alone or with other individuals in temporary association patterns (Reynolds & Reynolds, 1965; Nishida, 1979; Goodall, 1986). Spotted hyenas, Crocuta crocuta (Kruuk, 1972); lions, Panthera leo, of the Kalahari desert (Owens, 1984); spider monkeys, Ateles belzebuth (Klein & Klein, 1975) and whiptail wallabies, Macropus parryi (Kaufmann, 1974) are known to exhibit similar social organization. Unlike these other species, however, female chimpanzees transfer from the natal group into a new social group (Pusey, 1979; Nishida, 1979). Female chimpanzees are less gregarious (Halperin, 1979; Wrangham & Smuts, 1980) and range shorter distances than males (Reynolds & Reynolds, 1965; Wrangham & Smuts, 1980). Although an intensive study of female ranging patterns, feeding behavior and social interactions has not been conducted, some insight into the behavior of females has been attained from other studies on chimpanzees.

A core area is an area of the home range which is used disproportionately more than the rest of the range (Jennrich & Turner, 1969). Wrangham and Smuts (1980) found that female chimpanzees at Gombe spent 80% of their time in core areas that were about half the size of the males' area. The core areas of females in the wild are not exclusive, but may overlap extensively. However, the solitary nature of the females would indicate that they are temporally separating themselves in the overlapping areas.

The use of core areas by female chimpanzees in the wild has been hypothesized to be in response to feeding competition (Wrangham, 1979). Nishida (1989) found that protection of offspring and competition over food were the two main sources of conflict among female chimpanzees at Mahale. While a female was lactating she spent the majority of her time within her core area. Once she resumed cycling she left her core area and traveled more widely, accompanied by males (Pusey, 1979; Goodall, 1986).

Females benefit from a core area. By having a smaller area in which they range, they know where the closest food sources are located and, therefore, conserve energy by traveling shorter distances. Nishida (1989) proposed that female reproductive success may depend upon acquiring a core area near the center of the group's territory. He suggested that females with peripheral ranges will incur a greater risk of aggression from other female group members, as well as from resident males who "suspect" the paternity of those females' offspring.

Female chimpanzees are not considered to be territorial. If the best strategy is to have a core area near the center of the community's territory then there might be a mechanism working among the females that allows certain individuals to accomplish this end. Dominance in females is less clear than in males. Goodall (1986) reported that usually certain females are clearly dominant while others are clearly subordinate. Dominance in the group is usually associated with age, length of time in the group (Nishida, 1989) and relatives in close proximity (Goodall, 1986). Rowell's (1974) theory that dominance is maintained by respect from below rather than intimidation from above probably describes many female chimpanzee relationships. De Waal (1982) found this in the female chimpanzees of the Arnhem Zoo.

Although female chimpanzees are not territorial and do not have a well-developed social hierarchy this should not imply that they passively accept other females in their home range. Pusey (1983) reported that three females of high rank (2 at Gombe, 1 at Mahale) had daughters that remained in their natal group. These females were able to sufficiently increase the size of the mother's core area to accommodate them both. One set of females at Gombe was observed to chase and attack resident and newly immigrated adolescent females (Bygott, 1979) and one set was known to have taken, killed and eaten resident females' offspring (Goodall, 1977). By jointly harassing new females, residents may discourage them from settling nearby (Pusey, 1983). However, the presence of other females in the periphery of the group home range would provide a buffer between the core residents and other communities.

Considering this pattern among female chimpanzees, one may predict that natural selection would favor individuals that exhibit a primarily solitary existence in an established core area. This would allow a female to maximize her feeding efficiency and thus her reproductive success. Chimpanzees are capable of exhibiting behavioral plasticity. However, if given the opportunity to separate themselves from other group members in captivity, and if solitary behavior for females and social behavior for males is selected for in the wild, one may predict that this behavior would be found in captive groups as well.

To test the hypothesis that female chimpanzees tend to select certain areas of their habitat for heavier use and that these areas are recognized by other group members, a study was conducted on the four adult female chimpanzees at the Tulsa Zoo, all of whom were wild caught. The male (wild caught also) was included in the study to determine if he exhibited a more social behavior than the females and used the habitat differently than the females in this study, as would be predicted from data on wild male chimpanzees.

Comparing behavior between captive and wild chimpanzees is complicated. However, since the 9 chimpanzees at the Tulsa Zoo are housed in a large (approx. 10,600 sq foot) outdoor facility, they have the opportunity visually or physically to space themselves away from other group members. Although food is provided and there is no danger from neighboring males or predators, the females still compete. Possession of prized food items and protection of offspring are the major sources of conflict in this captive group.

This paper addresses the following questions: Do the female chimpanzees at the Tulsa Zoo use their island habitat randomly? If not, are they selecting certain areas for heavier use and is an individual's selected area recognized by other group members? How does the male's use of the island differ from that of the females'?

METHODS

The study was conducted on the chimpanzee (Pan troglodytes) population at the Tulsa Zoo, Tulsa, Oklahoma, from January 1989 through July 1990. The chimpanzees are housed on an island measuring approximately 26 by 52 meters. The island is surrounded on three sides by a water moat 6 meters wide and on the fourth side by the night den wall. The island has numerous vertical structures including ropes, poles, a platform, a synthetic termite mound, and cargo nets, as well as rocks and natural vegetation for climbing and resting upon. The island also has 4 concrete drainage pipes covered with dirt (referred to in the study as tunnels). The dense vegetation, tunnels and topographic variation of the island enable the chimpanzees visually to isolate themselves from each other and the public. The chimpanzees are on the island 6 to 10 hours a day, weather permitting.

Nine chimpanzees were present during the study (Table I). Data were collected on the 4 adult females and 1 adult male. Data were collected on the male to compare his behavior to that of the females. The composition of this group has been very stable. The adult female with the shortest tenure in the group was added in 1981. All 4 adult females and the male have been housed together on this island since that time. The only additions to the group have been by births from 3 of the females and the only deletions from the group have been through removal of offspring at 5 to 6 years of age. During this study there were no changes in group composition.

AF1 is clearly the dominant female in this group of chimpanzees. AF4 and AF5 are very subordinate females. Therefore, in this study high-ranking refers to AF1 and AF3 and low-ranking refers to AF4 and AF5.

AF1 has never reproduced. Although she regularly cycles, she does not allow mating by the adult male or infant males in the group. AF3 resumed post-partum cycling in January 1989 and may have become pregnant by the end of the study. AF4 gave birth in January 1989 and was lactating throughout the study. AF5 resumed post-partum cycling in July 1989.

Data were collected by instantaneous sampling on a focal animal (Lehner, 1979). Observations were recorded every 30 seconds for 10 minutes on each individual. Location, behavior and group member within 5 feet of the focal animal or in the same tunnel as the focal animal was recorded. Data were collected from January 1989 to August 1990 and 100 hours of data were used in this analysis. Each 10-minute session was considered one sample (Martin & Bateson, 1986). Therefore, there were 116 samples on AM2, 123 on AF1, 116 on AF3, 117 on AF4 and 120 on AF5.

The island was divided into 7 sections and each section was further broken down by characteristic of the space (Figure 1). The characteristics include horizontal space (on the ground), vertical space (cargo nets, poles, ropes or vegetation which support the individual off the ground), tunnels, platform and termite mound. This gave a possibility of 19 locations that the individuals could use. The divisions of areas on the island were not physical divisions. Landmarks on the island were used to distinguish one section from another.

Data were analyzed using non-parametric statistical tests. Tests performed on various components of the study are given in detail in the results section. Since this study was conducted on a captive group of chimpanzees, data points are dependent to some extent. The chimpanzees did not have the option of leaving the facility during sampling periods. To the extent possible, precautions were taken to keep data independent. Order of sampling of the individuals was randomly determined before arriving at the exhibit. Data were analyzed to determine each individual's use of the island and for diurnal, thermal and seasonal variation in each individual's usage. Data were also analyzed to determine if individuals recognized areas used by other group members.

RESULTS

Overall Usage - Females

Chi-square tests performed on each chimpanzee's usage of the 7 sections show that the chimpanzees are not using the island randomly. Each female is selecting a section for heavier use (Table II). AF1's and AF3's selected sections were different from those of all other females. AF4 and AF5 showed an overlap in their use of section 5. Each of the 7 sections contained various types of space: vertical, horizontal, tunnel, etc., but not all sections contained the same types of space. The rest of the analysis, therefore, addresses the 19 specifically identified areas which reflect not only the section but the characteristic of the space.

An analysis of the 19 possible locations shows the specific areas used by the chimpanzees. Each female used a different area most frequently. Figure 2 shows that by taking each individual's highest 2 to 3 usage areas almost half of each individual's time was allocated. Chi-square tests were performed on each individual against every other adult in the study. Table III shows that each chimpanzee is using the island independently of all other adult group members ($p < .005$, df=18) with the exception of AF4 and AF5 ($p < .10$, df=18). These 2 females show an overlap in their use of the platform in section 1 and the tunnel in section 5. However, they appear to be temporally separating themselves when they use these areas. For example, of the times AF4 was scored on the platform, AF5 was present 20% of the time. When AF5 was scored on the platform, AF4 was present 33% of the time. AF4 used the vertical space more frequently than other group members. Her usage was 14% greater than any other group member.

Diurnal Variation

To determine if each individual exhibited a diurnal variation in usage of the island, the time of day was divided into 3 categories: 1) before 10 a.m.; 2) 10:01 a.m. to 2 p.m.; 3) after 2:01 p.m. until the night den doors were opened (usually between 4-5 p.m.). Chi-square tests were performed on each individual's usage of the island between the 3 different categories. No significant variation was found for any group member (Table IV).

Thermal Variation

To test whether the chimpanzees showed a variation in their usage of the island as a result of temperature variation, temperature was divided into 3 categories: 1) below 60 degrees F; 2) 61 degrees F to 85 degrees F; 3) above 85 degrees F. Chi-square tests performed on each individual's use of the island in each category showed no significant variation for any group member (Table IV).

<u>Seasonal Variation</u>

Seasonal variation was analyzed by using 4 categories: 1) winter (Dec, Jan, Feb); 2) spring (Mar, Apr, May); 3) summer (June, July, Aug); 4) Fall (Sep, Oct, Nov). Chi-square tests were performed on each individual's usage of the island in these four categories. AF4 showed a significant ($p < .05$, df=51) variation in her seasonal use of the island. Other group members showed no variation due to season (Table IV).

AF4's variation in seasonal usage may be contributed to by her use of vertical space. In the winter and fall she showed an increase in her use of horizontal space and a decrease of her use of vertical space. Another factor causing her shift in use of the habitat may have been the age of her youngest offspring. She gave birth in January; this could account for her increased use of horizontal space during the winter months.

Female Recognition of an Individual's Area

Evidence to support the hypothesis that an individual's area is recognized by other group members is indirect. Females tended to avoid areas heavily used by higher-ranking females. Figure 3 shows AF1's heaviest used area. Other females seldom used this area whether AF1 was present or not. Figure 4 shows the area most heavily used by AF3. The subordinate females seldom used this area and the alpha female never used this area whether AF3 was present or not. Figure 5 shows the platform most heavily used by AF4. This area was used by other group members also but not as much as by AF4. Figure 6 shows the area most heavily used by AF5. The trend was the same as AF4's. Although AF5 used this area most frequently, other group members would also use this area.

Male Usage of the Island

Chi-square tests performed on the male's usage against each of the female's usage indicate that he used the island differently from the females ($p < .005$, df=6, Table II). Analysis of where he spent his time indicates that his most frequently used area was divided almost equally between the areas used by 2 of the cycling females (Figure 2). This was true for the analysis by section as well as analysis by specific area. The male exhibited no diurnal, thermal or seasonal variation in his use of the island (Table IV).

DISCUSSION

The disproportionate use of certain areas of the island habitat by the female chimpanzees at the Tulsa Zoo reflects a behavior comparable to the use of core areas in the wild. The function of this behavior in the wild has been hypothesized to be to increase feeding efficiency (Wrangham, 1979). However, it may also be a mechanism to reduce aggression. Females do not exhibit ritualized aggressive behaviors that can function to reduce injuries during conflict. Males typically intervene in female conflicts and will support the female with least tenure (Nishida, 1989). De Waal (1982) reported that there were more injuries in the Arnhem colony before the introduction of the males than there were even during the male power struggles. He suggested that females are not able to control their aggression as well as males. Another explanation may be the length of time the group had been housed together. Perhaps the group had not had time to work out their relationships.

Each female used a tunnel as her first or second most heavily used area (Figure 2). The tunnels provide protection from the elements - shade in the summer and shelter in the winter - but they also provide visual separation from other group members. This visual separation may be important for females in captivity. In some captive situations, females have no way to isolate themselves from one another, visually or spatially. Compared to chimpanzees in such situations, aggression is very low in the female chimpanzees at the Tulsa Zoo. One reason for this may be the amount and type of space present. If protection from the elements was the only feature desired there are other places on the island that could fulfill this need.

The 2 lower-ranking females showed an overlap in their use of the platform in section 1 and the tunnel in section 5. The female chimpanzees at the Tulsa Zoo spend at least half their time alone or only with their dependent offspring. In the 2 areas most frequently used by both AF4 and AF5, they tended to separate themselves temporally. Temporal separation reduced the amount of time they were in close proximity to one another. AF4 had 2 female offspring in the group during this study, one juvenile and one infant. AF5 had one infant male, to which she maintained close proximity. These offspring frequently played with each other. This may account for part of the overlap in the usage of the island by their mothers.

Overlap in the use of some areas cannot be attributed to lack of space. Some areas of the island were used very infrequently. A tunnel in section 2 was seldom used by any of the group members. The north side of the island which includes sections 2, 4 and 6 was also used less than the rest of the island. This may be because the chimpanzees were typically fed from the south side of the island. The keepers and the public usually approached the exhibit from the south. Another factor may be that the vegetation grew so dense on the north side of the island that the chimpanzees were forced to use trails to penetrate the area. They seldom went into the dense undergrowth.

The analysis of diurnal, thermal and seasonal variation includes many other variables. The chimpanzees were given access to the indoor den around 4 - 5 p.m. They had access until the following morning between 7:30 - 9 a.m. at which time they were locked onto the island. However, weather changes could cause this schedule to be altered. If the water in the moat froze and the keepers could not break it, the chimpanzees remained locked in their den from one day to several weeks. If the temperature was below 45 degrees F or if it was windy and wet (in the winter months) the chimpanzees were given access to the heated den all day long or may only be allowed out for a few hours. When the chimpanzees had access to the den, in any season, they usually went inside. As a result, fewer samples were taken in the winter, early mornings and evenings. Their behavior was altered by the new variable of the den area. Data were only collected when the chimpanzees were on the island.

The analyses of the data for diurnal and thermal variation demonstrated that these variables did not significantly affect usage for any group member. What may have affected diurnal usage was the time until feeding. The chimpanzees are fed 3 times a day at approximately the same time each day. About a half-hour before feeding times the chimpanzees began watching for the keepers from the vertical structures. The temperature did not affect the chimpanzees, however, sun and wind may have. In summer they appeared to go into the tunnels when the sun was shining. In winter they used areas that blocked the wind. However, this information was not recorded.

There was a seasonal variation for AF4. This female used the vertical space significantly more than any other group member. However, in the winter and fall she showed an increased use of the horizontal space and a decrease in her use of the vertical space. Another factor that may have caused what appeared to be a seasonal variation for this female is the age of her youngest offspring. Her infant was born in January 1989, the onset of the study. Her shift in usage may have been a result of the age of her offspring rather than the seasons. The Sacramento Zoo found the appearance of a seasonal variation in chimpanzees' use of their enclosure (Patty Gibson, pers. comm.). But individual chimpanzee use of the exhibit was not evaluated.

Another variable affecting the chimpanzees' usage of the island was the public. Public feeding of the animals was not allowed. The chimpanzees exhibit begging behavior which was reinforced by the public feeding them. When there were many visitors present the chimpanzees tended to gather along the edge of the moat in front of the public viewing area.

There are many variables that may affect the chimpanzees' use of the island. At the Tulsa Zoo these variables tend to show little real effect on the chimpanzees' spatial selection. The females' choice of selected areas appears to be stable.

Do the females recognize certain areas as being the preferred areas of other females? Indirect evidence indicates that they do. Lower-ranking females' avoidance of areas heavily used by higher-ranking females supports this hypothesis. This avoidance occurred despite no observation of a higher-ranking female taking an overt action to exclude a subordinate female from her occupied area. Only twice was another female observed in AF1's tunnel as she approached to go inside. Both times it was AF3, a high-ranking female subordinate to AF1. AF1 looked at AF3, and AF3 departed, bobbing her entire body. It appears that an area must be associated with a particular female and her rank. Low-ranking females, therefore, may never have an area that is recognized by other group members. The lower-ranking females both tended to use more of the island than the higher-ranking females. This may be in response to the higher-ranking females' presence in the subordinate females' areas.

Compared to many other captive facilities, the chimpanzee facility at the Tulsa Zoo provides an unusually large and diverse area to its occupants. Because this group has also been housed together for about 8 years, relationships between group members are well established. The stability of the social structure and the amount and type of space in which it is housed may affect the group's behavior. The chimpanzees seldom exhibit aberrant behaviors such as hair plucking, reingestion of vomit, coprophagy and rocking. Such behaviors may result from stress put on the chimpanzees as a result of their inability to separate themselves adequately. De Waal (1982) reported that by spring when the Arnhem Zoo chimpanzees are allowed back out on their island, after having spent the winter in the smaller indoor facility, many of the chimpanzees had large bare spots. The availability of areas in which the chimpanzees can separate themselves from other group members in captive situations may prove beneficial in reducing aberrant and aggressive behavior. This study of the Tulsa Zoo chimpanzees indicates that the individuals separate themselves from other group members by using different areas of their island habitat.

CONCLUSIONS

1. The female chimpanzees at the Tulsa Zoo use certain areas of their island habitat more extensively than other areas.

2. There was no diurnal or thermal variation in the

usage of selected areas.

3. One female, AF4, showed a seasonal variation in her usage of the island but the other group members did not.

4. The adult male tended to be present in areas most frequently used by cycling females.

5. Lower-ranking females appear to recognize areas used by the higher-ranking females and tend infrequently to use these areas.

6. High-ranking females will use areas heavily used by low-ranking females.

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TABLE I. Tulsa Zoo Chimpanzees, 1989.

I.D.*	D.O.B.	SEX	PARENTS	ARRIVED
AM2	1972	MALE	WILD	9-73
AF1	1962	FEMALE	WILD	6-63
AF3	1971	FEMALE	WILD	11-73
AF4	1973	FEMALE	WILD	4-77
AF5	1975	FEMALE	WILD	5-81
JF4	10-28-84	FEMALE	AM2/AF4	BORN
IF4	1-02-89	FEMALE	AM2/AF4	BORN
IM3	9-27-86	MALE	AM2/AF3	BORN
IM5	2-28-87	MALE	AM2/AF5	BORN

* First letter is age class: A=adult, J=juvenile, I=infant. Second letter is sex.
  # represents tenure in group for adults, 1 being longest tenure. # represents mother of juvenile or infant.

TABLE II. Chimpanzee Use Of The 7 Sections On Their Island, DF=6

I.D.	SECTIONS 1	2	3	4	5	6	7	Chi-Square
AM2	19%	9%	28%	2%	26%	8%	8%	49.0**
AF1	59%	2%	6%	5%	14%	3%	11%	207.9**
AF3	13%	10%	53%	4%	8%	1%	11%	150.5**
AF4	25%	11%	10%	4%	38%	7%	5%	73.1**
AF5	20%	13%	11%	3%	34%	15%	4%	56.0**

** p < .005

TABLE III. Results Of Chi-square Tests Performed On Each Adult Against Each Other Adult Group Member On Island Usage, DF=18

I.D.	Chi-Sq	Alpha	SAMPLE
AM2/AF1	69.1	.005	239
AM2/AF3	47.3	.005	232
AM2/AF4	50.9	.005	233
AM2/AF5	38.4	.005	236
AF1/AF3	116.7	.005	239
AF1/AF4	86.3	.005	240
AF1/AF5	83.2	.005	243
AF3/AF4	113.5	.005	233
AF3/AF5	108.1	.005	236
AF4/AF5	26.2	.100	237

TABLE IV. Results Of Chi-square Tests Performed On Each Adult Chimpanzee For Seasonal, Diurnal And Thermal Variation In Their Use Of The Island.

I.D.	AM2	AF1	AF3	AF4	AF5
Diurnal					
Chi-Sq	26.3	22.9	25.1	31.6	24.4
DF	34	34	34	34	36
Prob.	N.S.	N.S.	N.S.	N.S.	N.S.
Seasonal					
Chi-Sq	66.3	61.7	44.5	69.0	65.6
DF	51	51	51	51	54
Prob.	N.S.	N.S.	N.S.	<.05	N.S.
Thermal					
Chi-Sq	39.6	26.8	20.0	39.3	38.9
DF	34	34	34	34	36
Prob.	N.S.	N.S.	N.S.	N.S.	N.S.

Fig. 1. Chimpanzee island at the Tulsa Zoo. Island was divided into VII sections and structures where identified. T# represents tunnel and section number. PF represents platform in section I. TM represents termite mound.

CHIMP ISLAND AT THE TULSA ZOO

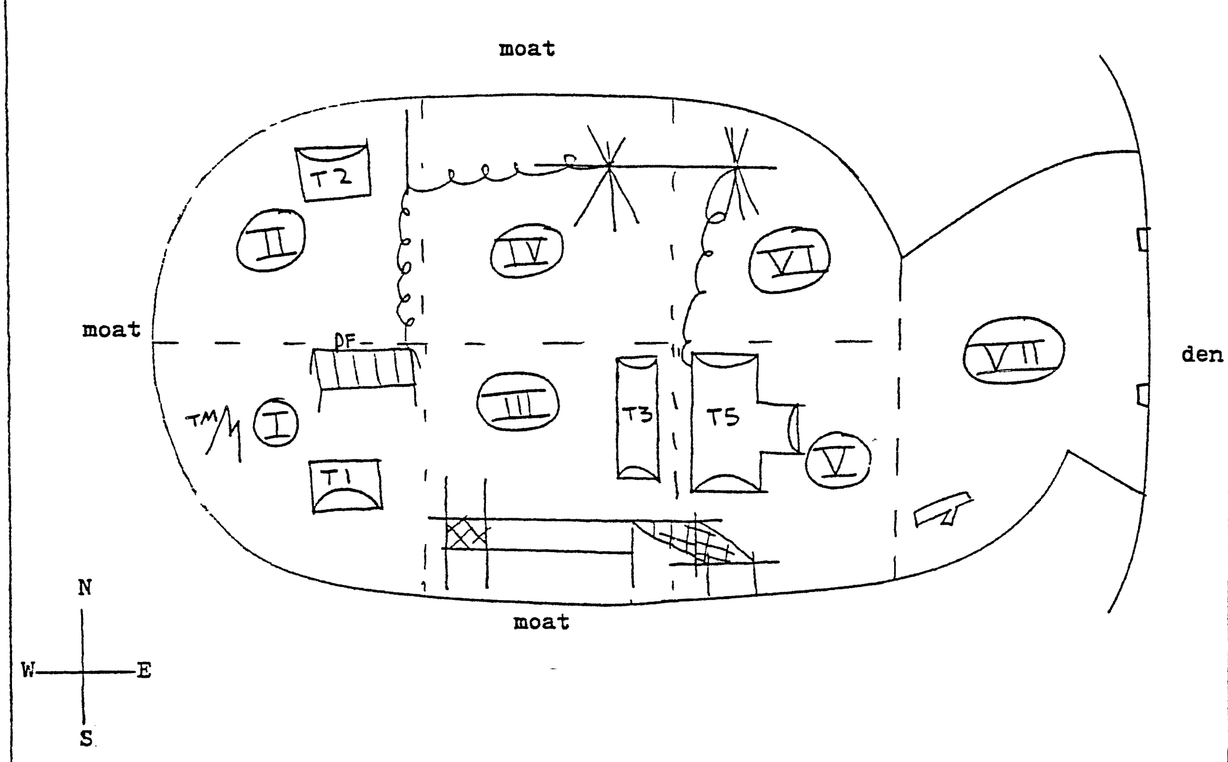


Fig. 2. Areas of the island most frequently used by each adult chimpanzee in the study.

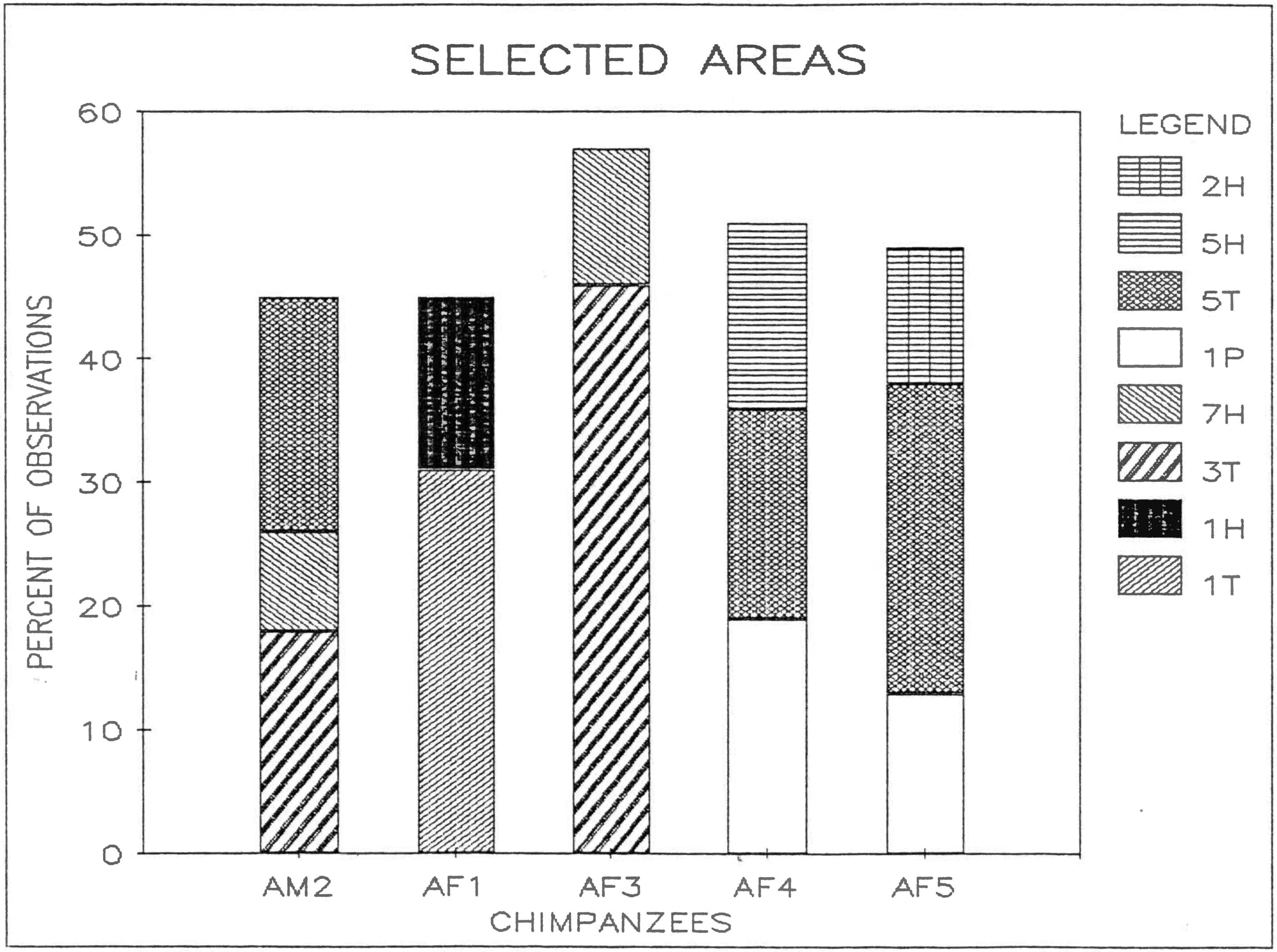

SELECTED AREAS
60
50
40
30
20
10
0
PERCENT OF OBSERVATIONS
AM2
AF1
AF3
AF4
AF5
CHIMPANZEES
LEGEND
2H
5H
5T
1P
7H
3T
1H
1T

Fig. 3. Comparison of AF1's usage of the tunnel in section 1 and the other females in the study.

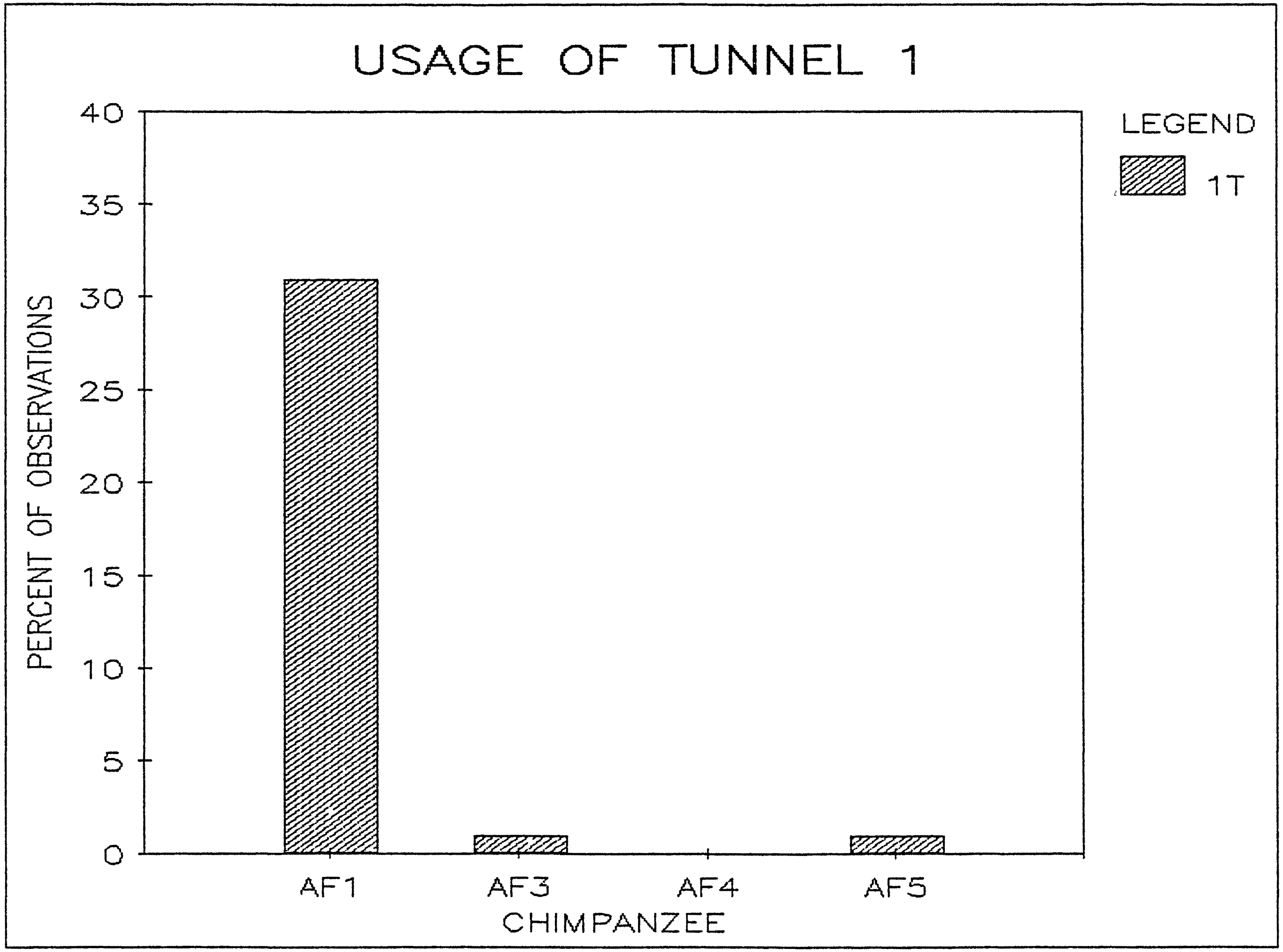

USAGE OF TUNNEL 1
PERCENT OF OBSERVATIONS
40
35
30
25
20
15
10
5
0
AF1
AF3
AF4
AF5
CHIMPANZEE
LEGEND
1T

Fig. 4. Comparison of AF3's usage of the tunnel in section 3 and the other females in the study.

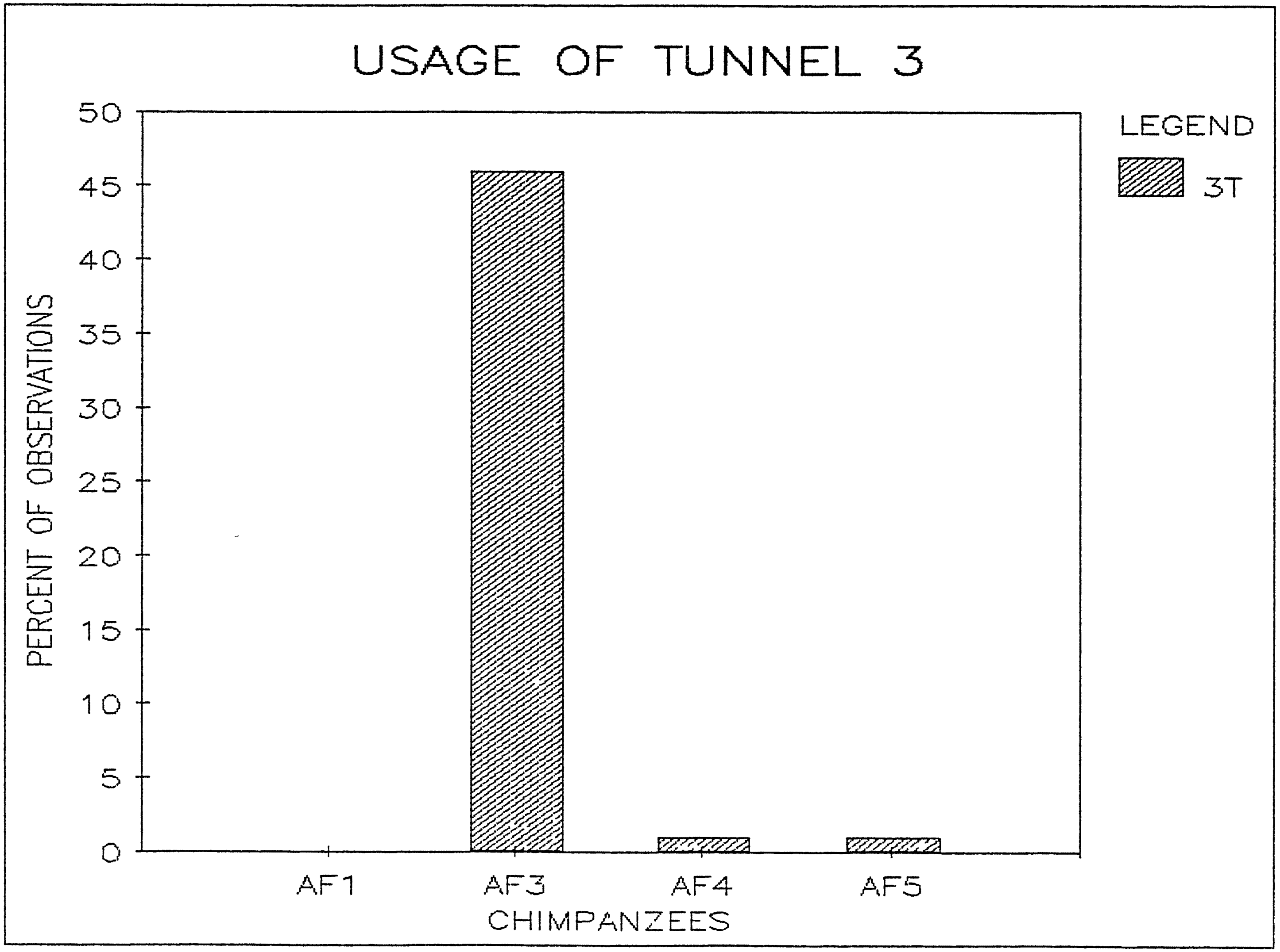

USAGE OF TUNNEL 3
PERCENT OF OBSERVATIONS
50
45
40
35
30
25
20
15
10
5
0
AF1
AF3
AF4
AF5
CHIMPANZEES
LEGEND
3T

Fig. 5. Comparison of AF4's usage of the platform and the other females in the study.

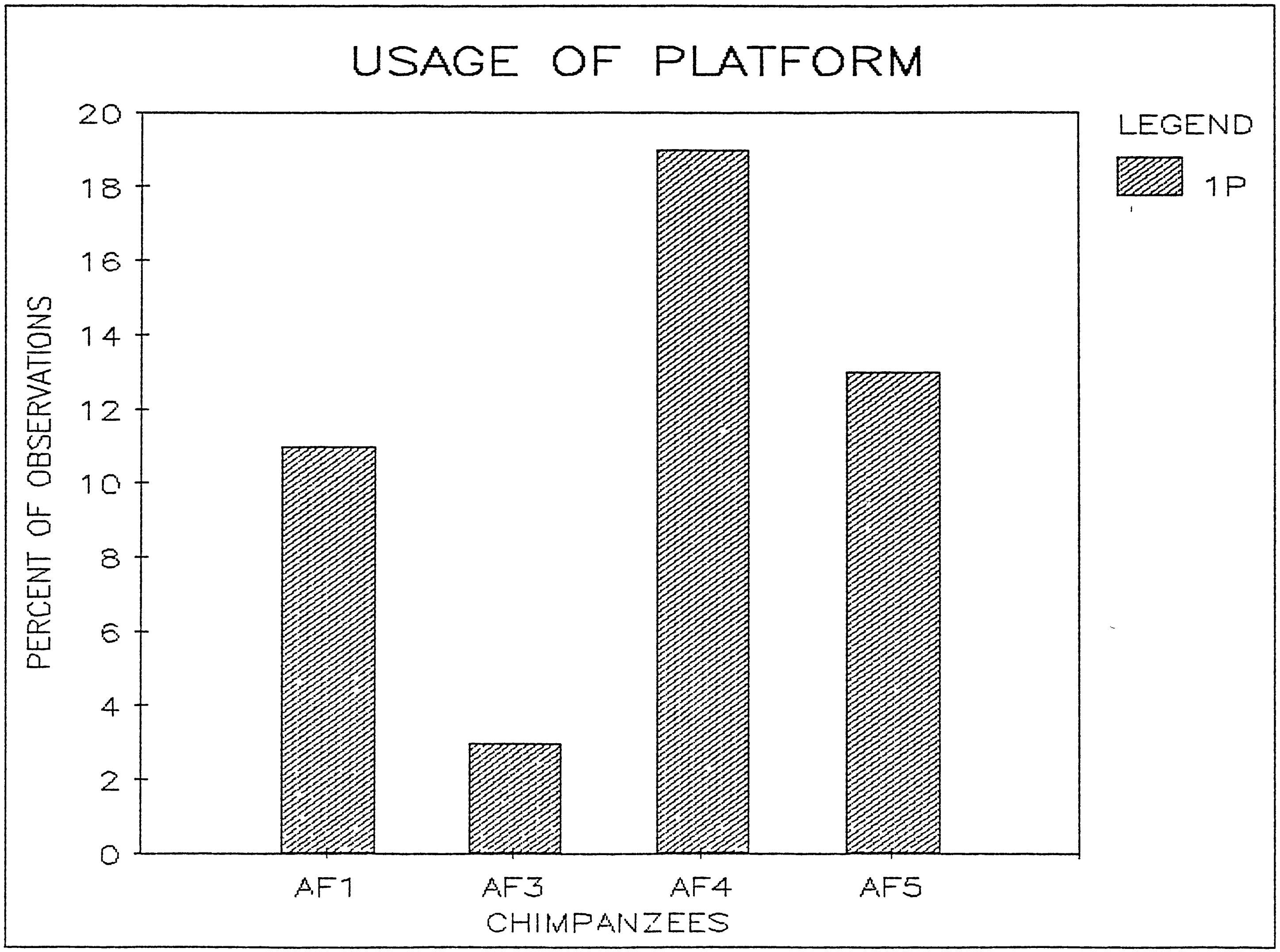
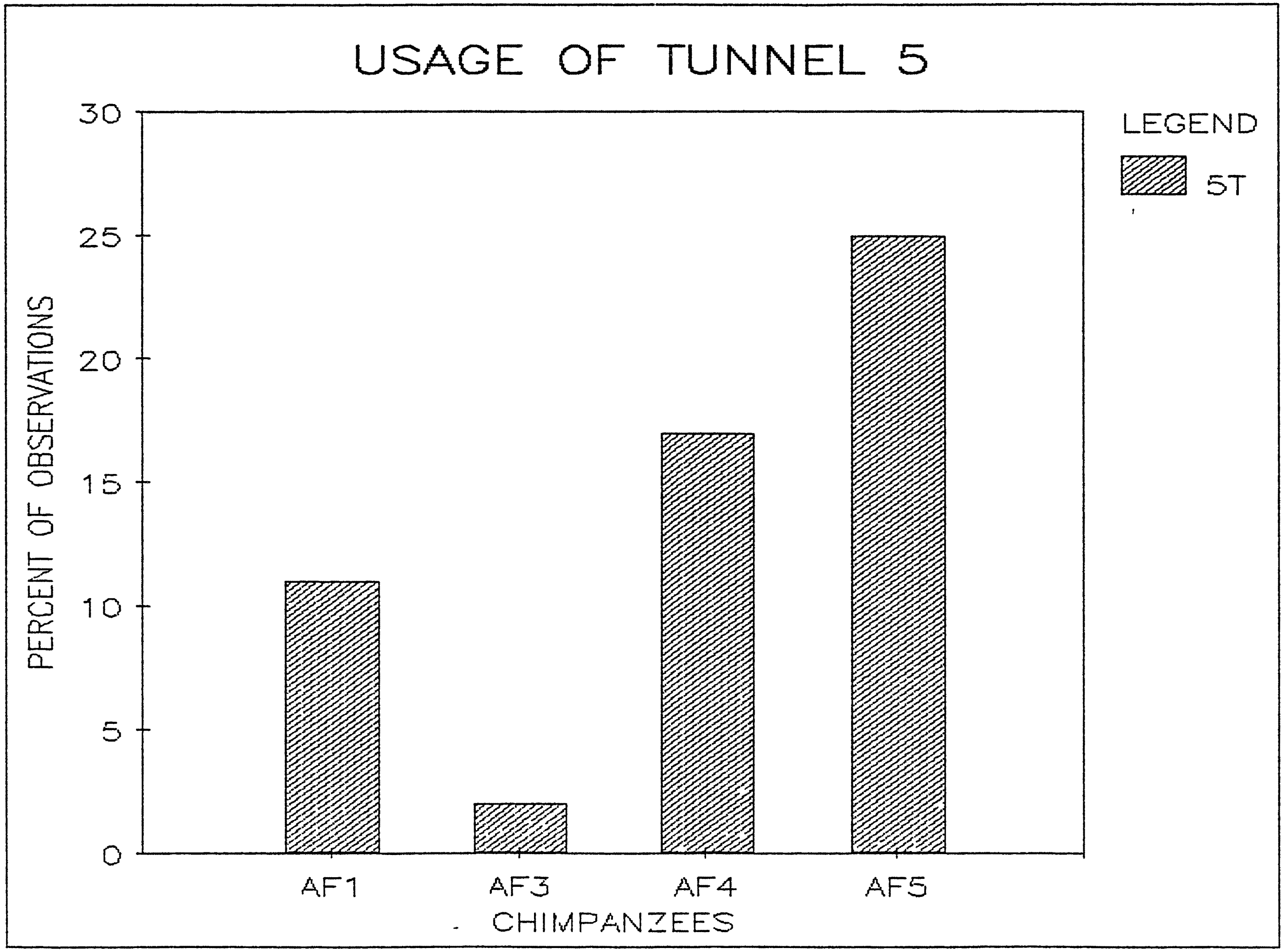

USAGE OF PLATFORM
PERCENT OF OBSERVATIONS
0
2
4
6
8
10
12
14
16
18
20
AF1
AF3
AF4
AF5
CHIMPANZEES
LEGEND
1P

Fig. 6. Comparison of AF5's usage of the tunnel in section 5 and the other females in the study.


USAGE OF TUNNEL 5
LEGEND
5T
PERCENT OF OBSERVATIONS
30
25
20
15
10
5
0
AF1
AF3
AF4
AF5
CHIMPANZEES

CHAPTER III

ASSOCIATION PATTERNS IN CAPTIVE ADULT CHIMPANZEES

ASSOCIATION PATTERNS IN CAPTIVE ADULT CHIMPANZEES

Association patterns of adult chimpanzees at the Tulsa Zoo were analyzed. Each chimpanzee showed a different association pattern. Adult females were observed alone or with their dependent offspring an average of 60% of the observations, while the male was alone only 26% of the observations. There was no diurnal variation in their association patterns. One adult female showed a significant seasonal variation; one female and the male showed a significant thermal variation. Two of the 3 cycling females showed a significant variation in association patterns resulting from their estrus state. These results reflect the different association patterns found between wild male and female chimpanzees.

Key Words: association pattern, social, solitary

INTRODUCTION

The social structure of chimpanzees was poorly understood for many years. The fusion-fission nature of the group caused researchers to assume the social organization was not a closed unit (Goodall, 1965; Reynolds & Reynolds, 1965). The long-term studies of habituated chimpanzees by

Lawick-Goodall (1968) and Nishida (1968) established the unit group (or community, Goodall, 1968) concept of social organization for chimpanzees. It is now known that a group of chimpanzees shares a common range and associates in temporary groups within this range. The complex nature of the fusion-fission society requires group members to identify members of their own group even when they are seen infrequently.

Relations between males of different unit groups are usually aggressive (Bygott, 1979; Goodall et al., 1979; Nishida, 1979). Females with sexual swellings may transfer between groups; however, once they give birth they typically settle in one group (Bygott, 1979; Pusey, 1979). Newly immigrated females are treated aggressively by resident females while males show a strong tendency to support newly immigrated females (Nishida, 1989).

Females are less sociable than males, spending most of their time with their own offspring (Nishida, 1968; Goodall, 1986). Anestrus adult female chimpanzees spent 65-70% of their time alone or with their offspring while adult males spent only 14-29% of their time alone (Halperin, 1979; Wrangham & Smuts, 1980).

Halperin (1979) found that females with more than one dependent offspring had the highest scores in the alone-with-offspring category while females with only one dependent offspring spent almost twice as much time in nursery groups (a nursery group consisted of multiple females with dependent offspring). Even the most gregarious females were less likely to be found in mixed social groups than the average male (Halperin, 1979). Females in estrus tended to travel more extensively than anestrus females and spent more time with adult males (Pusey, 1979).

The bond between mother and offspring is the strongest bond in chimpanzee society. Upon reaching adolescence (approximately 8 years of age) male offspring start leaving their mothers and associate more with adult males while females tend to associate with their mothers until they emigrate (Hayaki, 1988; Pusey, 1983; Goodall, 1986). Daughters that remain in their natal group may continue to have strong relationships with their mothers; a daughter may even share her mother's core area (Pusey, 1983). Although males begin associating less with their mothers once they reach puberty, Pusey (1983) found some adult males continued to interact with their mothers, associating with them more than with other anestrus females.

Males form strong relationships with other males in the group (Nishida, 1979) and brothers may form extremely strong bonds (Riss & Busse, 1977). Unlike other non-human primates, male membership in chimpanzee groups appears to be permanent (Itani, 1980). Since males remain in their natal group they are more likely to be closely related to one another. Males increase their inclusive fitness by cooperatively defending a territory (Wrangham, 1979; Ghiglieri, 1984). Since there will be more females in a larger area, males thus theoretically increase their chances of producing offspring (Wrangham, 1979). Older males and young males tend to be more solitary than males in their prime (Halperin, 1979).

The usual explanation for the solitary nature of female chimpanzees is that females maximize their feeding efficiency by spending their time primarily alone in a core area they know well (Wrangham, 1979; Wrangham & Smuts, 1980). Males, in contrast, sacrifice feeding efficiency by spending more time in social groups but increase their potential reproductive success by affiliative interactions with other males (Wrangham, 1979; Wrangham & Smuts, 1980).

In zoos, chimpanzees are typically housed in social groups. These usually consist of one adult male and females with offspring. Therefore, in captivity the social situation is the reverse of that found in the wild. Captivity requires females to be in close proximity to other females while the males typically do not have other adult males with whom to associate.

Studies of captive groups of chimpanzees have shown association patterns similar to those of wild chimpanzees (King et al., 1980; Nieuwenhuijsen and de Waal, 1982; de Waal, 1982; Gust, 1988). Nieuwenhuijsen and de Waal (1982) compared the social and solitary behavior of the Arnhem chimpanzees between the time the chimpanzees were kept in the indoor facility and the time they were kept in their outdoor facility (the indoor facility is 5.4% the size of the outdoor facility). They found that the adults did not engage in any more social behavior in the smaller facility. The solitary scores (which are based on proximity) decreased for the males in the winter (i.e. they spent more time in closer proximity to one another) but remained the same for the females. These data indicate that being in a small enclosure does not necessarily make chimpanzees become more social.

From a study conducted on the adult chimpanzees at the Tulsa Zoo, association patterns were analyzed to determine how frequently the chimpanzees associate with one another and how their association patterns compare with chimpanzees in other zoos and in the wild.

METHODS

This study was conducted on the chimpanzee (<u>Pan troglodytes</u>) population at the Tulsa Zoo, in Tulsa, Oklahoma, from January 1989 through July 1990. The chimpanzees were housed on an island measuring approximately 26 by 52 meters. The island was surrounded on three sides by a water moat 6 meters wide and on the fourth side by the night den wall. The island had numerous vertical structures, 4 concrete drainage pipes covered with dirt (referred to in the study as tunnels) and dense vegetation ranging from grass covering the ground to trees approximately 2 meters high. The dense vegetation and hilly terrain of the island enabled the chimpanzees to isolate themselves from one another visually and spatially. The chimpanzees were on the island 6 to 10 hours a day, weather permitting.

Nine chimpanzees were present during the study (Table I). Data were collected on the 4 adult females and 1 adult male. The composition of this group has been very stable. The adult female with the shortest tenure in the group was added in 1981. All 4 adult females and the male have been housed together on this island since that time. Additions to the group have been by births from 3 of the females and deletions have been through the surplus of these offspring at approximately 5 years of age (one infant died at 6 months of age). During this study there were no changes in group composition.

AF1 was clearly the dominant female in this group. AF4 and AF5 were subordinate females. Therefore, in this study high-ranking refers to AF1 and AF3 and low-ranking refers to AF4 and AF5.

AF1 has never reproduced. Although she cycled regularly, she did not allow mating by the adult male or infant males in the group. AF3 resumed post-partum cycling in January 1989 and may have become pregnant by the end of the study. AF4 gave birth in January 1989 and was lactating throughout the study. AF5 resumed post-partum cycling in July 1989.

Data were collected by instantaneous sampling on a focal animal (Lehner, 1979). Data were recorded every 30 seconds for 10 minutes on each adult chimpanzee. Location, behavior and group member within 5 feet of the focal animal or in the same tunnel as the focal animal were recorded. Data were collected from January 1989 through August 1990 and 100 hours of data were used in this analysis. Each 10-minute session was considered one sample (Martin and Bateson, 1986). There were 116 samples on AM2, 123 on AF1, 116 on AF3, 117 on AF4 and 120 on AF5.

Association patterns were determined by the presence of another group member within 5 feet of or in the same tunnel as the focal animal. The number of observations that each adult was scored alone, with dependent offspring (for adult females), with the adult male, with the adult male and dependent offspring, or in a mixed social group (with any of the above and/or another unrelated group member) was calculated. Association preferences were determined by the number of observations each adult associated with other group members. Effects of thermal, diurnal, seasonal and estrus cycle variation were analyzed. Statistical tests are discussed along with the results.

RESULTS

To compare data with other studies, association patterns were grouped into 3 categories: 1) alone or with offspring (for females with offspring, for AF1 and AM2 this category reflects alone scores only); 2) with the adult male or adult male and offspring (AF1 had no offspring, therefore, this category reflects observations with the male only); 3) mixed social group (any other individual or combination of individuals). Each female scored her highest number of observations in the alone or alone-with-offspring category while the male scored more observations in the mixed social group category. AF3 and AF4, both cycling females, spent more observations with the adult male than the other 2 females. Figure 1 shows each group member's association pattern during the study.

Association patterns were analyzed to determine if there were variations resulting from diurnal, seasonal, thermal or estrus cycles. Chi-square tests were run on each individual; therefore, tests reflect individual variation not group variation.

Diurnal Variation

Diurnal variation was broken into three categories: 1) before 10 a.m.; 2) from 10:01 a.m. until 2 p.m.; 3) from 2:01 p.m. until the night den doors were opened (usually between 4-5 p.m.). There was no significant variation for diurnal association patterns for any group member (Table II).

Seasonal Variation

Seasons were broken into 4 categories: 1) winter (Dec, Jan, Feb); 2) spring (Mar, Apr, May); 3) summer (June, July, Aug); 4) fall (Sep, Oct, Nov). AF1 showed a significant seasonal variation in her association patterns ($p < .05$, df=6). She was more solitary in the spring and more social in the summer. She became more social as a result of her increased use of the tunnel in section 5. It was the largest tunnel and has 3 openings which allowed a breeze through the tunnel. AF1 most frequently used the tunnel in section 1 which other group members seldom used. By increasing her use of the tunnel in section 5 in the summer, which was used by various other group members, she increased her association score. Other group members showed no significant variation as a result of seasons (Table II).

Thermal Variation

Temperature was broken into 3 categories: 1) below 60 degrees F; 2) 61 to 85 degrees F; 3) above 85 degrees F. AM2 and AF5 both showed a significant variation in association patterns as a result of temperature. Both AF5 ($p < .025$, df=4) and AM2 ($p < .025$, df=2) showed a decrease in their alone scores as temperature increased. Again, this is accounted for by an increase in the use of the tunnel in section 5 by most group members. Since all chimpanzees in a tunnel were scored together this would increase their association scores in the social group category. Other group members showed no significant variation (Table 2).

Estrus Cycle

Estrus cycles were broken into 3 categories: 1) no genital swelling (includes lactating females); 2) partial genital swelling; 3) full genital swelling. Three females were cycling during the study. AF1 showed no variation in her association pattern as a result of estrus ($p > .05$, df=4). This female does not copulate; therefore, her cycle state did not affect her association pattern with the male. AF3 ($p < .025$, df=8) and AF5 ($p < .025$, df=8) both showed a significant variation in their association patterns with the male as a result of their cycle state. As expected, both females interacted more with the male when they had a genital swelling than when they did not. AF5 associated with the male 74.7% of the time she had a full genital swelling. Her association with him dropped to 17.2% when she had a partial genital swelling. AF3 associated with the male 53.6% of the observations when she had a full genital swelling and 41.3% when she had a partial genital swelling. This is consistent with other data on chimpanzees; females associate more with males when they have a genital swelling than when they do not (King, et al., 1980; Pusey, 1979; Goodall, 1986). Table III shows the percent of observations the 3 cycling females spent with the adult male, AM2, during their different cycle states.

Location and Frequency

Each female having offspring scored her highest number of associations with her own offspring. The male was the adult all of the females associated with most frequently. The male associated most frequently with 2 of the cycling females, AF3 and AF5, and their offspring. Table IV shows frequency of associations with other group members.

All the adults except AF3 had their highest number of associations in the tunnel in section 5 of the island (Bettinger, in preparation). AF3 had her highest number of associations in the tunnel in section 3 of the island.

DISCUSSION

The chimpanzees at the Tulsa Zoo exhibit association patterns very similar to wild chimpanzees. The adult females averaged 60% of their observations alone or with offspring while the male spent only 26% of his observations alone. The most social female in the group, AF5, associated in a mixed social group only about half as frequently as the male.

The strongest bonds, determined by number of associations, were between the females and their offspring (Table IV). King et al. (1980) reported that the male in their group associated most with the cycling female in the group and her male offspring. They suggested that the male's association with the male offspring may be a result of males favoring male offspring as has been proposed by other researchers (Lawick-Goodall, 1968; Riss and Goodall, 1977). The male in this study also most frequently associated with the male offspring; however, it may simply be a result of their mothers' being the females cycling at the time.

AF4 had 2 female offspring in the group during the study. Her oldest offspring, JF4, was 4 years old at the onset of the study. AF4 scored her second highest number of associations with JF4, exactly half the number she scored with her infant daughter, IF4. This is consistent with the data on wild chimpanzees. As female offspring increase in age they begin spending less time with their mother; however, the association between mother and daughter remains strong as long as the daughter is in the natal group (Pusey, 1983). AF4 spent fewer observations alone than any other group member.

AF1's association patterns were unusual. Although she was a cycling female, she spent more observations alone than any other group member. She also showed no increase in association with the male during times of genital swelling

(Table III). This female does not copulate which would account for this unusual behavior. AF1 did associate with the male more than she did with other group members.

AF1's second and third highest associations were with the juvenile and infant daughters of AF4, JF4 and IF4 (Table IV). Although AF1 did not associate with AF4 significantly more than she did with any other group member, there appeared to be a relationship between them. AF1 and AF4 were supportive of each other during group conflicts and AF1 would also support AF4's offspring. De Waal (1982) found this same relationship between 2 females in the Arnhem colony of chimpanzees.

AF3 associated with group members other than the male and her offspring least of the females (Table IV). While she is a high-ranking female, she tended to stay away from the other group members. Even when other group members would congregate in the tunnel in section 5, she was seldom present.

AF5 had the most associations with non-related group members of the females in the group (Table IV). This female most frequently used the tunnel in section 5. This tunnel was the area where each adult chimpanzee, other than AF3, scored its highest number of associations. The tunnel in section 5 appeared to be an area of social activity. Horvat and Kraemer (1981) found that females with offspring interacted more frequently with individuals of the closest age class. AF5 frequently associated with AF4 and her offspring and IM3, but seldom with AF3.

AM2 scored his highest number of associations with AF5 followed closely by IM5, her offspring. His second highest associations with an adult were with AF3 followed by IM3, her offspring (Table IV). Both of these females were cycling during the study. AM2 associated least with AF4 and her offspring. AF4 gave birth at the onset of the study.

Each of the females in this group of chimpanzees exhibited an individual association pattern. Kawanaka (1984) found that the chimpanzees at Mahale do not associate indiscriminately. This was also true for the Tulsa Zoo chimpanzees. It is difficult to make comparisons between wild and captive studies since different parameters are used to determine solitary and social. The Tulsa Zoo chimpanzees appeared to have been minimizing their associations with each other. The results of this study indicated association values for the females at the Tulsa Zoo are very similar to those seen for wild chimpanzees. The male's association patterns were similar to those of wild males with the exception that he had no other males with which to associate.

CONCLUSIONS

1. Female chimpanzees were alone or with their dependent offspring an average of 60% of the observations,

while the male was alone only 26% of the observations.

2. There was no diurnal variation in association patterns, however, one female showed a seasonal variation and one female and the male showed a thermal variation.

3. Two of the 3 cycling females showed a variation as a result of their estrus state.

ACKNOWLEDGEMENTS

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TABLE I. Tulsa Zoo Chimpanzees, 1989.

I.D.*	D.O.B.	SEX	PARENTS	ARRIVED
AM2	1972	MALE	WILD	9-73
AF1	1962	FEMALE	WILD	6-63
AF3	1971	FEMALE	WILD	11-73
AF4	1973	FEMALE	WILD	4-77
AF5	1975	FEMALE	WILD	5-81
JF4	10-28-84	FEMALE	AM2/AF4	BORN
IF4	1-02-89	FEMALE	AM2/AF4	BORN
IM3	9-27-86	MALE	AM2/AF3	BORN
IM5	2-28-87	MALE	AM2/AF5	BORN

* First letter is age class: A=adult, J=juvenile, I=infant. Second letter is sex.
  # represents tenure in group for adults, 1 being longest tenure. # represents mother of juvenile or infant.

TABLE II. Results Of Chi-Square Tests On Variation In Association Patterns For 5 Adult Chimpanzees At The Tulsa Zoo.

Individual	Diurnal	Seasonal	Thermal	Estrus Cycle
AM2	N.S.	N.S.	*.025	Not applicable
AF1	N.S.	*.05	N.S.	N.S.
AF3	N.S.	N.S.	N.S.	*.025
AF4	N.S.	N.S.	N.S.	Not cycling
AF5	N.S.	N.S.	*.025	*.025

N.S. = not significant to at least $p < .05$

TABLE III. Frequency Of Association Of Cycling Females With The Male During Different Cycle States At The Tulsa Zoo.

Female	1.0	0.5	0.0
AF1	1.8%	8.7%	5.2%
AF3	53.6%	41.3%	10.9%
AF5	74.7%	17.2%	3.1%

1.0 represents full genital swelling
0.5 represents partial genital swelling
0.0 represents no genital swelling

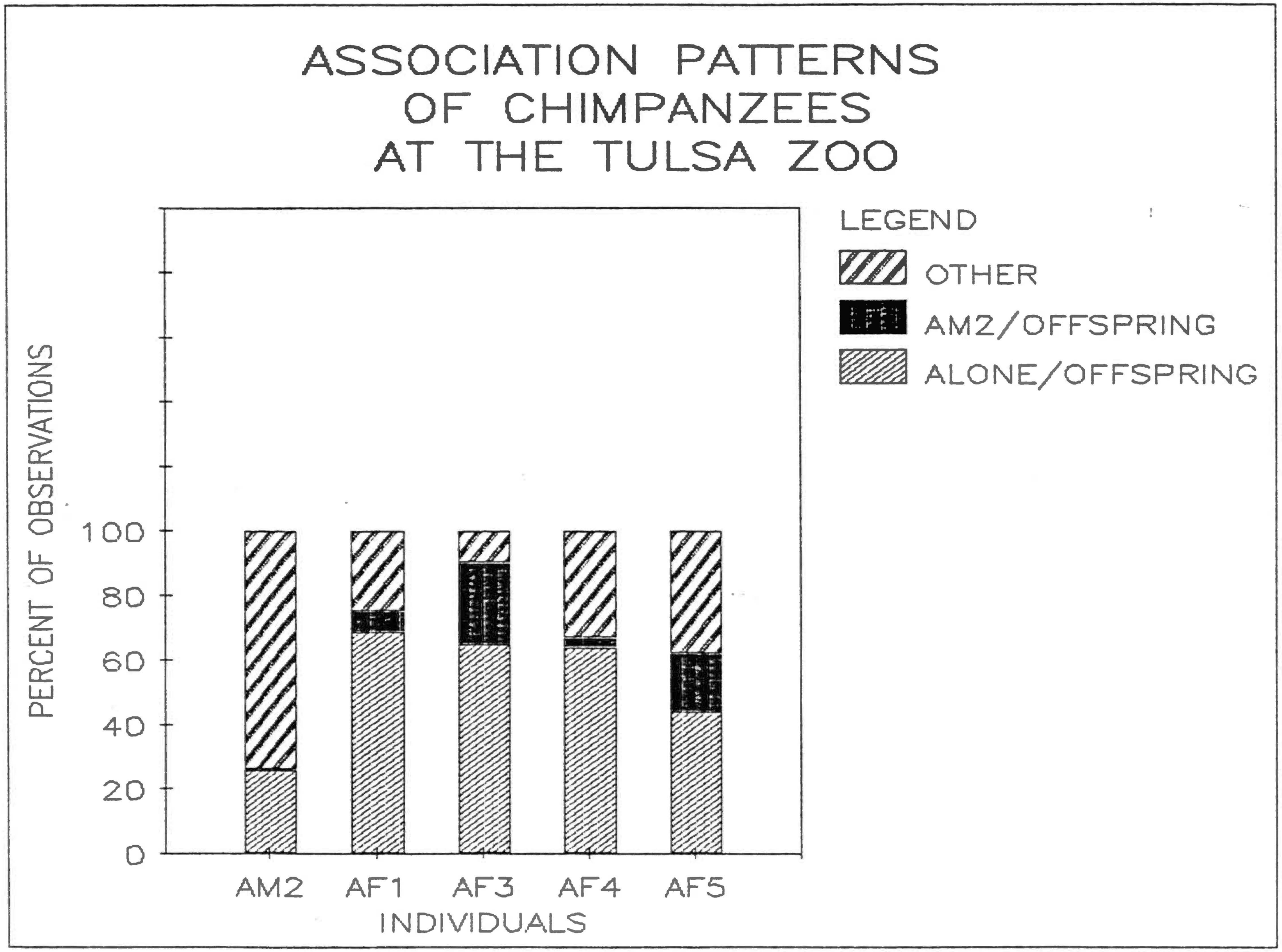
TABLE IV. Percent Of Observations That Each Adult Associated With Other Group Members.*

Group Member	AM2	AF1	AF3	AF4	AF5
ALONE**	26%	69%	33%	10%	19%
AM2	---	6%	19%	6%	16%
AF1	8%	---	2%	6%	5%
AF3	12%	2%	---	1%	2%
IM3	9%	1%	38%	3%	5%
AF4	6%	4%	1%	---	9%
JF4	6%	5%	3%	19%	6%
IF4	7%	5%	1%	39%	8%
AF5	14%	4%	2%	8%	---
IM5	12%	4%	1%	8%	30%

* These numbers reflect percentage of all associations. Percent includes times when each adult was with another individual, either singly or in a group.

** Alone in this table refers to no other group member (including offspring) within 5 feet of the focal animal.

Fig. 1. Percent of observations each adult chimpanzee spent in different association patterns.


ASSOCIATION PATTERNS
OF CHIMPANZEES
AT THE TULSA ZOO
LEGEND
OTHER
AM2/OFFSPRING
ALONE/OFFSPRING
PERCENT OF OBSERVATIONS
100
80
60
40
20
0
AM2
AF1
AF3
AF4
AF5
INDIVIDUALS

CHAPTER IV

BEHAVIOR EXHIBITED BY CAPTIVE ADULT CHIMPANZEES

BEHAVIOR EXHIBITED BY CAPTIVE ADULT CHIMPANZEES

Wild chimpanzees spend more than half their waking hours foraging and traveling between foraging sites. In captivity, where food is provided, chimpanzees must occupy their time with other activities. At the Tulsa Zoo, traveling, foraging, laying/sitting and grooming accounted for 74% of the behaviors observed. All behaviors observed have been found in both wild and other captive groups, although variation existed in frequency and technique. This group showed the same trends in choice of interactive partners as has been found in wild chimpanzees. Although some behaviors occurred infrequently, they may still have had an important impact on group structure and behavior.

Key Words: behavior, captivity, forage, groom, play, public, watch

INTRODUCTION

In the wild, chimpanzees spend a large portion of their time foraging. At Gombe Stream Reserve in Tanzania, the chimpanzees averaged 47% of their time foraging (Goodall, 1986) while in Kibale Forest in Uganda, they averaged 57% (Ghiglieri, 1984). Time spent traveling between food sources accounted for another 13% at Gombe (Goodall, 1986) and 11% at Kibale (Ghiglieri, 1984). Therefore, available time for other activities is directly related to food availability. Riss & Busse (1977) found that feeding time and inactive time are inversely proportional. Wild chimpanzees devoted only 30% to 40% of their active time to other behaviors.

In captivity, where food is provided, chimpanzees have considerably more time to engage in other social and solitary behavior. What do chimpanzees do in captivity? De Waal (1989) reported that the chimpanzees at the Arnhem Zoo "do remarkably little most of the time. They move slowly, eat grass, sleep for a long while, groom one another." In this study, at the Tulsa Zoo, these activities accounted for 74% of the observed behaviors.

Traveling, eating and sleeping provide chimpanzees with the essentials for existence, while grooming helps maintain social relationships. Grooming serves many functions in chimpanzee life. It calms excited group members, provides reassurance and appeasement, allows contact between group members, maintains and improves relations and rids the body of ectoparasites and debris (Goodall, 1986). Chimpanzees appear to relax during grooming.

Most behaviors observed in captivity have also been observed in wild chimpanzees. Variation may exist in frequency and technique. For example, most chimpanzees use tools. At Gombe they fish for termites with thin sticks; at Bossou they use large sticks to pull branches with fruit within reach; in Guinea, Liberia and Ivory Coast they use rocks as hammers (Goodall, 1986) and at the Tulsa Zoo they use branches to reach objects floating in the water moat. Aberrant behaviors are found in both wild and captive groups, although they may be more common in captivity.

This paper will discuss behaviors observed in a captive group of chimpanzees at the Tulsa Zoo. Most commonly observed behaviors, interactive partners and variation within the group and with other groups of chimpanzees will be discussed.

METHODS

The study was conducted on the chimpanzee (*Pan troglodytes*) population at the Tulsa Zoo, in Tulsa, Oklahoma, from January 1989 through July 1990. The chimpanzees were housed on an island measuring approximately 26 by 52 meters. The island was surrounded on 3 sides by a water moat 6 meters wide and on the fourth side by the night den wall. The island had numerous vertical structures, 4 concrete drainage pipes covered with dirt (referred to in the study as tunnels) and vegetation ranging from grass to thick bushes and trees approximately 2 meters high. The dense vegetation and topographic relief enabled the chimpanzees to isolate themselves both visually and spatially. The chimpanzees were on the island 6 to 10 hours a day, weather permitting. All data were collected when the chimpanzees were on the island.

Nine chimpanzees were present during the study (Table I). Data were collected on the 4 adult females and 1 adult male. These adults have been housed together on this island since 1981. Three of the females (AF3, AF4, AF5), had offspring present during the study. There were 3 females cycling during the study: AF1, AF3 and AF5. AF4 gave birth at the onset of the study and had 2 offspring in the group.

Data were collected by instantaneous sampling on a focal animal (Lehner, 1979). Data were recorded every 30 seconds for 10 minutes on each adult. Location, behavior and group member within 5 feet or in the same tunnel as the focal animal were recorded. Data were collected from January 1989 to August 1990 and 100 hours of data were used in this analysis. Each 10-minute session was considered 1 sample (Martin & Bateson, 1986). There were 116 samples on AM2; 123 on AF1; 116 on AF3; 117 on AF4 and 120 on AF5. Statistical tests were not conducted on the behavior portion of the data.

The chimpanzees were fed 3 times a day. The first feeding was in the morning between 7:30 and 9 a.m. Vegetables were typically spread out on the island along with sunflower seeds; at random times the termite mound would be filled with mustard. The chimpanzees were then released onto the island. At approximately 1 p.m. they were fed fruit. Fruit was thrown by the keepers across the moat to each chimpanzee. The last feeding, monkey chow, was at approximately 4:30 p.m. when the chimpanzees were given access to the night den. Data were not collected during feeding times. Collection of data resumed 15 minutes after feeding. Foraging/eating in this study primarily refers to feeding on natural vegetation (however, an individual sometimes found a vegetable, peels or seeds that had been overlooked during a feeding).

RESULTS

Due to the presence of the dense vegetation and tunnels on the island, behavior could not always be determined. Therefore, 25% (3,025 out of 11,907) of the observation points were "bad observations". An observation was considered "bad" if the observer could not see the chimpanzee clearly enough to determine the behavior. This was frequently the case if the focal animal was in the heavy vegetation on the north side of the island. Some observations could be recorded when the chimpanzees were in the tunnels, depending on number of individuals present and amount of ambient light.

Some individuals were easier to observe than others. AF3 spent 46% of her observed time in the tunnel in section 3 (Bettinger, in preparation). In this tunnel she is difficult to observe; therefore, 40% of the observations of her behavior could not reliably be determined. AM2 also spent a great deal of time in tunnels. Behavior was undetermined on 32% of the observations of him. The other females were easier to observe and the percent of "bad observations" of them were as follows: AF1, 15%; AF4, 19%; and AF5, 21% (Figure 1).

The percent of "bad observations" on the different individuals reflects their different behavioral characteristics. AF3 was particularly solitary, isolating herself from other chimpanzees and the public, while AF1 and AF4 interacted with the public more than other group members. Goodall (1986) reported that some chimpanzees are more difficult to observe at Gombe also.

Eighteen behaviors were recorded, excluding "bad observation", on 8,882 observation points. Table II lists the behaviors and frequency for each adult. Some behaviors occurred very infrequently. Greeting behavior, including greeting an individual and being greeted, occurred only 7 times. Copulation was recorded only 4 times although there were cycling females present and this is a reproductively active group (except for AF1, who does not copulate).

The most frequently recorded behavior was lay/sit. This behavior accounted for 37% of the behaviors recorded. Traveling accounted for 10% and foraging accounted for another 11%. Although data were not recorded until 15 minutes after feedings, the chimpanzees were recorded foraging on 11% of the observations. Certain individuals foraged more frequently than other group members. AF5 accounted for 32% of the foraging recorded while AF3 accounted for another 29%. Both of these females were observed eating vegetation growing on the island. Foraging on the vegetation or for sunflower seeds thrown around the island was a slow process. Individuals would move slowly from place to place picking through the vegetation. Leaves and twigs were sometimes wadged.

Grooming, which includes grooming another individual, being groomed by another individual or self-grooming, was the second most frequent behavior (Figure 2), accounting for 16% of the behavioral observations. Grooming patterns were similar to those found in wild chimpanzees. Females with offspring most frequently groomed their own infants. AF3 and AF5 were never recorded to groom other infants, while AF4 groomed all other infants. AF1 seldom groomed any other group member. Only 3 times was she observed grooming others, all of whom were infants. The male most frequently groomed the cycling females. IF4 was the only infant he was observed grooming.

Individually, each chimpanzee groomed itself more often than it groomed any other individual. In the social grooming category, the male groomed other individuals twice as frequently as did any other group member, but received the least amount of grooming (Figure 2).

All of the females were groomed most frequently by the male. AF4, who had a juvenile daughter in the group, was groomed by her almost as much as she was by the male. Most of the grooming the male received was provided by JF4 (12 out of his 19 grooming scores were from JF4).

Watching was another behavior frequently exhibited, accounting for 13% of the observations. Each group member most frequently watched the public (which includes zoo visitors, keepers, and observer). AF1 and AF4 watched the public twice as much as did the rest of the group. The females with offspring watched their infants second most frequently. Figure 3 shows the percent of observations for the 5 most common behaviors.

Thirteen behaviors made up the remaining 13% of the observations. Since they occurred infrequently, they will be discussed and compared to other studies in the discussion section.

DISCUSSION

Seventy-four percent of the observations were travel, lay/sit, forage and groom. Instantaneous sampling of focal animals, often precludes recording of rare behaviors. Wild chimpanzees spend the majority of their time foraging and traveling and when resting they frequently groom. It is not surprising to find the same trend in captivity. Although a behavior may occur infrequently, it can have a large impact on the group.

Grooming and watching were the predominant social behaviors exhibited by this group of chimpanzees. Grooming provides contact with other group members. Consistent with other data on chimpanzees, grooming was not performed randomly. In the wild, adult females are most likely to groom their offspring while males most frequently groom one another (Ghiglieri, 1984; Goodall, 1986; Nishida, 1988). Females at the Tulsa Zoo also most frequently groomed their infants. There was only one male present in the group; therefore, the male at the Tulsa Zoo did not have the opportunity to groom other adult males.

Males have been reported to groom females with genital swellings more frequently than females without genital swellings (Lawick-Goodall, 1968; Merrick, 1977). This was true for AM2. He most frequently groomed females when they had a genital swelling. Tutin (1979) found that females were more likely to copulate with males that had groomed them. Goodall (1986) reported that at Gombe, when a male and female were in a consort, the male groomed the female more frequently than the female groomed the male. This was also found at the Tulsa Zoo. The females infrequently groomed the male.

Watching provides chimpanzees with information about other group members and their environment. Goodall (1986) reported that scanning the environment was quite common for the chimpanzees at Gombe. Visual vigilance probably evolved as an anti-predator behavior. In many species of monkeys, watching for predators is crucial to their existence. The major predator of chimpanzees is humans, but infant chimpanzees have been reported to be killed by male chimpanzees from neighboring groups (Goodall, 1986). To non-human predators, the adult chimpanzee is too formidable an opponent; however, infants which stray too far from the protection of their mothers may be susceptible to predation from leopards or other animals. Goodall (1986) reported no incidents of chimpanzees actually being attacked by non-human predators; however, she has reported incidents of chimpanzees responding aggressively toward leopards and lions (Goodall, 1986).

Watching may be the most important component of chimpanzee communication. Many signals used in chimpanzee communication are silent: facial expressions, body posture, piloerection and eye contact. Unlike most other non-human primates, eye contact in chimpanzees is used during friendly and reconciliatory interactions (Goodall, 1986). Both humans and chimpanzees avoid eye contact during strained relationships. De Waal (1989) found that eye contact was critical for reconciliation to take place in both chimpanzees and bonobos (Pan paniscus). He found the opposite to be true in rhesus monkeys (Macaca mulatta) and stump-tailed macaques (Macaca arctoides). They look opponents in the eye during aggressive behavior but avoid eye contact during friendly interactions.

Although chimpanzees may avoid making eye contact with one another during times of tension, they frequently watch one another. During periods of change in the male hierarchy at the Arnhem Zoo, males watched one another's behavior (de Waal, 1982). At the Tulsa Zoo, the male would watch the females with a swelling. If they moved to a different location he would move also, positioning himself where he could watch them. During periods when a female had a full swelling, he would also watch the infant males in the group. If they inspected a female he frequently pushed them away.

By watching other group members' behavior, an individual can adjust its own behavior accordingly. Piloerection is an autonomic response given during periods of excitement and aggression. When a male is preparing to display, the first signal often is his hair standing on end. For other group members this communicates his forthcoming behavior and allows them to make adjustments in their behavior such as submissive gestures, fleeing the area or retrieving infants that may get in the path of the displaying male.

Most communication between chimpanzees relies on visual cues (Goodall, 1986). They have well-developed facial musculature and a hairless face which allows for the evolution of facial expression to be used as signals in communication. Facial expressions are used in close proximity. Goodall (1986) reported that males patrolling the periphery of the territory at Gombe used a silent full closed grin (an expression that looks like a wide smile exposing both teeth and gums) when they heard or saw neighboring males. For this signal to be useful it must be seen by other members on the patrol.

Other signals, such as the pink genital swelling of females can communicate across long distances such as the valleys of Gombe. Chimpanzees appear to be able to recognize other group members by their posture and gait. Goodall (1986) reported that a juvenile separated from his mother stopped whimpering when he apparently recognized her across a valley at which time he returned to her.

One adult female at the Arnhem Zoo was deaf. She relied solely on visual cues from other group members and the environment. De Waal (1982) reported that she had no problem adjusting to group life, although sometimes she was slower to react than other group members. By watching other group members' behavior she could determine what was occurring in the group.

Young chimpanzees in the wild learn by watching and imitating other group members. Chimpanzees in captivity also learn by watching and imitating keepers and the public. The Tulsa Zoo chimpanzees often watched the public. This behavior may have served to alleviate boredom. Watching plays an important role in chimpanzee life. The complex nature of the social structure and the necessity of learning behaviors such as mothering and tool use require chimpanzees to maintain high levels of visual contact with their surroundings.

Aggression was recorded only 65 times in this group of chimpanzees, but the male was responsible for 88%. During 42 of his 57 total aggression scores, he was not displaying at any group member. Sometimes he displayed for no apparent reason. Goodall (1986) reported that males at Gombe sometimes displayed for no apparent reason also. Whenever the male did display, other group members stayed out of his way or were submissive toward him. The most frequently attacked group members were JF4 (7 times) and her mother AF4 (4 times). The other females were each attacked once and IM3 was attacked once.

Begging is another behavior that was not recorded frequently but does affect the group. Begging was recorded 39 times. AF1 was responsible for 79%. She begged from the public but not from other group members. AF1 was the dominant female, so when the public threw food across the moat (despite the prohibition of public feeding) she would take it away from group members who tried to obtain it. Only 3 times was begging directed at or from another group member; twice from infants to AF4, once from AF5 to the male. Begging frequency was probably higher than recorded. The presence of an observer usually inhibited most zoo visitors from throwing objects.

Play behavior was recorded 240 times (3%). All adults played; however, no adult was recorded playing with another adult. Adult females play with other adults very infrequently (King et al., 1980; Goodall, 1986). The females with offspring played primarily with their own offspring. The three mothers with infants played more than the female without offspring. AF1 had no offspring but she was recorded playing 32 times. Ninety-four percent of her play was with the offspring of AF4, JF4 and IF4.

The male played most frequently; 38% of play recorded was by the male. He played with all the infants and the juvenile in the group. He played with IF4 2.4 times more than he played with any other group member. This contradicts what King et al. (1980) found for the Washington Park Zoo chimpanzees. They found that the male preferred the male offspring. Their finding is consistent with Goodall's (1968) data indicating that males preferred male infants. The other infants in the Tulsa Zoo group were both males and their mothers were cycling. AM2's choice of play partners may reflect the age of the infants and their behavioral characteristics. IF4 was the youngest infant in the group and very outgoing. Her older sister, JF4, frequently groomed AM2. IF4 would climb on AM2 and was even observed riding on his back on 2 occasions. The other 2 infants, IM3 and IM5, were both approaching what in captivity may be considered the juvenile stage. Their behavior toward him was more guarded than that of IF4.

Savage et al. (1973) found that play was the dominant behavior if at least one infant was involved. This was also true of the Tulsa Zoo group. The majority of the interactions involving infants (other than by the infants' mothers) was in play.

The Tulsa Zoo chimpanzees use tools in various ways. Tool use was recorded in the category "manipulate". This category includes: sponging behavior -- the use of chewed sticks or leaves which are dipped into the moat and then sucked; fishing behavior -- the use of a branch or stick broken off the bushes and trees on the island to get mustard out of the termite mound or objects out of the moat; cups -- any object retrieved from the moat that can be filled with water for drinking (this includes plastic cups, lids, cans, orange peels, etc.); weapons -- miscellaneous objects such as sticks and rocks which are used as projectiles either being thrown across the moat at the public or at other animals that get on the island with the chimps (birds, squirrels, and bullfrogs are most common).

Two aberrant behaviors were recorded "sway" and "inspect feces". Sway refers to a slight side-to-side rocking movement. This behavior was recorded 47 times. AF4 accounted for 45 of the observations. She began this behavior after the birth of her last infant, IF4, and typically does it when she is sitting idly.

Inspect feces is when the chimpanzee defecates into its hand (typically) or onto a structure and then inspects the feces. This behavior was recorded 28 times. Ingestion of the feces, which was included in this category of behavior, was only recorded 3 times, all by AF5. The male was recorded inspecting his feces 17 times. All chimpanzees except AF4 were recorded inspecting their feces at least once. Whether this behavior is aberrant or not is subjective. To adult humans it is aberrant; however, it may not be to chimpanzees. The male was recorded to urinate, defecate and inspect feces at least twice as much as any female. Perhaps because males are territorial these behaviors are more common. Coprophagy has been observed in wild chimpanzees; however, it is unusual (Goodall, 1986).

The chimpanzees at the Tulsa Zoo exhibit a wide variety of behaviors. Most behaviors occur infrequently, while resting, traveling, foraging and grooming occur frequently. A goal of the ChimpanZoo project, coordinated by the Jane Goodall Institute, is to establish a long-term data base on captive chimpanzees. It is hoped this project will reveal similarities and differences between groups of captive chimpanzees.

CONCLUSIONS

1. Seventy-four percent of the observations on the chimpanzees at the Tulsa Zoo were either traveling, foraging, grooming or lay/sit.

2. All of the group members most frequently groomed themselves. In social grooming, the females most often groomed their own infants. The females most frequently were groomed by the male. The male received the least grooming of any adult.

3. The chimpanzees watched other group members and the public. They most frequently watched the public.

4. All of the adults played with the infants in the group. Adults did not play with one another and females most frequently played with their own infant.

5. Two aberrant behaviors, sway and inspect feces, were recorded; however, their frequency was low.

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TABLE I. Tulsa Zoo Chimpanzees, 1989.

I.D.*	D.O.B.	SEX	PARENTS	ARRIVED
AM2	1972	MALE	WILD	9-73
AF1	1962	FEMALE	WILD	6-63
AF3	1971	FEMALE	WILD	11-73
AF4	1973	FEMALE	WILD	4-77
AF5	1975	FEMALE	WILD	5-81
JF4	10-28-84	FEMALE	AM2/AF4	BORN
IF4	1-02-89	FEMALE	AM2/AF4	BORN
IM3	9-27-86	MALE	AM2/AF3	BORN
IM5	2-28-87	MALE	AM2/AF5	BORN

* First letter is age class: A=adult, J=juvenile, I=infant. Second letter is sex.
  # represents tenure in group for adults, 1 being longest tenure. # represents mother of juvenile or infant.

TABLE II. Frequency Of Behaviors Exhibited By Adult Chimpanzees At The Tulsa Zoo.

BEHAVIOR	AM2	AF1	AF3	AF4	AF5	TOTAL
Aggressive	57	6	1	1	0	65
Beg	2	31	2	3	1	39
Copulate	2	0	0	0	2	4
Excretion	28	9	3	9	4	53
Forage/Eat	106	124	283	160	310	983
Groom: GR						1455
Solitary:						
GR Self	156	66	56	155	155	(588)
Social:						
GR other	219	3	61	110	102	(495)
Being GR	19	86	94	44	129	(372)
Greet	3	1	0	1	2	7
Hold	1	4	32	157	44	238
Inspect	14	2	9	1	9	35
Inspect Feces	17	2	1	0	8	28
Lay/Sit	458	1022	522	655	580	3237
Manipulate	8	13	13	8	26	68
Play	92	32	33	46	37	240
Stand	41	134	12	30	43	260
Travel	184	217	169	183	177	930
Scratch	6	5	4	3	2	20
Sway	0	0	0	45	2	47
Watch	180	345	111	318	219	1173
SUBTOTAL	1593	2102	1406	1929	1852	8882
BAD OBSERV.:	744	388	942	458	493	3025
TOTAL	2337	2490	2348	2387	2345	11907

Fig. 1. Percent of good and bad observations on each adult chimpanzee at the Tulsa Zoo.

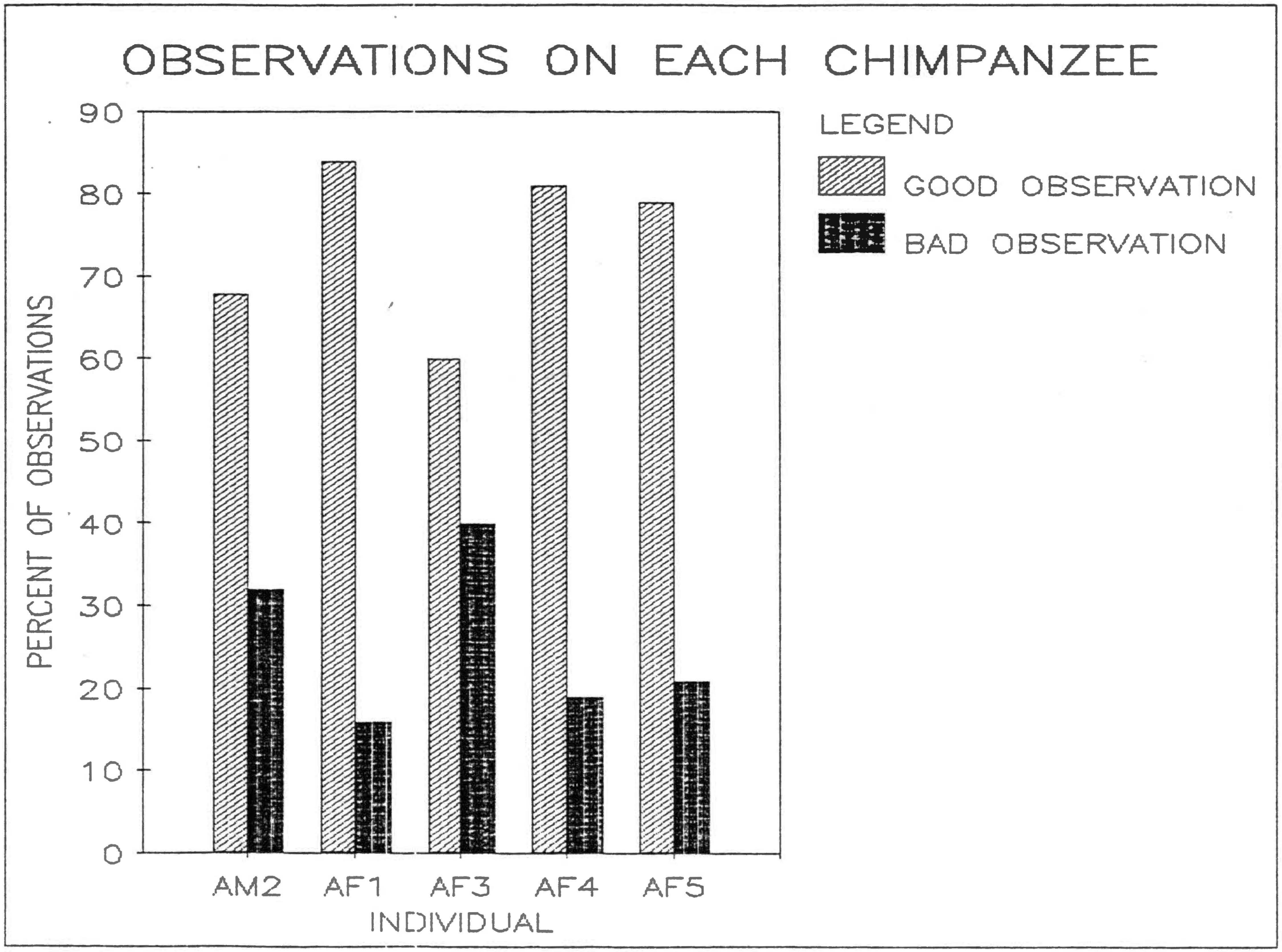

OBSERVATIONS ON EACH CHIMPANZEE
LEGEND
GOOD OBSERVATION
BAD OBSERVATION
PERCENT OF OBSERVATIONS
0
10
20
30
40
50
60
70
80
90
AM2
AF1
AF3
AF4
AF5
INDIVIDUAL

Fig. 2. Frequency of observations each adult chimpanzee at the Tulsa Zoo spent grooming itself, other group members or being groomed.

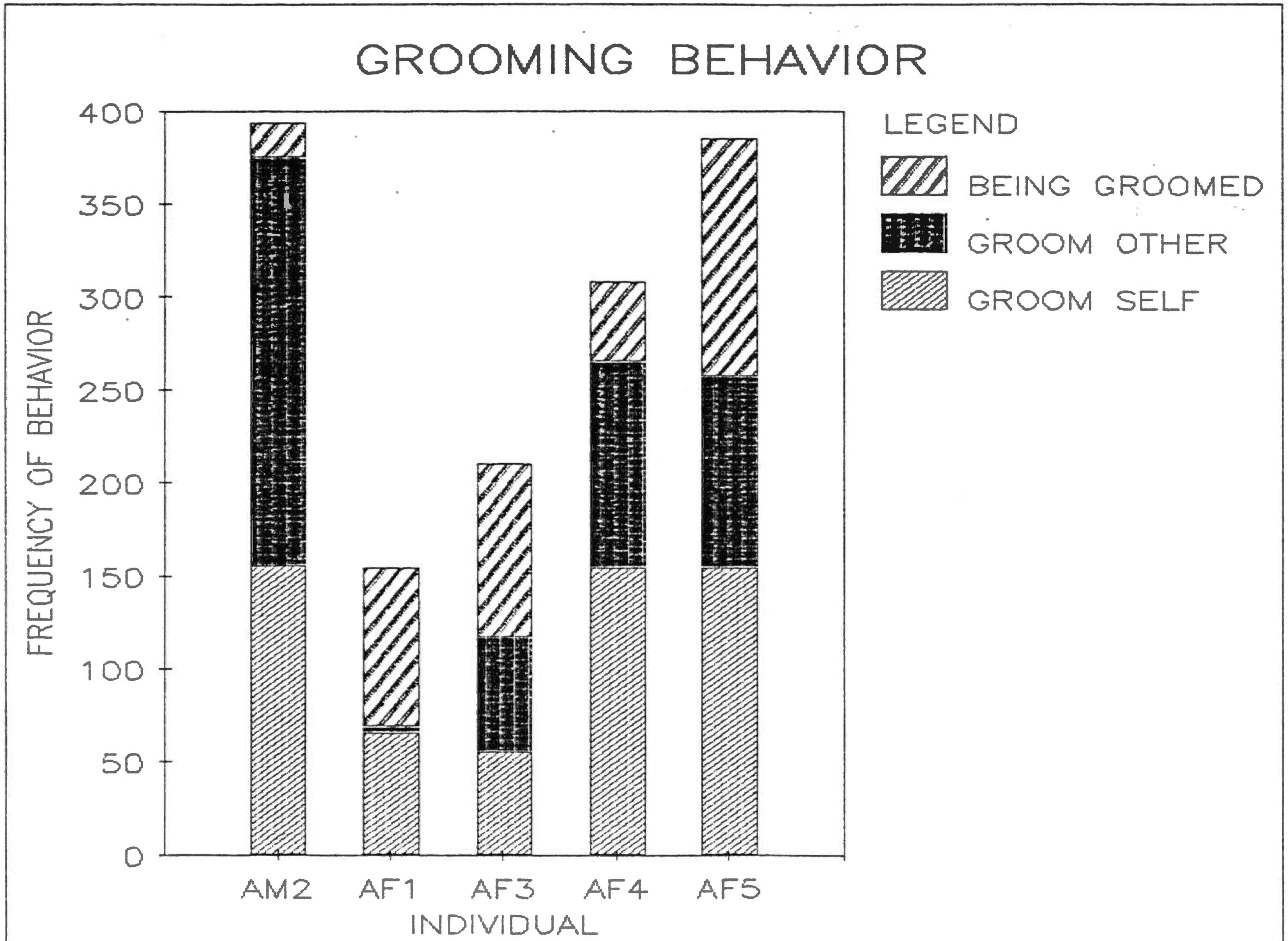
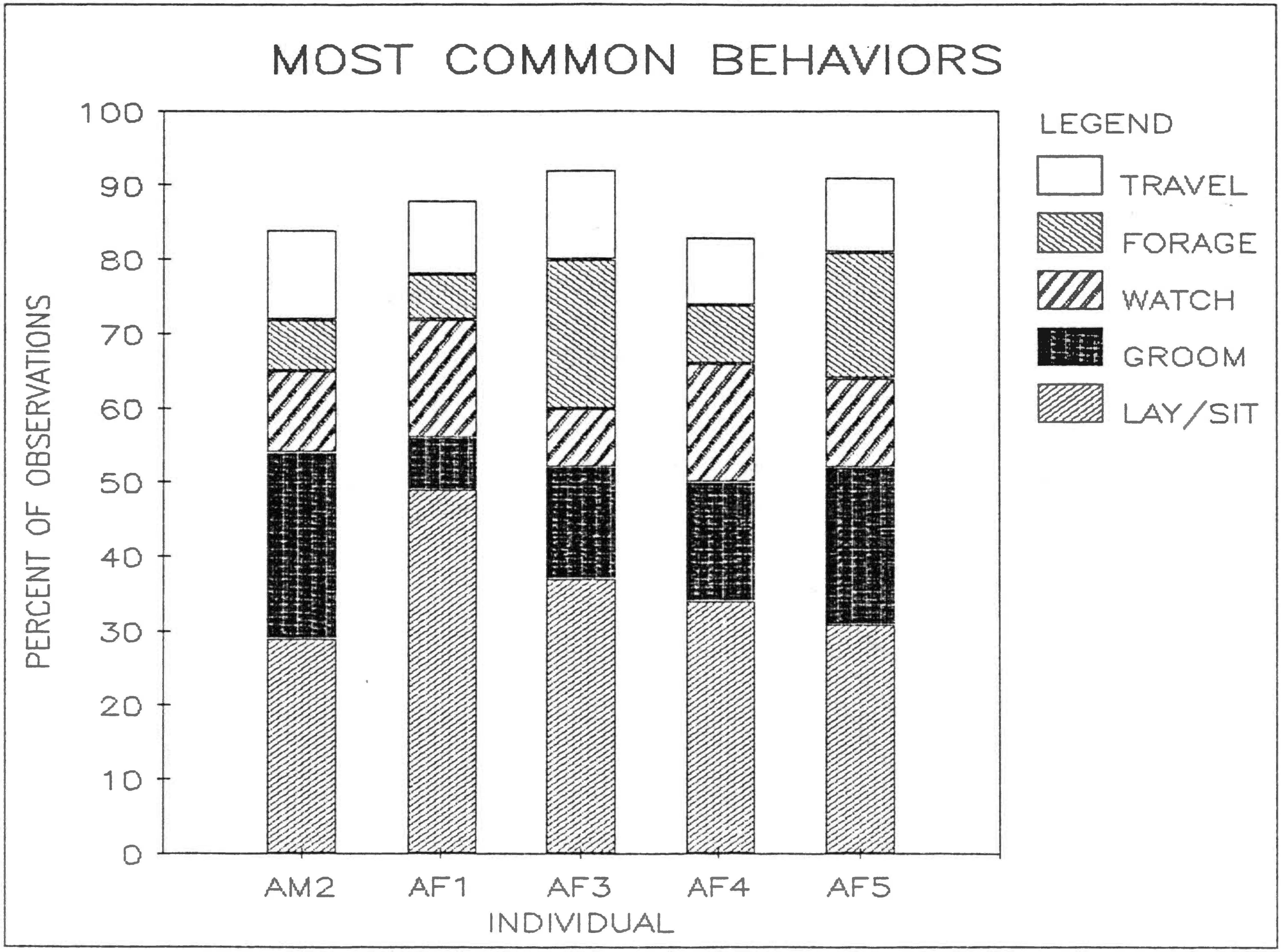

GROOMING BEHAVIOR
FREQUENCY OF BEHAVIOR
400
350
300
250
200
150
100
50
0
AM2
AF1
AF3
AF4
AF5
INDIVIDUAL
LEGEND
BEING GROOMED
GROOM OTHER
GROOM SELF

Fig. 3. The five most commonly recorded behaviors of the adult chimpanzees at the Tulsa Zoo.


MOST COMMON BEHAVIORS
LEGEND
TRAVEL
FORAGE
WATCH
GROOM
LAY/SIT
PERCENT OF OBSERVATIONS
0
10
20
30
40
50
60
70
80
90
100
AM2
AF1
AF3
AF4
AF5
INDIVIDUAL

VITA

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