BEHAVIORAL PATTERNS AND SPACE UTILIZATION IN A CAPTIVE GROUP OF DIANA MONKEYS, *CERCOPITHECUS DIANA*

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BEHAVIORAL PATTERNS AND SPACE

UTILIZATION IN A CAPTIVE

GROUP OF DIANA MONKEYS,

CERCOPITHECUS DIANA

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CHAPTER I

PREFACE

There are four chapters in this thesis. Each chapter is written in the format for a specific scientific journal. Chapter II is written in the format for a brief report in the journal Folia Primatologica. Chapter III is written in the format for publication in the journal Zoo Biology. The fourth chapter is a synopsis of the thesis. This work was funded by Tulsa Zoo Friends and Tulsa Zoo (Tulsa, OK, USA).

CHAPTER II

FACTORS AFFECTING AGGRESSION IN CAPTIVE GROUPS OF DIANA MONKEYS, *CERCOPITHECUS DIANA*

Introduction

Diana monkeys are highly arboreal, rainforest dwelling guenons native to lowland West Africa [1,2]. As with many other primate species, these monkeys are threatened with extinction [3]. Forest destruction and over-hunting are the primary causes of their decline [1,4-6]. Due to their arboreal nature and tendency to inhabit mid to upper-canopy layers of primary and secondary forest, tracking and observing Diana monkeys in the wild is difficult; therefore, few field studies have been conducted [2,7]. Upper canopy layers of the rainforest may be structurally complex. This complexity could limit the amount of visual contact between monkeys in a social group and thus influence social behavior.

The social group compositions observed in the field have consisted of one adult male, multiple adult females (presumed to be related) forming a female bonded core, and immature offspring [7-9]. In captivity, however, managers have encountered difficulties establishing and maintaining

groups which contain more than one adult female [10]. Tulsa Zoo recently conducted a survey of international and U.S. zoos housing Diana monkeys which showed that only 11 of 45 groups (24%) currently maintain multiple adult females in a social group. Of this 11, seven contained related adult females. Attempts made by zoos to establish and maintain multiple adult females in a group have resulted in high levels of aggression and, in some instances, failure to achieve the desired, natural group composition [M.G. Williams, unpubl. data]. In addition to problems with aggression, captive animals are declining in numbers due to low rates of reproduction [10]. Competition for limited space or other resources may also affect the success of Diana monkeys in captivity. In addition, the lack of visual barriers in a captive setting could conceivably affect the success of a species adapted to this type of environment.

Tulsa Zoo (Tulsa, OK, USA) has exhibited Diana monkeys since 1963. During a 13 year period, 1983 to 1995, Tulsa housed Diana monkeys in nine different group compositions. Most of these groups were reproductively active. This contrasts what has been reported for Diana monkeys at many other captive facilities [10]. My objectives for this study were to determine whether levels of aggression differed among captive Diana monkey groups of various sizes and compositions. If levels of aggression did differ, what

factors were associated with aggression.

Materials and Methods

Data on aggressive interactions were obtained from 13 years (1983-1995) of daily keeper reports. Tulsa Zoo staff are trained to record, on a daily basis, all observed occurrences of aggression, sexual interactions, and reproductive states for primates housed at the zoo. A genealogy of the Diana monkeys at Tulsa Zoo and animal holding records from the zoo's records department were used to obtain group compositions during different time periods. Data on aggression were then summarized by month. When possible, the identity (age, gender and relatedness) of the individuals involved and the direction of the aggressive interactions were recorded. All of the Diana monkey groups used in the analyses were housed in the same exhibit, which differed over time only in structures and substrates located within the exhibit. In all groups containing multiple adult females, these females were related.

ANOVA was used to test for differences among the groups in overall levels of aggression and aggressive interactions which resulted in injury, referred to as wounding aggression. A Tukey's *a posteriori* test was performed to identify which group compositions differed in overall levels

of aggression. A multiple regression model was then constructed to examine factors affecting levels of aggression. The factors tested in the regression were chosen *a priori* to represent group size and composition changes. Statistical analyses were performed using the SAS statistical package [11].

Results

Nine different group compositions were housed at Tulsa Zoo over the 13 year sampling period; of this nine, only five groups had differing adult compositions (Table 1). Overall levels of aggression differed among the nine Diana monkey group compositions ($F=3.73$, $p=0.0005$). Frequency of wounding aggression, however, showed no differences between group compositions ($F=1.14$, $p=0.337$). Tukey's *a posteriori* test indicated three clusters of group compositions, corresponding to low, medium, and high levels of aggression. The Tukey's chart was as follows:

012	022	113	122	130	112	210	131	132

For this diagram, each three digit sequence represents the number of males, number of females, and number of immatures, respectively. The group composition which contained one adult male, three adult females, and two immature animals showed the highest levels of aggression. I classified the

group composition with two adult males and one adult female plus the composition consisting of one adult male, three adult females, and one immature together in one cluster which exhibited medium levels of aggression.

Significant relationships existed between levels of aggression and group size, the number of immatures, the number of adult females, and the interaction between the number of immatures and the number of adult females (Regression model $F=7.2$, $p=0.0001$). The number of immatures and the interaction between immature animal and adult female abundances were linearly related to levels of aggression ($T=-2.30$, $p=0.023$ and $T=3.5$, $p=0.0006$, respectively). The overall regression equation was:

$$\text{Aggression} = 0.24 \times \text{Group Size} + -0.9 \times \text{Number of Adult Females} + -1.6 \times \text{Number of Immatures} + 0.76 \times \text{Adult Female-Immature Interaction}$$

Most aggressive interactions occurred between two or more related adult females (55%).

Discussion

Overall levels of aggression differed among the nine Diana monkey group compositions; however, when levels of wounding aggression were examined, no differences were found. Most of the aggressive encounters were without injury, indicating that these interactions were primarily of

the visual display type (i.e. yawns, chases, stares, etc.). Visual threat displays may serve to reduce the risk of injury to individuals by thwarting physical confrontations, thus lowering the frequency of wounding aggression [12,13]. Threat displays have been observed in wild and captive Diana monkeys [2, 8, M. Williams, unpubl. data].

In general, the data indicated that levels of aggression increased with more than one adult female and more than one immature animal in a social group. In addition, the group composition consisting of two related adult males and one unrelated adult female also exhibited high levels of aggression. In the wild, Diana monkeys are thought to be polygynous [7-9]; therefore, this composition may be unnatural.

Levels of aggression increased as group compositions became more complex. Regression analysis indicated a linear relationship between levels of aggression and the interaction between the number of adult females and the number of immature animals in a group. As mentioned in the introduction, captive Diana monkeys differ in attainable group compositions from their wild counterparts [7-10]. Due to high levels of aggression and poor reproductive output, these animals are primarily housed in male-female pairs. Wild Diana monkeys are not reported to exhibit monogamous

behavior; in fact, only one species of *Cercopithecus*, the DeBrazza monkey (*Cercopithecus neglectus*), occurs in uni-male / uni-female groups. However, DeBrazza monkeys only exhibit monogamy in a portion of their native range [14]. The endangered Golden Bellied Mangabey (*Cercocebus galeritus chrysogaster*) has also been reported to be difficult to maintain in captivity due to increased levels of aggression with larger group sizes. As with Diana monkeys, this species cannot be maintained in group compositions similar to those reported for wild populations [Leslie Field, N.A. Regional Studbook Coordinator and Mangabey SSP Coordinator, pers. comm.].

Most recorded aggression in the Diana monkey groups at Tulsa Zoo occurred between related adult females. This high incidence of aggression between related females is perplexing due to this animal's polygynous nature in the wild [7-9]. It is assumed that female Diana monkeys do not disperse and thus are incorporated into the female-bonded core of the group [7-9, 14-16]. In addition, other factors not measurable given data limitations, such as competition for food and space or reproductive competition, could be influencing the observed levels of aggression [15, 17-18]. In all of my study groups with multiple related adult females, only one female was producing offspring at a time.

In fact, the same female would produce all of the offspring for the group over a period of years, despite the presence of other reproductive aged females. Although there were high levels of aggression between adult females within groups, the captive population at Tulsa Zoo has been reproductively active for nearly 30 years. This is of particular importance considering that only one-third of the captive population of Diana monkeys are reproducing [10]. The reproductive success of Diana monkeys at Tulsa Zoo may be related to the "family" structure of these groups over our study period. In all group compositions we examined, most of the individuals were related with changes in composition only occuring through deaths, births, removal of offspring, or, rarely, the introduction of a new group member. The social structure of these groups thus mimics the social dynamics of wild groups [7-9].

I believe that levels of aggression may be influenced not only by competition among group members in captivity, but also by the lack of visual barriers in the captive environment. Visual barriers allow individuals to conceal themselves from other group members. In the upper forest canopy where Diana monkeys reside, animals may not be in constant visual contact or even close proximity to one another. Captive environments, which lack structural complexity, may serve to increase stress within the social

group, causing the number of agonistic interactions to rise [19,20].

In summary, I found that levels of aggression tended to rise as group compositions became more complex. These results have particular significance because of the Diana monkey's threatened status and the paucity of ecological and behavioral data on this species in the wild [21]. Studies of Diana monkeys in captivity can provide valuable information for captive managers interested in maintaining and breeding this species. These studies may also provide insight into the species' behavioral ecology in the wild. This is particularly true of captive studies which utilize long-term data. Future areas of research on Diana monkeys should focus on the effects of competition within the captive environment. Studies conducted on larger more complex groups may provide insight as to whether competition for resources such as exhibit space or food, as well as reproductive competition, act to structure the social dynamics of this species. Also, studies of exhibit complexity and the role of visual barriers may provide guidelines for more efficient captive management.

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References

1 Oates JF: The distribution of *Cercopithecus* monkeys in West African forests; in Gautier-Hion A, Bourliére F, Gautier J-P, Kingdon J (eds): A Primate Radiation: Evolutionary Biology of the African Guenons. Cambridge, Cambridge University Press, 1988, pp 79-103.

2 Bourliére F, Hunkeler C, Bertrand M: Ecology and behavior of Lowe's Guenon (*Cercopithecus campbelli lowei*) in the Ivory Coast; in Napier JR, Napier PH (eds): Old World Monkeys: Evolution, Systematics and Behavior. New York, Academic Press, 1970, pp 297-349.

3 Wolfheim J: Primates of the World: Distribution, Abundance, and Conservation. Cambridge, Harvard Press, 1983.

4 Sanderson IT: The Monkey Kingdom. Philadelphia, Doubleday and Co, 1957.

5 Davies AG: Conservation of primates in the Gola Reserves, Sierra Leone. Primate Conservation 1987;8:151-153.

6 Nowak RM: Walker's Mammals of the World, Volume 1, Fifth Edition. Baltimore, Johns Hopkins University Press, 1991.

7 Byrne RW, Conning AM, Young J: Social relationships in a captive group of Diana monkeys (*Cercopithecus diana*). Primates 1983; 24:360-370.

8 Hill CM: The role of female Diana monkeys, *Cercopithecus diana*, in territorial defense. Animal Behavior 1994;47:425-431.

9 Whitesides GH: Interspecific associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: biological significance or chance? Animal Behavior 1989;37:760-776.

10 Stevenson MF: International Studbook for the Diana Monkey (*Cercopithecus diana diana*). Edinburgh, Royal Zoological Society of Scotland Unpublished Report, 1991.

11 SAS Institute: SAS User's Guide: Basics, Statistics. SAS Institute, Cary, North Carolina, 1982.

12 Wilson EO: Sociobiology: The New Synthesis. Cambridge, The Belknap Press of Harvard University Press, 1975.

13 Nieuwenhuijsen K, de Waal FBM: Effects of spatial crowding on social behavior in a chimpanzee colony. Zoo Biology 1982;1:5-28.

14 Cords M: Forest guenons and Patas monkeys: male-male competition in one-male groups; in Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds): Primate Societies. Chicago, The University of Chicago Press, 1987, pp 98-111.

15 Shields WM: Dispersal and mating systems: Investigating their causal connections; in Chepko-Sade BD, Haplin ZT (eds): Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. Chicago, University of Chicago Press, 1987, pp 3-24.

16 Cheney DL, Seyfarth RM: Nonrandom dispersal in free-ranging Vervet monkeys: Social and genetic consequences. American Naturalist 1983; 122:392-412.

17 Wasser SK, Starling AK: Reproductive competition among female yellow baboons; in Else JG, Lee PC (eds): Primate Ontogeny, Cognition, and Social Behavior. Cambridge, Cambridge University Press, 1986, pp 343-354.

18 Wasser SK: Reproductive competition and cooperation among female yellow baboons; in Wasser SK (ed): Social Behavior of Female Vertebrates. New York, Academic Press, 1983, pp 349-390.

19 Brent L, Eichberg JW: Primate puzzleboard: a simple environmental enrichment device for captive chimpanzees. Zoo Biology 1991; 10:353-360.

20 de Vries A, Taylor LL: Enclosure utilization and time budgets of Japanese macaques (Macaca fuscata) at the Calgary Zoo. AAZPA Regional Proceedings 1989; 1989:377-382.

21 Oates JM: Action Plan for African Primate Conservation 1986-1990. Washington D.C., IUCN/WWF, 1986.

Table 1. Compositions of Diana monkey groups housed at Tulsa Zoo from 1983-1995.

Group Comp #	# Adult ♂	# Adult ♀	Immature	Total
1	0	1	2	3
2	0	2	2	4
3	1	1	1	3
4	1	1	2	4
5	1	1	3	5
6	1	2	2	5
7	1	3	0	4
8	1	3	1	5
9	1	3	2	6

CHAPTER III

BEHAVIORAL PATTERNS AND UTILIZATION OF EXHIBIT SPACE IN CAPTIVE DIANA MONKEYS

ABSTRACT

Diana monkeys (*Cercopithecus diana*) are highly arboreal, rainforest dwelling guenons native to West Africa. The persistence of this species in the wild is threatened due to habitat destruction and over-exploitation. In addition, its numbers are declining in captivity due to poor reproductive success. To provide additional information for successful captive management of this species, behavioral frequencies and space utilization data were collected for a reproductively active group of Diana monkeys housed at Tulsa Zoo (Tulsa, Oklahoma, USA). I determined that the most frequently occupied area of the exhibit was an enclosed overhead run connecting the indoor and outdoor exhibits. In addition, the monkeys most often occupied arboreal exhibit structures. The female and the infants were the most gregarious, while the adult male and the juvenile female were the most solitary. The adult male and the juvenile female were involved in more agonistic encounters, indicating that the adult male was the most dominant

individual while the juvenile female was the most subordinate (as determined by the rate and direction of aggressive interactions). These results support behavioral patterns documented in both captive and wild studies. These types of captive studies may provide useful information for the conservation of a species, particularly in the absence of field data. Captive studies can aid in our understanding of rare, elusive, or inadequately studied animals by bridging gaps in previously acquired behavioral and ecological data.

INTRODUCTION

Diana monkeys, *Cercopithecus diana*, are highly arboreal guenons native to primary and secondary rainforests of Sierra Leone, Southeast Guinea, Ghana, Ivory Coast, and Liberia. This species is currently threatened with extinction in the wild due to habitat destruction and over-hunting [Sanderson, 1957; Bourliére et al., 1970; Wolfheim, 1983; Davies, 1987; Oates, 1988; Nowak, 1991; Oates, 1996]. Diana monkeys have been maintained in captivity for over 50 years [Stevenson, 1993]; however, the captive population is declining due to poor reproductive success. Supplementing this declining population with wild stock is not feasible due to the Diana monkey's CITES Appendix I status and

African governmental restrictions on the trade of this threatened species [Stevenson, 1993].

Few studies have been conducted on Diana monkeys [Byrne et al., 1983]. In fact, much of the information on its ecology and behavior in the wild has come from studies where this type of data or this species was not the primary focus [Bourliére et al., 1970; Davies, 1987; Oates and Whitesides, 1990]. Field observations have shown that Diana monkeys are diurnal frugivores that live in harem or polygynous groups in the mid to upper canopies of West African rainforests [Bourliére et al., 1970; Oates and Whitesides, 1990; Hill, 1994].

Studies conducted in captivity may provide insight into the natural behavior and ecology of animals in the wild and, thus, become valuable tools for field biologists studying animals in their natural setting. Captive studies can also provide managers with knowledge enabling them to formulate solid management practices related to exhibit characteristics, husbandry, and enrichment [Eisenberg and Kleiman, 1977; Kawata, 1980; Byrne et al., 1983]. Since Diana monkeys are listed as a threatened species [Oates, 1996] and are the focus of a "Species Survival Plan" in captivity, the maintenance and growth of current captive populations is necessary for the persistence of this species. To develop optimal captive management practices

for the Diana monkey, it is essential that more studies on behavior and ecology be conducted in the wild. Further, successful groups in captivity must also be the focus of scientific investigations to address questions pertaining to reproduction, management practices, and health of Diana monkeys in the captive environment [Byrne et al., 1983].

Tulsa Zoo (Tulsa, Oklahoma, USA) has exhibited Diana monkeys since 1963. Currently, Tulsa houses a reproductive pair with several of their immature offspring. The objectives of this study were twofold. My first objective was to determine how this reproductively active group was utilizing their exhibit space. My second objective was to examine the behavioral repertoire of Tulsa Zoo's Diana monkeys to determine how they allocate their time in captivity. In addition, my findings were compared to those of previously published wild and captive studies. Because low reproductive success has been documented in captivity [Stevenson, 1993], information on the Tulsa Zoo group may provide valuable insight for managers of reproductively inactive groups.

MATERIALS AND METHODS

Study Subjects and Facilities

At the start of this study, Tulsa Zoo housed a social

group consisting of: one adult male, one adult female, and two immature offspring (one male and one female). One year after our study began, a third offspring (female) was produced and, shortly thereafter, one of the older immatures (juvenile female) was transferred to another zoo. All of the animals in our study were born in captivity, with the possible exception of the adult female (Table 1).

The Diana monkey exhibit at Tulsa Zoo is made up of an outdoor area (7.62 m × 2.13 m × 2.44 m), enclosed on the top and public side by chain-link fencing. The remaining three sides are concrete block and wood. One side wall of the outdoor exhibit is shared with siamangs (*Symphalangus syndactylus*) and the other side wall is shared with Celebes macaques (*Macaca niger*). An overhead run (1 m × 1.5 m × ~1 m) connects the outdoor area with an indoor area. The indoor exhibit (5.49 m × 2.44 m × 3.05 m) is fronted with glass for public viewing and has concrete block walls and ceiling (Figure 1). Cage furnishings for both indoor and outdoor areas consisted of: wooden platform ledges, tree limbs and logs, rocks, and ropes. The indoor area is equipped with sky-lights to provide natural lighting. During this study, animals were given access to both indoor and outdoor areas most of the time. Only when the exhibit was being cleaned or the temperature was below freezing were the

animals excluded from a particular area.

Data Collection

Data were collected from October 1994 to May 1996 using instantaneous scan and instantaneous focal sampling [Martin and Bateson, 1993; Lehner, 1996]. A total of 161.5 hours of behavioral data were collected. A minimum of 14 hours of behavioral data and 70 hours of locality data were collected for each individual. For all statistical analyses performed, I standardized these data by the number of observations. I created an ethogram of behaviors from pilot observations made in August and September 1994 (Appendix). This ethogram was used to characterize behaviors and contexts of the behaviors (i.e. agonistic, social or solitary) of focal animals throughout the study. The focal animal was considered "social" in context if there was a partner near or interacting with it. For example, if the focal was involved in a grooming interaction with another individual, the context would be "social". The behavior, in this instance, would be groom. The context was considered "agonistic" if the focal animal was involved in aggression or was submissive. The partner in these types of interactions was recorded as well. The context "solitary" was used if the focal animal was alone and was not

interacting with a partner. For focal animal sampling, data on context and behavior were recorded at 30 second intervals for 10 minutes. The order of focal observations was randomized prior to data collection.

I divided the exhibit into seven zones: three inside, three outside, and the overhead run (Figure 1). These zones were further subdivided into areas based on exhibit structures. Immediately following the focal sample, an instantaneous scan sample of the exhibit was made and the location (zone and cage furniture) within the exhibit of each group member was recorded. If an animal was located between two zones during a sample, the zone containing the largest proportion of its body was recorded.

Data Analyses

Space Utilization: The instantaneous scan samples of locality were used to characterize the Diana group's use of exhibit space. A frequency analysis was performed to examine how each individual utilized the exhibit. Spearman Rank Correlations were used on the ten most commonly utilized areas to determine if a particular individual's use of exhibit space correlated with any other individual's use. Spearman Rank Correlations were used because data did not meet assumptions of normality. The ten most commonly

utilized areas of the exhibit were used for this test to avoid spurious results due to rarely utilized areas, and the individual correlations were Bonferroni adjusted to reduce the probability of Type-I error [Sokal and Rohlf, 1994].

Chi-square tests were used to analyze a series of questions pertaining to exhibit use. First, I wanted to determine if the most frequently occupied area within the exhibit was used by all group members equally. Second, I tested whether the group members used arboreal or terrestrial structures most frequently. For this analysis I combined all structures above the ground into an "arboreal" category and the ground or floor of the exhibit into a "ground" or terrestrial category. A test was also performed to see if there were seasonal differences in arboreality. Finally, I examined whether the animals utilized indoor or outdoor areas most frequently. This relationship was also tested for seasonal differences.

Behavioral Patterns: Focal animal samples were used to analyze behavioral patterns within the Diana monkey group. A chi-square test was performed to determine if all of the animals in this social group exhibited similar behavioral frequencies. A second chi-square test was used to determine if there were differences in contextual frequencies.

Seasonal differences in contextual frequencies were also tested. The effect of time of day (morning or afternoon) on behavior was also examined with a chi-square test. A McNemar Symmetry Chi-square test [Sokal and Rohlf, 1994] was then used to determine which individuals were most often involved in agonistic interactions. Finally, I examined how aggression related to the age and sex of immature animals.

RESULTS

Space Utilization: A list of the ten most commonly utilized areas within the exhibit by individual was compiled (Table 2). Spearman Rank Correlations were then used to determine if any individual's use of space was associated with another group member's use of space (Table 3). There was a significant correlation of exhibit use between the adult female and the two infants ($K=0.77$ and 0.78, $p<0.01$). The most frequently occupied area of the exhibit by all individuals in the group was the overhead run, which connects the indoor and outdoor areas. However, this overhead run was not used by all group members equally ($X^2=2823$, $p<0.001$). The juvenile female used this area least frequently, while the adult male utilized this area most frequently. When the overhead run was excluded from the analysis, the animals still showed preferences for

certain areas (Table 2; $X^2=1759$, $p<0.001$).

Tulsa's Diana monkeys most often occupied arboreal cage structures ($X^2=1334$, $p<0.001$). The most terrestrial group member was the juvenile female (Figure 2). No significant seasonal effects were found for arboreality. I also determined that animals spent more time in the indoor portion of their exhibit ($X^2=1101$, $p<0.001$). There were significant seasonal effects, with indoor areas occupied more in the winter and outdoor areas occupied slightly more in the summer ($X^2=48$, $p<0.001$).

Behavioral Patterns: The monkeys in this social group did not behave with similar frequency ($X^2=9070$, $p<0.001$). The adult animals were involved in aggressive interactions more frequently than the immatures; the adult male was involved in the most non-contact aggressive interactions (visual or threat displays) while the adult female had the highest frequency of contact aggression within the group. The juvenile female exhibited more submissive behaviors, followed by the oldest infant male. Play behavior was exhibited with similar frequency among all of the immature animals and was rarely exhibited by adults. In fact, the adult male was the most idle or inactive group member, followed by the adult female. The adults and the juvenile

female were involved in grooming interactions with similar frequencies. The adult male exhibited the highest frequency of grooming interactions, while the two infants showed the lowest frequencies. The adult male was the recipient of grooming from the adult female and the juvenile female. Just as often, the adult male was observed grooming these two individuals. The juvenile female spent the most time foraging, followed by the oldest infant male. The adult female vocalized most frequently, followed by the juvenile female.

Individuals differed in the contexts of their behaviors (X^2=2680, $p<0.001$). The infants and the adult female were the most social animals while the adult male and the juvenile female were the most solitary. The adult male was involved in the most agonistic encounters, followed by the juvenile female. Agonism included both aggressive and submissive interactions. When seasonal differences in context were tested, a significant effect was found (X^2=516, $p<0.001$). Animals were more agonistic in the winter and solitary most often in the spring. In the winter months, Diana monkeys were confined to the indoor portion of their exhibit when temperatures fell below freezing. Social interactions were lowest in the spring.

Behaviors of the group differed by time of day (X^2=162, $p<0.001$). Play behavior was most common in the morning

while animals were more idle in the afternoon. In general, animals appeared to be more active in the morning than in the afternoon.

Certain individuals were involved in aggression more often than others (X^2=23, p=0.012). The adult male was most frequently involved in aggressive interactions with the juvenile female and the infant male. The adult female was most often involved in aggressive interactions with the juvenile female. Following this test, I graphed the relationship between the age and sex of an immature and the number aggressive interactions (Figure 3).

DISCUSSION

Kawata [1980] studied Diana monkeys at Tulsa Zoo and determined that they were arboreal 95% of the time. I found that the current group was also arboreal a large percentage of the time (84%; Figure 2). Zucker et al. [1988] found similar patterns for a group of Diana monkeys housed at Audubon Zoo. In the wild, these monkeys occur in the upper canopies of primary and secondary rainforests [Bourliére, 1970]. Animals occupied the indoor portion of the exhibit more frequently in the winter months. This could largely be due to the fact that these animals were locked indoors during periods of freezing temperatures. Also, keepers

often fed the animals indoors when temperatures were cold but not below freezing. Agonistic interactions among group members were highest during the winter months. This is likely due to the groups confinement to the indoor area when temperatures were freezing. Studies by Nieuwenhuijsen and de Waal [1982] and de Vries and Taylor [1989] also documented the effects of crowding on increasing agonistic interactions.

The area of the exhibit most often occupied by all group members was the overhead run. More frequently utilized areas within an exhibit usually contain qualities such as better vantage points, better resources, etc. [Traylor-Holzer and Fritz, 1985]. The overhead run is elevated above the ground and provides the animals more privacy from the public than any other area of the exhibit. It is also the greatest distance away from the public viewing areas of both indoor and outdoor facilities. This area sits directly above the keeper access hallway, providing the animals with a vantage point to watch a keeper approach as well as providing the animals visual contact with their neighbor's (Celebes macaques) overhead run. I determined that the adult male utilized this area more frequently than any other group member, while the juvenile female was the group member which utilized this area the least. This could be due to the low rank of juvenile

animals within the social group [Byrne et al., 1983] as evidenced by the direction of a majority of the aggressive interactions within my study group. Therefore, it is possible that the juvenile female was actually excluded from this "preferred" area.

Byrne et al. [1983], Zucker et al. [1988], and Kawata [1980] all found that the adult male was the most dominant individual in captive Diana monkey groups. This study supported their findings. The adult male not only utilized the overhead run most frequently, he also instigated more aggressive interactions than any other group member. The juvenile female exhibited submissive behavior most frequently and received more aggression than any other member of the group. Byrne et al. [1983], in a study of captive Diana monkeys at Edinburgh Zoo, found this pattern to be true for his study subjects as well. In chimpanzees (*Pan troglodytes*), Nieuwenhuijsen and de Waal [1982] demonstrated that juvenile females were the most attacked age-sex class while adult males were the most aggressive (dominant) age-sex class. In addition, my study found that the adult male and the juvenile female were the most solitary and peripheral group members, also supporting the findings of Nieuwenhuijsen and de Waal [1982] and Byrne et al. [1983].

The adult individuals were involved in aggressive interactions more frequently than immature animals. Much of this aggression was directed toward immature animals, especially the juvenile female and the infant male. The adult male was involved in more non-contact or display aggression (i.e. yawn threats, mock chases, displays, stare threats, etc.) than any other group member. The adult female was involved in more contact aggression (i.e. grabs, bites, etc.) than any other group member. Zucker et al. [1988] discussed similar findings for a Diana group housed at Audubon Zoo. Likewise, Hill [1994] found that Diana monkeys in the wild exhibited this same pattern. During a territorial dispute with another group, males would stay in the trees and display to each other while the females and sub-adults were likely to chase and exhibit physical aggression toward the offending group.

The rate of aggressive interactions directed toward juvenile animals in the current study increased as these animals aged (Figure 3). The oldest infant male received the highest level of aggression. Byrne et al. [1983] documented increases in aggression between adults and offspring from age 5-6 months. Aggression directed in higher frequencies toward the infant male could be related to dispersal patterns for this supposedly female-bonded species. It is assumed that Diana monkey groups in the wild

consist of a female-bonded core with juveniles and adult males as peripheral group members [Byrne et al., 1983; Hill, 1994]. In this type of social system it is assumed that male offspring are most often the individuals that disperse out of the natal group [Shields, 1987]. Natural dispersal of offspring from the natal group is not possible in the captive environment; therefore, it is feasible that this inability to escape or leave the social group at the correct stage of development may cause increases in aggression and crowding of the exhibit if new offspring are being produced [Nieuwenhuijsen and de Waal, 1982]. A survey conducted by Tulsa Zoo in 1995 of international zoos housing Diana monkeys revealed that juvenile male offspring were more often removed from social groups than were female offspring (average age of immature removal for both males and females was 2.4 years). Oates and Whitesides [1990] document the departure of juveniles from several wild groups yet fail to mention the sex of these individuals and the causes of their departures (i.e. increases in aggression directed toward these individuals by the social group, death, illness, etc.). The gender of an immature Diana monkey is difficult to determine. Stevenson [1993] provides measurements for the distances between the anus and penis or vagina of immature Diana monkeys. Without a close inspection of an animal, which would require the animal to be caught, it is

almost impossible to ascertain its gender.

The highest frequency of social behaviors observed within the group occurred between the infants and the adult female. The infants also showed significant overlap in use of exhibit space with the adult female. Byrne et al. [1983] found that infant Diana monkeys are responsible for maintaining social contact with the adult female and other group members. It should be noted that I recorded the adult female as social in her behavioral context if she and her infant were in contact. However, Nieuwenhuijsen and de Waal [1982] recorded an adult female as solitary in context if she was with her infant. This is a controversial and debatable topic; however, I feel that the female is often behaving socially when with the infant due to her probable awareness of the infant's presence on or near her and her acquiescence to its presence by not moving away or discouraging the infant (i.e. threat, bite, etc.).

In contrast to Byrne et al. [1983] and Zucker et al. [1988], I found that the adult male was frequently involved in grooming. This is congruent with the findings of Kawata [1980]. In chimpanzees, Nieuwenhuijsen and de Waal [1982] speculated that grooming served to alleviate tension within the social group and, therefore, offset aggression. The individuals most often involved in grooming within our study group were the adults and the juvenile female. These

individuals were also most often involved in aggressive interactions. Individuals least involved in grooming were the infants. Infants were groomed most often by the adult female and rarely participated in the grooming of any group member. Similar patterns were observed by Byrne et al. [1983].

I observed two additional behavioral patterns that were similar to previously reported findings. Calling, or vocalizing behaviors, were most frequently exhibited by the adult female, followed by the juvenile female. Hill [1994] documented that in wild Diana monkey groups, females were most likely to participate in territorial calling bouts. In addition to the above pattern, the juvenile female spent more time foraging than any other group member followed by the infant male. These individuals are often the lowest ranking group members [Byrne et al., 1983] and are likely to be excluded from food resources during feeding. These monkeys must therefore spend more time foraging for food than more dominant individuals who can monopolize clumped food resources and resource rich areas [Brent and Eichberg, 1991].

In summary, I found that the captive group of Diana monkeys housed at Tulsa Zoo exhibited several behavioral patterns previously documented in other captive and/or wild groups. These monkeys utilized arboreal structures within

the exhibit most frequently. This parallels the findings of other captive studies [Kawata, 1980; Byrne et al., 1983; Zucker et al., 1988] and the limited field studies [Bourliére et at., 1970]. Wilson [1982] documented the importance of considering the natural behaviors and ecology of animals when designing their captive environment. Due to the highly arboreal tendencies of Diana monkeys, captive managers should attempt to maximize the amount of vertical space within an exhibit.

The social structure of my group was similar to that documented for a captive group of Diana monkeys housed at Edinburgh Zoo [Byrne et al., 1983]. However, Kawata [1980] cautioned that captive groups may be unnaturally smaller than wild groups and often contain differing, artificial group compositions; therefore, it is possible that these variations in group size and composition may affect normal behavioral patterns of this species. My group of Diana monkeys most frequently used the exhibit area which provided the most isolation from the public and the most keeper visibility (overhead run). de Vries and Taylor [1989] speculated that animals in constant view of the public may exhibit higher levels of aggression. Providing animals with a private area, an adequate distance away from the public, may serve to reduce aggression within the group. It is becoming increasingly evident that the quality of an exhibit

and its structures, taking into account the natural ecology and behaviors of the animal, are essential for stimulating the natural behavior patterns of the animal. Exhibit quality can also be a valuable tool for conservation efforts by potentially increasing reproductive success [Clarke et al., 1982; Wilson, 1982; Traylor-Holzer and Fritz, 1985].

Studies conducted in captivity can provide valuable insight into the behavioral ecology of animals in the wild. These types of studies, together with field studies, may be utilized by captive managers in the development of conservation efforts. In some cases, when field data are limited, these studies can be used to approximate missing or unknown data; however, this use of captive data should be approached with caution. Most captive studies are limited in that only one social group may be available for observation, and manipulating the composition and size of social groups or the exhibit is usually not possible. Further studies on Diana monkeys in captivity and in the wild will be essential to formulate an effective conservation plan for this highly threatened species.

CONCLUSIONS

1. I found that many behavioral/spatial patterns for a captive group of Diana monkeys supported those of previously

documented groups, both captive and wild.

2. Due to this species' arboreal nature and preference for arboreal structures in the captive environment, I feel that managers of this captive species should maximize the amount of vertical space in exhibits.

3. The literature is depauperate for this highly threatened species of guenon; therefore, more field studies should be conducted to gather data on its behavior and ecology.

4. When field data are lacking, captive studies can be used to provide information on behavior and ecology, if the limitations of these studies are fully understood.

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REFERENCES

Bourliére, F., Hunkeler, C., Bertrand, M. Ecology and behavior of Lowe's Guenon (*Cercopithecus campbelli lowei*) in the Ivory Coast. Pp. 297-349 in OLD WORLD MONKEYS: EVOLUTION, SYSTEMATICS, AND BEHAVIOR. J.R. Napier; P.H. Napier, eds. New York, Academic Press, 1970.

Brent, L., Eichberg, J.W. Primate puzzleboard: a simple environmental enrichment device for captive chimpanzees. ZOO BIOLOGY 10:353-360, 1991.

Byrne, R.W., Conning, A.M., Young, J. Social relationships in a captive group of Diana monkeys (*Cercopithecus diana*). PRIMATES 24:360-370, 1983.

Clarke, A.S., Juno, C.J., Maple, T.L. Behavioral effects of a change in the physical environment: a pilot study of captive chimpanzees. ZOO BIOLOGY 1:371-380, 1982.

Davies, A.G. Conservation of primates in the Gola reserves, Sierra Leone. PRIMATE CONSERVATION 8:151-153, 1987.

de Vries, A., Taylor, L.L. Enclosure utilization and time budgets of Japanese macaques (*Macaca fuscata*) at the Calgary Zoo. AAZPA REGIONAL PROCEEDINGS 1989:377-382, 1989.

Eisenberg, J.F., Kleiman, D.G. The usefulness of behavior studies in developing captive breeding programmes for mammals. INTERNATIONAL ZOO YEARBOOK 17:81-89, 1977.

Hill, C.M. The role of female Diana monkeys, *Cercopithecus diana*, in territorial defense. ANIMAL BEHAVIOR 47:425-431, 1994.

Kawata, K. Notes on comparative behavior in three primate species in captivity. ZOOL. GARTEN N.F., JENA 4:209-224, 1980.

Lehner, P.N. HANDBOOK OF ETHOLOGICAL METHODS, SECOND EDITION. Cambridge, Cambridge University Press, 1996.

Martin, P., Bateson, P. MEASURING BEHAVIOR: AN INTRODUCTORY GUIDE, SECOND EDITION. Cambridge, Cambridge University Press, 1993.

Nieuwenhuijsen, K., de Waal, F.B.M. Effects of spatial crowding on social behavior in a chimpanzee colony. ZOO BIOLOGY 1:5-28, 1982.

Nowak, R.M. WALKER'S MAMMALS OF THE WORLD, VOLUME 1, FIFTH EDITION. Baltimore, Johns Hopkins University Press, 1991.

Oates, J.F. The distribution of *Cercopithecus* monkeys in West African forests. Pp. 79-103 in A PRIMATE RADIATION: EVOLUTIONARY BIOLOGY OF THE AFRICAN GUENONS. A. Gautier-Hion; F. Bourliére; J-P Gautier; J. Kingdon, eds. Cambridge, Cambridge University Press, 1988.

Oates, J.F. AFRICAN PRIMATES: STATUS SURVEY AND CONSERVATION ACTION PLAN, REVISED EDITION. Switzerland, IUCN/SSC Primate Specialist Group, 1996.

Oates, J.F., Whitesides, G.H. Association between olive colobus (*Procolobus versus*), Diana guenons (*Cercopithecus diana*), and other forest monkeys in Sierra Leone. AMERICAN JOURNAL OF PRIMATOLOGY 21:129-146, 1990.

Sanderson, I.T. THE MONKEY KINGDOM. Philadelphia, Doubleday and Co., 1957.

Sokal, R.R., Rohlf, F.J. BIOMETRY. New York, W.H. Freeman and Company, 1994.

Stevenson, M.F. INTERNATIONAL STUDBOOK FOR THE DIANA MONKEY (*Cercopithecus diana diana*). Edinburgh, Royal Zoological Society of Scotland, 1993.

Traylor-Holzer, K., Fritz, P. Utilization of space by adult and juvenile groups of captive chimpanzees (*Pan troglodytes*). ZOO BIOLOGY 4:115-127, 1985.

Wilson, S.F. Environmental influences on the activity of captive apes. ZOO BIOLOGY 1:201-209, 1982.

Wolfheim, J. PRIMATES OF THE WORLD: DISTRIBUTION, ABUNDANCE, AND CONSERVATION. Harvard, Harvard Press, 1983.

Zucker, E.L., Hidalgo, M.L., McQueen, M.A. Social relationships among adults in a small group of Diana monkeys (*Cercopithecus diana*). AMERICAN JOURNAL OF PRIMATOLOGY 14:455, 1988.

TABLE 1. Diana monkeys at Tulsa Zoo during the time of this study (October 1994 to May 1996).

Individual	Birth	Origin
Adult Male	April 1987	Tulsa Zoo, OK
Adult Female[1]	Est. August 1976	Natural Bridge Zoo, VA
Juvenile Female[2]	July 1993	Tulsa Zoo, OK
Infant Male[2]	September 1994	Tulsa Zoo, OK
Infant Female[2]	July 1995	Tulsa Zoo, OK

[1]Tulsa Zoo acquired the adult female from Jacksonville Zoo in October 1991.

[2]All juveniles and infants are the offspring of the adult male and adult female listed in this table.

TABLE 2. The ten most commonly utilized areas by each individual, standardized by the number of observations. These numbers represent counts of each individual in a particular area.

Area	Adult ♂	Adult ♀	Juvenile ♀	Infant ♂	Infant ♀
1G	532	972	989	918	739
2G	752	817	748	1002	414
3G	519	767	980	867	497
AL	816	1310	860	1165	1104
AT	737	1134	1002	980	641
BL	1024	679	895	789	402
BT	585	1437	845	1124	976
CL	533	535	891	1032	537
CT	278	180	846	752	516
OR	8539	7161	3554	5136	8333

Note: The first digit or letter under the category "area" corresponds to divisions within the exhibit as per Figure 1. The second letter corresponds to the structure or cage furniture: G=Ground, L=Ledge, T=Tree, OR=Overhead Run.

TABLE 3. Matrix of Spearman Rank Correlation Coefficients using the 10 most commonly utilized areas by individual. Each cell in this matrix represents R, the correlation coefficient.

	ADT-♂	ADT-♀	JUV-♀	INF-♂	INF-♀
ADT-♂	1.000				
ADT-♀	0.552	1.000			
JUV-♀	0.188	0.273	1.000		
INF-♂	0.564	0.770*	0.042	1.000	
INF-♀	0.236	0.782*	0.309	0.758	1.000

* Significant relationship ($p<0.01$).

FIGURE 1. Diagram of the Diana monkey exhibit at Tulsa Zoo. Indoor and outdoor area subdivisions (zones) used in space utilization analyses are illustrated (indoor = A, B, and C; outdoor = 1, 2, and 3; overhead run = OR).

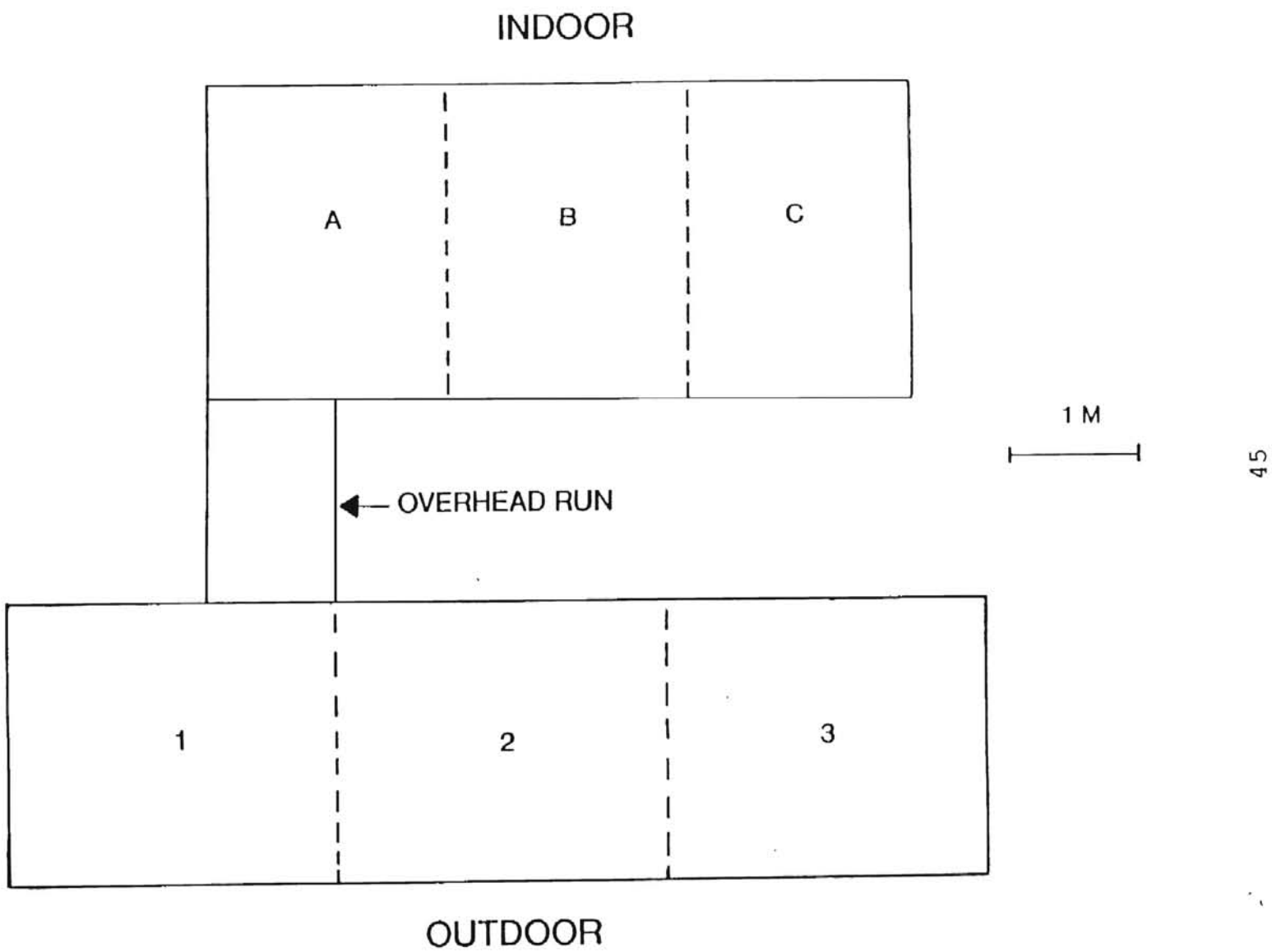

INDOOR
A
B
C
1 M
OVERHEAD RUN
1
2
3
OUTDOOR

FIGURE 2. The amount of time each individual spent arboreal versus terrestrial (ADM = adult male, ADF = adult female, JUVF = juvenile female, INFM = infant male, and INFF = infant female).

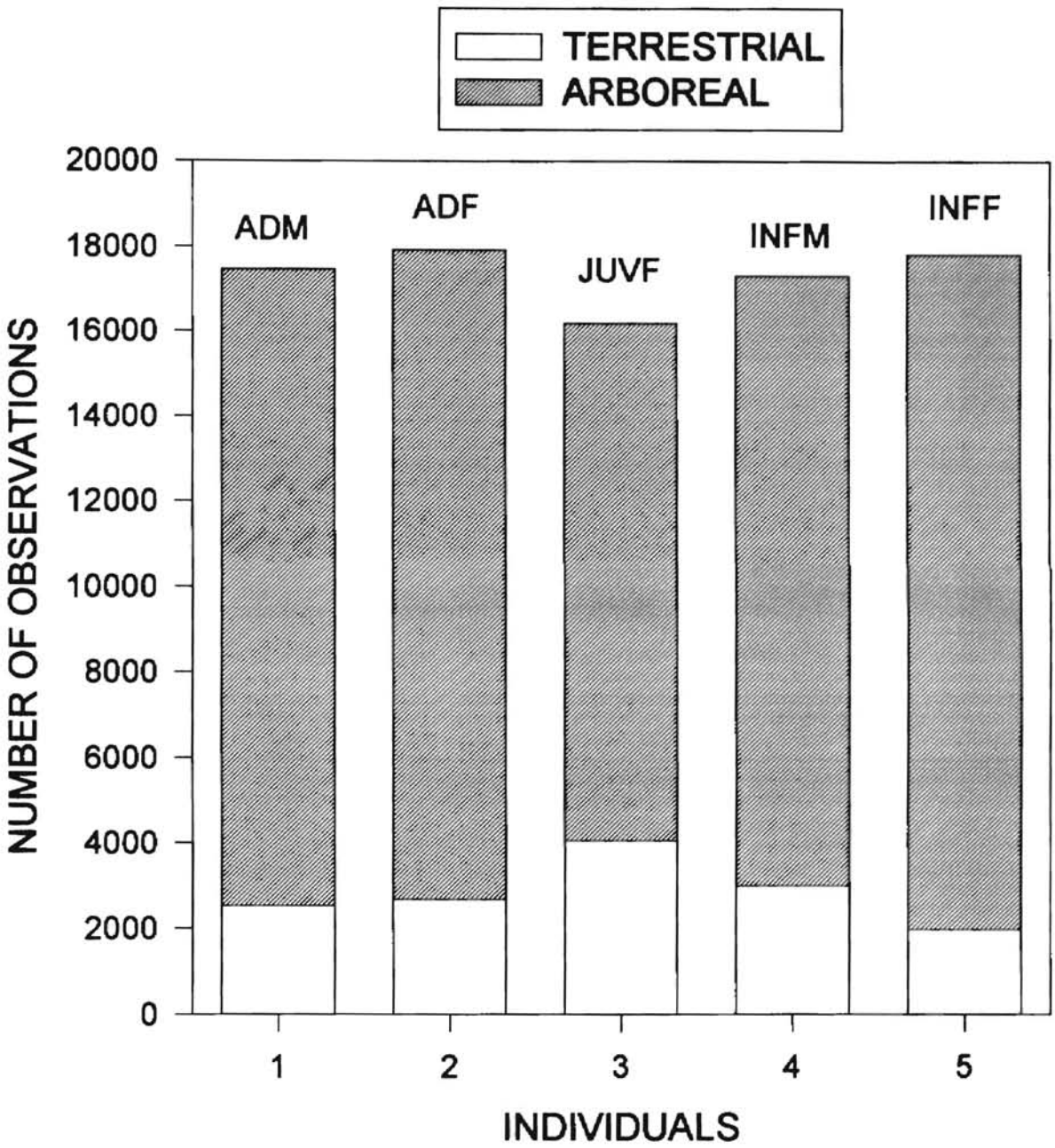
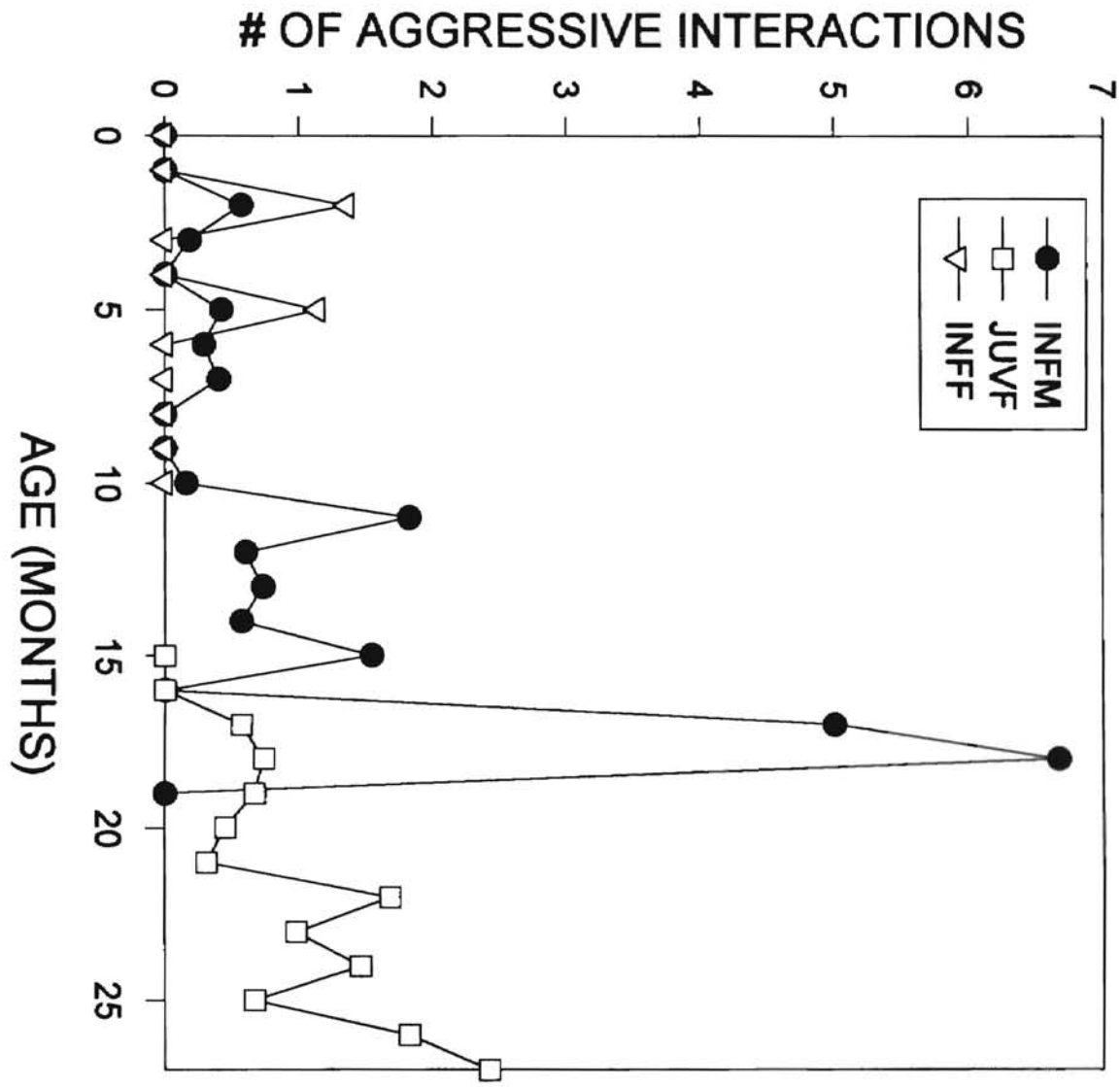

TERRESTRIAL
ARBOREAL
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
NUMBER OF OBSERVATIONS
ADM
ADF
JUVF
INFM
INFF
1
2
3
4
5
INDIVIDUALS

FIGURE 3. The number of aggressive interactions for immature animals of varying age and sex.


OF AGGRESSIVE INTERACTIONS
0
1
2
3
4
5
6
7
AGE (MONTHS)
0
5
10
15
20
25
INFM
JUVF
INFF

CHAPTER IV

SYNOPSIS

When past groups of Diana monkeys housed at Tulsa Zoo were examined, higher levels of aggression were attributed to group compositions which contained multiple adult females and immatures. Most of the aggressive interactions, however, occurred between related adult females (55%, CHAPTER II). Diana monkeys in the wild are thought to consist of uni-male, multi-female troops with their associated offspring. The dispersal pattern of immature Diana monkeys is thought to be male-biased which would lead one to believe that females in wild groups are related. If this is the case, the high occurrence of aggression between related adult females in captivity is perplexing and warrants further study. A survey conducted by Tulsa Zoo in 1995 found that adult pairs had a higher reproductive success in captivity than did harem groups. Studies of larger harem groups could determine whether competition for reproduction occurs in this species. These studies could also be used to determine what role competition for space and resources have on the social dynamics and success of captive groups.

The data presented in Chapter III of this thesis support the findings of previously published studies conducted on Diana monkeys. Diana monkeys in the wild are highly arboreal primates. Tulsa Zoo's current group (1994-1996) was also highly arboreal, spending approximately 84% of their time off the ground. The social dynamics of the current group strongly resembled other captive groups for which data were available. The adult female and infants were the most social or "core" group members while the adult male and juvenile female were the most solitary and peripheral. The adult male was the dominant group member and the juvenile female was the lowest ranking, most subordinate, group member. The rank of an individual was determined by the rate and direction of agonistic interactions. The adult male and juvenile female were involved in agonistic encounters most frequently. The juvenile female was the recipient of most of the aggression within the group. As juveniles and infants aged, aggression directed towards them increased (CHAPTER III, Figure 3).

Knowledge of the behavioral ecology of Diana monkeys in the wild is limited. Future directions for research on this threatened primate should focus on field observations. These studies would provide captive managers with valuable information pertaining to the social dynamics of wild groups, thus, allowing a better understanding of

reproductive and social requirements of this species in captivity. Until this information becomes available, it appears that Diana monkeys may need to be maintained in smaller groups if increasing the reproductive success and decreasing competition and aggression is to be attained.

APPENDIX

Diana Monkey Ethogram

Contexts: AGG=Agonistic, SOC=Social, SOL=Solitary

Behaviors to be recorded for this study:

CODE	BEHAVIOR	DEFINITION
AGC	Aggressive Contact	Hit, bite, or grab (specify). Hit=animal swings arm and impacts with another individual. Bite=animal bites another individual causing the individual to vocalize. Grab=animal reaches out and clutches another animal.
AGN	Agg. Non-Contact	An animal chases/displays another or threatens another animal with a head bob, yawn, stare, or grin (specify).

SUB	Submissive	An individual avoids or flees from another animal or lipsmacks in response to a threat. An animal may present to another animal by turning its buttocks toward the face of another animal.
COP	Copulation	Animals are seen to mount and thrusting is observed. Name partners.
PLA	Play	Wrestle, gymnastics, or chase without aggression. Indicate whether social or solitary and participants.
NUR	Nurse/Suckle	Indicate partner.
CTI CTO	Carry/Hold Infant Carry/Hold Object	Who/What is being carried and by whom?
IDL	Sleep/Rest/Idle	Animal is lying down or sitting and is not exhibiting any other type of behavior.

MAN	Manipulate/Examine	Animal is holding/manipulating an object with interest. The manipulation is by sight, smell, or touch.
TRA	Travel	Animal is moving from one place to another.
WAT	Watch	Animal is intently watching or staring at another animal or person. Specify who is being watched.
GRM	Groom	Context can be SOC or SOL. Animal grooms self or a group member. Give direction of the interaction.
FOR	Food/Forage/Water	Animal eats, drinks, manipulates enrichment for food (reward), or catches insects.
CON	Contact	Animal touches or embraces another animal. Specify partners and direction of interaction.

FOL	Follow	Animal follows directly behind another individual while traveling. Specify who is being followed.
APP	Approach	Animal walks directly up to or purposely walks toward another animal. Specify who is being approached.
VOC	Vocalize	Animal vocalizes.
DIS	Display	Aggression not directed toward another individual. An attention getting behavior. For example: Adult male runs from tunnel to inside ledge, jumps to tree branch and causes branch to hit against the cage roof producing a loud thud.
BAD	Bad Observation	When animal is out of view or the behavior or identity of an animal is undeterminable at that instant.

OTH	Other	Aberrant behaviors or behaviors that are unusual and have no known biological significance. Ex. Begging, drinking urine, or eating feces. Specify or describe behavior.
RET	Retrieve Infant	Adult female picks up infant, or travels to retrieve infant in distress.

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