THE SOCIOSEXUAL BEHAVIOR OF MALE JAPANESE MONKEYS

PERIPHERALIZATION AND SPATIAL STRUCTURE: FACTORS INFLUENCING THE SEXUAL BEHAVIOR OF MALE JAPANESE MONKEYS

By

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A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Master of Arts

McMaster University

November 1984

MASTER OF ARTS (1984)
(Anthropology)

McMASTER UNIVERSITY
Hamilton, Ontario

TITLE: Peripheralization and Spatial Structure: Factors Influencing the Sexual Behavior of Male Japanese Monkeys

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SUPERVISOR: Dr. E.J.E. Szathmary

NUMBER OF PAGES: 123 + ix

ABSTRACT

The present study examines the concept of peripheralization and spatial structure in the Arashiyama West troop of Japanese macaques (Macaca fuscata), and employs an objective method to assess the existence of a central-peripheral tendency in the spatial organization of this Japanese macaque troop. By calculating each adult male's mean distance in meters from the 'alpha' male of the troop, it was possible to rank males according to their distances from the alpha male. The resultant linear gradation of males illustrates the troop's spatial organization. This study did not find evidence supporting the notion that a rigid central-peripheral structure exists in the Arashiyama West troop. Indeed, there appears to be no objective criterion whereby some males can be labelled "central" and others "peripheral", for the linear gradation of distances that defines the spatial organization of adult males can be bisected arbitrarily at any point along its continuum.

In this thesis "spatial status" is defined as a gradation of the distance between each male and the alpha male, where the shortest mean distance corresponds to the highest spatial status. The predictors age, dominance rank and maternal lineage are examined for their influence in determining a male's spatial status within the troop. The isolated and cumulative effects of the aforementioned variables are also examined to explain variations in male sexual behavior.

Results from this study indicate that a male's spatial status is directly influenced by the combined effects of age, rank and lineage, as well as by the isolated effects of any one of the previously mentioned variables. Furthermore, the results indicate that a male's age and spatial status explain the most variability in male mating behavior.

Whether the process of peripheralization and the existence of adult male spatial status are "exaptations", that is, traits which probably were NOT selected for during the course of evolution of *Macaca fuscata*, cannot be proved by the data in this thesis. However, the available evidence does suggest that spatial status in particular is more likely to be an "exaptation" rather than an "adaptation", and accordingly it probably does not contribute to male fitness.

Acknowledgments

I would like to extend my heartfelt thanks to my supervisor, Dr. Emoke J. Szathmary, whose constructive criticsm, editing and encouragement made this thesis a reality. To my committee members, Dr. Shelley Saunders and Dr. Susan Hornshaw I express my thanks for their continual moral support throughout this endeavour.

I would also like to thank the Arashiyama West Institute for allowing me to conduct research on Japanese macaques. A special thanks to Lou Griffin, manager of the Institute, for the many hours she spent helping me with animal identification.

To Mr. Anami Bhargava, who helped me write the computer programs necessary for the analysis of my data, I am forever grateful, for without his knowledge, patience and eagerness to help this thesis would not have materialized.

I would also like to acknowledge the insight gained from my fellow researcher and colleague, Mary McDonald, who shared this field experience with me.

To my parents, I say thank you for giving me their emotional support throughout this project and in believing that an end is in sight.

Finally, immeasurable thanks are extended to Mrs. Mary McKinnon for her expertise and professionalism in the typing of this thesis.

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CHAPTER I

INTRODUCTION

The present study examines the concept of peripheralization and spatial structure in the Arashiyama West troop of Japanese macaques (Macaca fuscata), and examines the association of age, dominance rank and maternal lineage on a male's 'spatial status' within a troop. The aforementioned variables are also used to attempt to explain variations in male sexual behavior. Finally, Gould and Vrba's (1981) concept of 'exaptation' is employed as a possible explanation for peripheralization and the spatial organization in this species.

The Central-Peripheral Group Structure of *M. fuscata* Society

Japanese macaque society is structured around sets of matrilineal kin groups that are closely associated with a small number of central adult males, usually unrelated (Fedigan, 1982). Individual males which are loosely associated with these kin groups and live on the outskirts of the central (or core) region of the troop, are referred to as peripheral males. Japanese researchers have conceptualized the social structure of this species as consisting of a series of concentric circles, where older central males, females and their offspring constitute the core of the troop; peripheral lower-ranked, younger females are located in an outer circle, and peripheral males (of varying rank) occur in the outermost circle (Imanishi, 1963).

The literature documents that an animal's inclusion into either of the "central" or "peripheral" structural groups has been based on qualitative geographic distinctions and/or intuitive, impressionistic judgments of researchers. Although the precise features of Japanese macaque central-peripheral group structure bear elucidation, and although arguments abound about what the cause and/or function of such a structure may be, it is not disputed that this species has "a central core and a periphery in a behavioral and interactive sense" (Fedigan, 1982:219).

This report assesses an animal's degree of centrality or peripheralization quantitatively. The results will show that two readily identifiable and geographically distinct groups of animals do not exist. Rather, on average, the adult males can be ordered in a linear sequence from most central to most peripheral in the area in which the troop is found. This linear grading was determined by a measurement of each individual male's mean distance from the "alpha" male of the troop, who best represents the troop core. The results also suggest that while there may be central tendencies for particular behaviors within a Japanese macaque society, the central-peripheral concept is not likely to predict the behavior of individual animals (see Chapter 5 for a more detailed discussion). Hence, the functional or explanatory values of labelling animals as "central" and "peripheral" appear to be limited. Nonetheless, several explanations have been offered to explain the apparent duality in the spatial organization of this species. Dominance rank is one of the more important "explanations", and some may feel this study is another exploration of the dominance concept. To show that this is not the case, I will briefly review what is known about dominance and Japanese macaque spatial organization.

Dominance Rank

The concept of dominance has been used repeatedly by primatologists to explain practically every facet of nonhuman primate behavior and social organization. The word "dominance" as defined in the dictionary, is "the rule or control over others by superior power or influence". The use of the dominance concept for explaining social structure in animals was first used in the early 1920s. In his now classic study on the pecking order in domestic chickens, "Schjelderup-Ebbe equated dominance with the ability to aggress on an individual without having that individual respond aggressively" (Holt, 1980:1), and consequently, "this ability was considered to form the basis of social structure" (Holt, 1980:1). The peck order definition of dominance "implies that animals organize themselves according to the ability to physically defeat, or intimidate others in conflicts" (Fedigan, 1982:93).

Schjelderup-Ebbe's (1922) study measured dominance by direction of aggression and this soon led primatologists to focus on the functional benefits of being dominant (Fedigan, 1982). Thus, numerous and controversial measures of dominance came to exist. Some of the various measures of dominance used in behavioral studies today are as follows: priority of access to incentives, e.g. water, food (Boelkins, 1967; Mason, 1961); direction of agonistic signals (Hinde, 1978; Bernstein, 1970; Bramblett, 1976); threat responses (Rowell, 1966, 1974); approach-retreat interactions (Rowell, 1966); mating success (Conoway and Koford, 1965; Altmann, 1962); grooming behavior (Seyfarth, 1977); social spacing (Emory, 1975; Hall, 1967) and display behavior (Nishida, 1970). The list of behaviors used to measure dominance continues to grow as does the amount of controversy surrounding the concept itself. It is important to stress that the ability to win in conflicts and to intimidate others is an observable and important social skill. It is, however, situation and context-dependent (Fedigan, 1982). The inherent inability to find correlations between the different measures of dominance

> indicates that it is incorrect to think of dominance rank as a unitary characteristic possessed by an individual, and incorrect to think of dominance relations in dyads, and dominance hierarchies in groups, as a single phenomenon generalizable and applicable to all social interactions (Fedigan, 1982:100).

Given this, one may ask just how important are the various forms and measures of dominance in nonhuman primate social life in general? It is important to stress that dominance in the sense of winning conflicts through individual effort is important in primate social life, however, use of the concept is somewhat limited, as it does not offer an explanation for all social behavior, interactions and relationships (Fedigan, 1982).

It is my contention that the study of spatial structure is not necessarily synonymous with the study of dominance in this species. I think that too much emphasis has been placed on the importance of dominance in the social behavior of nonhuman primates. As Gartlan (1968) argues, the dominance paradigm is too narrow a foundation on which to build a thorough understanding of primate behavior.

The tendency among primatologists has been to explain an individual's behavior by his rank within the troop, and to explain an interaction between two monkeys on the basis of their relative position within a hierarchy (Fedigan, 1976). One must realize that dominance-related behavior "is only one of a characteristic set of behaviors attributable to an individual as a functioning member of a group" (Fedigan, 1976:2). When viewed as an isolated variable, dominance rank is _not_ a sufficient explanation for nonhuman primate social or spatial organization, nor should it be solely used to explain or predict the outcome of behavioral interactions. Other sociological and biological variables which affect an individual's behavior and the nature of an interaction between two individuals are: age, sex, uterine group, and the personal variables of temperament and past experience (Fedigan, 1976).

This study examines the association of _age_, _uterine group_ and _dominance rank_ on a male's 'spatial status' within a troop. The same three variables are also used to explain variations in male sexual behavior.

Researchers have also relied on sociological and biological variables to explain various naturally occurring processes among nonhuman primates; one of these processes is peripheralization.

Peripheralization Among Japanese Macaques

Peripheralization, defined as the act of male emigration from the center of a troop leading to emigration from the natal troop, was first employed by Japanese primatologists in the early 1960s. Since then it has been adopted by numerous researchers in discussions of sociological and psychological development, as well as in discussions of the maturation process of young Japanese macaque males (e.g., Alexander and Bowers, 1967; Fedigan, 1976, 1982; Imanishi, 1960; Nishida, 1966; and Tokuda, 1961).

Whereas females are likely to stay in their natal troop throughout their lives, males when they reach the age of 2½ to 3½ years, tend to move toward the edge of the troop and form close associations in a peer group of young males (Fedigan, 1976; Nishida, 1966). After spending a period of time in the periphery of the troop, the majority of these males emigrate from their natal group and either go through a period of 'solitarization', where they literally live on their own, or they join neighboring macaque troops. This stage of peripheralization and/or solitarization is one which all males, with very few exceptions, pass through (Nishida, 1966).

In an attempt to explain the process and role of male peripheralization among Japanese macaques, some researchers make reference to the dominance concept as a viable explanation for this stage in the maturation process correlation. As Drickamer (1974) was able to show, reduced observability of low ranking animals may be responsible for reports of reduced mating activity. It is important to stress that although a high ranking male may be able to drive away competing males, it does not automatically follow that he can form a successful consort with every female, or that he will have the greatest reproductive success (Fedigan, 1982).

Evidence does suggest, however, that there is a relationship between dominance rank and spatial status; specifically that peripheral males tend to be low ranking (Fedigan, 1976). This relationship may best be explained by considering the fact that peripheralization is a stage in the life cycle of almost all macaque males, a stage that occurs fairly early in life. For the most part, peripheral males tend to be young animals, and groups of peripheral animals are commonly comprised of juveniles and sub-adults. The apparent relationship between rank and peripheralization may in fact be a result of the undisputed relationship between age and peripheralization (Fedigan, 1976), because many researchers report that age is highly correlated with rank more than any other factor (e.g., Drickamer, 1975; Hausfater, 1975; Stephenson, 1975). This is related to the fact that an animal's "seniority" or "tenure" with a group may correlate significantly with rank (Norikoshi and Koyama, 1975). These relationships may best be understood by considering that as an animal matures and becomes a more integrated member of society, its social skills will improve. Seniority in a group may thus reflect an individual's social skills. Accordingly, as Drickamer and Vessey (1973) and Wilson (1968) report, dominance rank is a function of both age and seniority in a troop.

It is necessary to point out that among Japanese macaques offspring rank according to the rank of their mothers (Kawamura, 1958) and sons of high-ranking females will achieve high ranks only in their natal troops. If a male leaves his natal troop and joins another, he <u>does not</u> carry his rank with him, but needs to acquire it in each troop he joins. It has yet to be demonstrated whether sons of higher-ranked females show a decreased tendency for peripheralization; and whether a male stays in his natal troop because he has high rank or obtains high rank because he stays (Bernstein, 1976). It is also evident that correlations drawn between a male's rank and the tendency to peripheralize do not indicate causality. I therefore conclude that dominance rank, when viewed as an isolated variable, is insufficient as an explanation for male peripheralization in this species. It is thus necessary to examine the effects of other variables (e.g., age, lineage, "tenure", "spatial status"), as well as dominance rank, to gain a deeper understanding of the underlying factors which possibly dictate nonhuman primate behavior.

Having briefly reviewed the concept of dominance, this thesis will not concern itself with dominance *per se*. However, some issues concerning rank, spatial status and mating behavior will be considered. I will turn now to some background information on Japanese macaque mating behavior.

The Mating Behavior of Japanese Macaques

The mating season of Japanese macaques usually lasts anywhere from four to five months and among the Arashiyama West troop extends through the months of September to January. During this time, sexually mature animals form "consorts", defined as temporary, exclusive attachments between two individuals (Fedigan, 1982). Animals can establish a number of consorts with different partners, lasting anywhere from a short period in a day to over two weeks.

Japanese macaques are "series mounters", which means that a consort relation between two animals is characterized by a series of mounts, each involving intromission and multiple thrusting. The number of mounts in a consort relation is extremely variable, and the male only ejaculates after several successive mounts. Once the male has ejaculated, the pair enters a "refractory period" where they will separate from each other for a period of time, after which they will seek out new partners (Bullard, 1983).

It is evident that the mating behavior of Japanese macaques is clearly identifiable and unambiguous, in that it is not likely to be confused with any other type of behavior. Accordingly, the influence of other factors on mating behavior can be rigorously assessed. This thesis investigates the effect of 'spatial status' on male mating behavior and considers, at the theoretical level, whether the spatial organization in this troop of macaques is an adaptation or has any adaptive significance. Specifically, is a male's reproductive success enhanced by his 'spatial status' within the troop? Since it is proposed in this study that the central-peripheral structure in the Arashiyama West troop is not a rigid reality, and that in fact a linear gradation exists, is selection favoring strict centrality (i.e. a short mean distance from the "alpha" male)? What, if any, are the (evolutionary) mechanisms responsible for the positioning of animals within this troop?

Adaptation vs. Exaptation

Within the realm of evolutionary thought, there has developed, since the time of Darwin, confusion among the taxonomy of terms used to "reflect (or even create) different theories about the structure of the world"

(Gould and Vrba, 1981:4). The term 'adaptation', for example, when used in the study of evolutionary biology, has two different meanings. The term adaptation is used firstly to discuss features which have evolved through the process of natural selection for the specific function or task they now perform; and secondly, it is used in reference to any feature that enhances fitness, regardless of its historical origin (Gould and Vrba, 1981). Confusion exists because adaptation refers to both an evolutionary process and a current state of being (Gould, 1981).

Williams (1966) recognized this confusion and stated that:

> we should speak of adaptation only when we can attribute the origin and perfection of this design to a long period of selection for effectiveness in this particular role...and we must distinguish adaptations and their functions from fortuitous effects (cited in Gould and Vrba, 1981:4).

In Williams' terminology, "function" refers explicitly to the operation of adaptations. Such a restricted and functional definition of the term adaptation refers specifically to "historical processes of change, or creation for definite functions" (Gould and Vrba, 1981:3).

Darwin, in his book The Origin of Species, provides an example of the existing dilemma of subsuming different criteria of historical genesis and current utility under a single term. For example, Darwin (1859) wrote:

> The sutures in the skulls of young mammals have been advanced as a beautiful adaptation for aiding parturition, and no doubt they facilitate or may be indispensable for this act; but as sutures occur in the skulls of young birds and reptiles, which have only to escape from a broken egg, we may infer that this structure has arisen from the laws of growth, and has been taken advantage of in the parturition of the higher animals (cited in Gould and Vrba, 1981:5).

As Gould and Vrba (1981) suggest, Darwin asserts the utility, and indeed, the necessity, of unfused sutures but declines to label them an adaptation, as they were not built by natural selection to function as they now do in mammals. The duality of the term 'adaptation' when used by evolutionary biologists "presents little problem in cases of true adaptation, where a process of selection directly produces the state of fitness" (Gould and Vrba, 1981:14). The question arises, therefore, what to call useful structures which presently exist, but were not built by natural selection for their current role?

In an attempt to answer the preceding question, Gould and Vrba suggest that a new word be added to the dictionary of evolutionary terms. The term 'exaptation', as defined by Gould and Vrba (1981), should be used to refer to features that presently enhance fitness, but were not built through the process of natural selection for their current role. Such features are fit (in the Darwinian sense) for their current role, but were not specifically designed for it and are therefore not pushed towards fitness (Gould and Vrba, 1981). The central thesis of Gould and Vrba's argument is that "adaptations have functions, exaptations have effects" (1981:6). The authors suggest that the operation of an adaptation is its function, and that the operation of an exaptation should be labelled an 'effect'.

The use of the term 'exaptation' not only identifies a common flaw in evolutionary reasoning--the inference of historical genesis from current utility, it also focuses attention upon the somewhat neglected but paramount role of non-adaptive features in the evolutionary pathway (Gould and Vrba, 1981). It is important to stress, as Gould and Vrba do, that features which can presently be classified as 'exaptations' may have, at some point in time, been either adaptations for another function, or they may have been non-adaptive structures.

The distinction made between 'exaptations' and 'adaptations' offers an interesting alternative to discuss how similar characteristics could have arisen through processes other than natural selection. The term 'exaptation' has proven to be applicable in this study to explain two naturally occurring phenomena present in a Japanese macaque troop. The present study is the first of its kind to discuss peripheralization and the concept of 'spatial status' in terms of 'exaptations'.

CHAPTER II

RELATED STUDIES

The literature on Japanese macaque social organization and sexual behavior is extensive (e.g., Casey and Clark, 1976; Fedigan, 1976, 1982; Imanishi, 1965; Lancaster, 1973; Nishida, 1966; Sugiyama, 1976; Tokuda, 1961 and Yamada, 1966, 1971). The concept of peripheralization has been discussed in numerous papers which deal specifically with the socialization and maturation process of macaque males (e.g., Fedigan, 1976, 1982; Nishida, 1966; Yamada, 1966). Nishida (1966) has conducted the most definitive work on the development and sociability of male monkeys and his work offers an in-depth analysis of solitary macaque males in the breeding and non-breeding season, as well as a detailed review of the existence and organization of solitary males.

Peripheralization

Studies which offer explanations for why peripheralization occurs in nonhuman primates are quite plentiful. Tokuda (1961) asserts that peripheralization of young males occurs mainly due to the exclusion of less dominant males by females. This explanation, however, remains dubious as it has not been adequately shown that females use their dominance status to attack young, low ranking males with the intent of driving them into the periphery of the troop.

Tokuda (1961:11) also asserts that the peripheral region is

> an important structural area as it accepts juvenile males which grew up in the central region. Namely, it has relation to a social mechanism that allows the troop size to expand to a certain extent.

This is an interesting explanation if one considers that the central region probably does have a limit in accommodating the yearly increase in troop members born to females living in the center of the troop. Thus, the peripheral region serves as a buffer mechanism to the expansion of the central region (Tokuda, 1961).

Nishida (1966) concludes that peripheralization is not a phenomenon which occurs because leader males and females focus outward aggression towards young males, but it is a stage males arrive at during their natural course of development; a stage which all males eventually go through. This is an interesting and viable interpretation, especially if one accepts the notion that peripheralization be viewed as an animal's first step in gaining independence from their matrilineal family. As Fedigan (1976:70) states:

> Young males of the Arashiyama West troop begin their lives with a period of ecocentric growth and development, which emphasizes their physical development, although socialization is also important. Their major ties at this time are to mothers and siblings. They begin to show independence from their matrilineal family either as juveniles and subadults, and move to the edge of the troop where they form close associations in a peer group of young males.

In accordance with Nishida (1966), Enomoto (1978) asserts that peripheralization should be viewed as a biological, not a sociological phenomenon, which functions as an outbreeding (or incest-avoiding) mechanism, as well as a method of maintaining the behavioral integration of the species. If an animal leaves his natal troop and subsequently joins another troop, peripheralization may indeed promote the transfer of new genetic material from one troop to another, thus facilitating genetic variability in the species. It is important to stress, however, that outbreeding is a result of peripheralization, but peripheralization is not a consequence of outbreeding.

A less sophisticated yet acceptable explanation is offered by Lancaster (1973) and Nishida (1966), who assert that peripheralization is simply a voluntary process which satisfies the propensity of young males to roam. This indeed may be the case, as it was evident among the Arashiyama West troop that juvenile and subadult males did wander extensively from the troop's home range and were able to explore areas uninhabited by other adult monkeys. Sugiyama (1976) and Itoigawa (1974), for example, have concluded that

> male Japanese monkeys are simply more mobile than previous studies have indicated. These monkeys may wander for any number of reasons, such as following the example of a playmate or elder brother, because of a weak bond with the mother and matrilineal kin...or simply to seek a richer food distribution outside the troop's home range (cited in Fedigan, 1982:129).

Whichever the case may be, peripheralization or solitarization is an option available to Japanese macaque males from adolescence until death (Fedigan, 1976).

In reviewing the literature, it is evident that numerous theoretical explanations have been proposed to explain why peripheralization occurs. To date, however, neither the mechanism nor the exact function of this process is clearly understood.

Empirical Evidence for Central/Peripheral Social Structure

Researchers who have reported on the social structure of Japanese macaques agree that it is necessary to take into consideration the apparent duality of the social organization of this species--the center and the periphery (e.g., Nishida, 1976; Tokuda, 1961; Yamada, 1966). As mentioned in the introductory pages of this thesis, Japanese researchers discuss the social organization of *M. fuscata* as being made up of concentric circles, where the leader males and females constitute the core of the troop and subleader males and younger, low ranking females form the periphery (e.g., Imanishi, 1963; Nishida, 1966; Yamada, 1966, 1971). This concentric circle theory offers a schematic model for understanding nonhuman primate social organization; however studies which incorporate this theory have largely been based on subjective, impressionistic or intuitive interpretations of the spatial arrangements of troop members.

If one accepts the concentric circle theory, whereby certain animals inhabit specific areas of a troop's home range, some predictions should be possible regarding the distance between sub-groups of animals and the 'alpha' male. For example, one would expect that the mean distance, over a period of time, of members of a specific sub-group (i.e. subadult males) to be homogeneous. In other words, sub-group membership should predict mean distance from the center of the troop. Clearly, this is not the case among the Arashiyama West macaques, and as shall be shown in this thesis, sub-group membership does not predict mean distance from the center of the troop. As Fedigan (1982) points out, however, concentric circles are simply a graphic illustration of an abstract concept in social theory, and suggests that justice be given to the theoretical sophistication of this idea.

In general, according to Kummer (1971), social affinity and spatial proximity are so highly correlated that the distribution of animals in space can be used as a first reading of their social structure.

Essential to our understanding of nonhuman primate social organization are studies which quantitatively support impressionistic interpretations regarding an animal's 'spatial status' within a troop. Such studies are noticeably absent from the literature. Clearly, a definite need exists for studies which quantitatively determine an animal's spatial proximity within a troop, and secondly, studies which offer a quantitative analysis to determine whether a central-peripheral structure exists in a given troop.

Variation in Male Sexual Behavior

Studies which analyze variations in male sexual behavior based on either an animal's degree of centrality or peripheralization, or his geographic grouping (i.e., whether he/she is part of the center or peripheral structure of the troop) are also rather scant. Fedigan (1976) has completed the most extensive research on the role behavior of central and peripheral animals. Using the variables age, sex and spatial status, Fedigan reports on the variations in behavior peculiar to each group and concludes "that spatial status has a strong though not quite statistically significant effect on monkey behavior"

(1976:48). Furthermore, she asserts that 'spatial status' is either a phenomenon unique to Japanese macaques, or a concept unique to Japanese primatologists for use in the analysis of primate behavior.

Recent studies on the sexual behavior of male Japanese monkeys have attempted to determine whether a correlation can be drawn between male dominance rank and mating success. Enomoto (1974), in his study on the Shing-A troop of Japanese macaques, found no significant correlation to exist between frequency of copulation and a male's dominance rank. Similar results are reported by Eaton (1976) in the Oregon troop, Wolfe (1976) in the Arashiyama West troop and Loy (1971) in a rhesus monkey troop. Contrary to these findings, Tokuda (1961) and Stephenson (1975) reported that a positive correlation exists between male rank and mating success. Early studies conducted on rhesus monkey troops (e.g., Carpenter, 1942; Kaufman, 1965) reported similar correlations.

In a recent study by Takahata (1981) on the sexual behavior of Japanese monkeys of the Arashiyama B troop, he reports that no positive correlation exists between the rank order of males and their mating activity. He condludes "that high rank males did not always attain high reproductive success, as females did not invariably choose them as partners" (1981:105). The assertion being tested by Takahata is whether high ranking males have priority of access to estrous females. Sugawara (1980) defines a dominant animal as one who can gain access to others without any trouble. But as Takahata (1981) points out, among Japanese monkeys mere dominance, when defined as priority of access to females, may be insufficient to attract estrous females into courtship interactions with males.

Studies have also been conducted to see if a correlation exists between age and mating success among nonhuman primates. Shively, Clarke, King, Schapiro and Mitchell (1982) conducted a comparative study on the patterns of sexual behavior in three species of macaques (*M. mulatta*, *M. fascicularis* and *M. radiata*). One of the many documented results in this report is that a positive correlation was found to exist between rank and male sexual activity, as well as between age and male sexual activity. The authors conclude that the youngest and most subordinate males were the most sexually active among the *M. mulatta* troop. This is an interesting result in light of Eaton's (1978) study, where the author concludes that one cannot over-emphasize the importance which learning and experience play in the attainment of a male's sexual maturity.

Hanby and Brown (1974) in their study of the Oregon troop macaques, stress the importance of development and integration of sociosexual behaviors (e.g., mounting, presenting, thrusting, intromission, ejaculation) to male sexual maturity. The authors conclude that the expression of such sociosexual behaviors by adult male macaques "depends on the condition which an animal is reared in and his immediate social environment" (1974:191). Various laboratory studies conducted on rhesus monkeys (e.g., Harlow 1962; Mason 1961; Missakia 1969) and chimpanzees (e.g., Davenport and Rogers 1968; Reisen 1971), support Hanby and Brown's theory that

> social deprivation interferes not only with the copulatory aspects of mounting and presenting, but with their comforting and conciliatory aspects as well (1974:191).

In the literature on the sexual behavior of Japanese monkeys, age-related behavioral changes have often been obscured by an emphasis made on social factors such as dominance rank and kinship affiliations. Recent studies have indicated that fully adult males require fewer mounts to ejaculation and also have an increased number of mount sequences that end in ejaculation (e.g., Enomoto 1974; Hanby and Brown, 1974). Fedigan (1976) reports that among the Arashiyama West troop, a comparison of group means between adult, subadult and juvenile males, revealed that adult males scored the highest on male courtship behavior (p = .0348, mean = 50.50). This result indicates that adult males exhibit courtship towards females significantly more than subadult or juvenile males do. This result quantifies the notion that age has a statistically significant effect on male courtship behavior.

One area of research potential is the relationship between kinship and mating patterns among nonhuman primates. In a preliminary report which is part of a five-year longitudinal study, Baxter and Fedigan (1979) found that for the Arashiyama West troop, avoidance of mating with relatives extends to the entire matriline. A definite need exists for researchers to conduct long-term studies that will answer some of the many unanswered questions regarding mate preference and kinship avoidance.

Summary

This brief review of the available literature reveals that the functional value of peripheralization and the central-peripheral structure among Japanese macaques remains unanswered. A study on the complete life history of male Japanese monkeys would offer great insight into the social, biological and evolutionary functions of these phenomenon.

It is also evident from the literature that there exists an absence of an objective means for assessing an animal's inclusion into either the "central" or "peripheral" regions of a Japanese macaque troop. It is amazing that so much importance has been attached to the structural differentiation of a troop when there is such a lack of quantitative assessment of the reality of such a troop structure. In spite of this fact, numerous assertions continue to be made by researchers concerning mating success according to an animal's inclusion into either of the structural groups (i.e., his 'spatial status'). It is necessary therefore, to re-emphasize Fedigan's (1976) notion, that this structural separation of "central" and "peripheral" troop members may be nothing more than an abstract device used by Japanese primatologists, for it is apparent that this dual "structure" is not a rigid reality.

The present study differs from the rest, as it offers an objective and quantitative assessment of an animal's 'spatial status' and discusses how this variable is associated with the other predictors of mating behavior--namely age, dominance rank and lineage.

CHAPTER III

SAMPLE AND METHODS

Study Troop

The Arashiyama West troop of Japanese monkeys is a semi-free ranging group of animals that have been living in a fifty acre enclosure near Dilley, Texas since 1980. Prior to 1972 the troop was located at the Arashiyama Primate Monkey Park near Kyoto, Japan, and extensive studies have been undertaken on the troop since 1954. In 1966 the original Arashiyama troop fissioned into two troops: Arashiyama A and Arashiyama B, and in 1972 the entire Arashiyama A troop (numbering approximately 150 monkeys) was captured and transported to a 108 acre ranch near La Moca, Texas. The monkeys stayed at La Moca for eight years, and it was during this time that the troop was renamed Arashiyama West. In the spring of 1980 the entire troop was once again captured and transported to their present site near Dilley, Texas.

Since their relocation in 1980, the Arashiyama West troop has more than doubled in size and presently numbers just over 300 individuals. The situation at Arashiyama West offers an excellent opportunity for researchers to collect behavioral data on free-ranging animals, as all age/sex classes are represented within the troop and all dominance relations are known. Furthermore, the Institute makes available to all researchers complete life histories and maternal genealogies of each animal that go as far back as 1954.

The structure of the Texas environment is one which grossly differs from the environment in which Japanese monkeys evolved. The present site has many 'desert-like' features: extremely high temperatures, low humidity, drying winds and limited rainfall. Thus, heat exhaustion and dehydration pose serious health problems for the monkeys. Within the confines of the enclosure are two artificially maintained waterholes, numerous man-made shade structures and a few tall deer towers.

The enclosure is surrounded by an electrified fence, thus threats of predation from dangerous wildlife (e.g., coyotes, wild pigs, bobcats) is minimal. However, poisonous snakes do live inside the enclosure and therefore are a daily challenge to the monkeys' lives.

The monkeys are fed daily at 3:00 p.m. They are provisioned with Purina Monkey Chow, cow-breeder range cubes, two buckets of grain and corn combined, and when available, a large sack of peanuts. Day-old produce is donated periodically to the monkeys by local merchants. Planted yearly within the enclosure are two large wheat fields in which the animals forge.

After the monkeys are fed the major activities of the troop are basically non-social (e.g., foraging, sleeping). Preliminary observation revealed that few sexual interactions occur at this time and thus data for this study were not collected after 3:00 p.m.

Study Sample

At the end of the 1982 birth season, a population census revealed that the Arashiyama West troop numbered approximately 311 monkeys. In September 1982 when this study began, there were a total of 27 adult males (24 of which were living within the confines of the fifty acre enclosure) that had reached sexual maturity ($\geq$ 5 years of age). Three adult males were being held captive in a holding structure outside the main enclosure and were thus physically separated from and inaccessible to the rest of the troop. The sample size (N = 24) for this research was therefore dictated by the number of sexually mature and accessible males which, for the most part, stayed inside the fenced enclosure and lived as permanent, 'stable' members of the Arashiyama West troop. The 24 males varied in age from 5 to 18 years and represented 11 different matrilines (for a complete list of lineage membership and characteristics, see Appendix A). Over 700 hours were spent observing behavioral interactions between the monkeys and a sample of seven one-hour focal animal sessions were recorded for each subject, totalling 168 hours of focal animal data.

Fedigan (1976) delineated the existence of distinct social roles among the Arashiyama West troop. She specifically defined and showed the existence of twelve role groups in this troop. Of the twelve groups defined by Fedigan in 1976, three were adopted for the present research, namely: adult central males ($\geq$ 7 years of age), adult peripheral males ($\geq$ 7 years of age), and young peripheral males (4-6 years of age) (see Table 1 for group membership).

Data Collection

Data collection for this study took place during the 1982 mating season, namely between the months of October to December, 1982. Preliminary baseline data were collected during the month of September. This initial observation time allowed me to learn animal identification, practice focal animal sessions, become familiar with the daily routine of the troop, to orient myself as to the geographic distribution of my focal animals (i.e., which animals constituted the main core of the troop), and to develop a behavioral ethogram.

From October 1982 to December 21, 1982 intensive data collection was undertaken from the initial daylight

Table 1 - Group Membership List

Adult Central	Adult Peripheral	Young Peripheral
Rh 6271 (1)	Rh 58636975 (12)	Mat 586376 (53)
P 70 (2)	P 6573 (16)	Ra 76 (54)
N 6272 (3)	Pet 6470 (29)	Mat 616776 (81)
Suma '64 (28)	Wa 70 (55)	Me 6776 (135)
Ro 6370 (74)	Sy 67 (61)	Bl 6777 (139)
Me 65 (128)	B 586475 (108)	Sh 6477 (245)
B 586471 (129)	Pet 6175 (131)	
P 68 (143)	Ran 68 (134)	
Me 69 (146)		
Momo '64 (250)		

The numbers in parenthesis are the original tatoo numbers of the animals.

Table 2 - Focal Animal List

Tatoo Number	Maternal Lineage Name
1	Rheuse 6271
2	Pelka 70
3	Nose 6272
12	Rheuse 58636975
16	Pelka 6573
28	Suma '64
29	Petimone 6470
53	Matsu 586376
54	Ran 76
55	Wania 70
61	Syara 61
74	Rotte 6370
81	Matsu 616776
108	Betta 586775
128	Meme 65
129	Betta 586471
131	Petimone 6165
134	Ran 68
135	Meme 6776
139	Blanche 6777
143	Pelka 68
146	Meme 69
245	Shiro 6477
250	Momo '64

hours (6:30 a.m.) to approximately 2:30 p.m. daily. It was only during inclement seasonal weather (e.g., rain, wind storms) that deviations from the schedule were made.

Since each member of the Arashiyama West troop has been tatooed with a specific number for identification purposes, a list was compiled of the 24 males according to their given tatoo numbers (1-245). Behavioral data were obtained in one-hour observational sessions on each male on the list (see Table 2). In the case where the first animal on the list could not be found within a reasonable period of time in each observational day, the next animal on the list was sought. This system was continued until an equal number of tests were attained for each subject on the list. A total of 7 one-hour behavior sessions were recorded for each of the 24 focal males. When the first round of these 7 focal sessions was completed, the second round of observations was begun. For example, each animal at the end of round two would have exactly two hours of focal animal data collected on him. Round three would not start until this criterion was met.

Observations were recorded on a focal animal data sheet for the duration of the study. The use of such a data sheet allows one to calculate the frequency, duration and sequence of numerous behavioral units. It was possible to record the specific behavior in which the animal was engaged, as well as the direction in which the behavior was performed. For example, if a subject was being groomed by another animal, the words groom-received were recorded. Alternatively, if a subject was grooming another animal the words groom-directed were recorded. Whenever possible the ID number and sex of the interacting animal (if known) were written in the comment section of the data sheet (see Appendix B). The major behaviors that the specific animal performed were thus recorded. In addition, a stopwatch was used to record the duration of specific behaviors (e.g., grooming, locomoting, foraging) which were performed for a long enough period of time to render measurement. Such durational data are referred to as states in subsequent discussions in this thesis. It was virtually impossible to record the duration of momentary, instanteous behaviors (e.g., a threat), as they occurred too rapidly for accurate measurement.

Pre-existing ethograms pertaining specifically to the Arashiyama West troop (e.g., Fedigan 1976; Wolfe 1976), as well as preliminary personal observation of troop behavior during the month of September, were combined to create an ethogram of male sociosexual behaviors. A total of 103 independent units of behavior were identified, named, defined and numerically coded (see Appendix C). A system of weighting was used when it came to the actual recording of an animal's behavior. Since the primary focus of this research was on social interactions, behaviors such as grooming, mounting or chasing were always given priority in recording when they occurred simultaneously with non-social behaviors (e.g., sitting). If, for example, a subject was 'sitting' and 'grooming' another animal at the same time, only 'grooming' would be recorded.

In addition to collecting focal animal data, locational data were collected using a modified version of the scan sampling method (Lehner, 1979). Keeping within a 45 minute framework, the following data were recorded on each of the 24 males twice daily, at 7:00 a.m. and 2:00 p.m.:

(1) If the subject was seen during the 45 minute limit, a yes/no entry was recorded.

(2) If the subject was seen, his location was plotted (by the mark of an X) on a photocopied map of the enclosure.

It is evident to observers that the 'alpha' male of a Japanese macaque troop acts as a focus for troop activity and it is common for other adult central males and females to congregate in close proximity to him, thus forming the core of the troop. The 'alpha' male of the Arashiyama West troop is named Suma. He is 18 years old and has been 'alpha' male for approximately nine years. Preliminary observations made during the month of September revealed that Suma's presence and movement does act as a "focus or magnet for other troop members" (Fedigan, 1976). It was on this basis that the rationale for the analysis of the locational data was formed.

Study Objectives

The major objectives of this study were: (1) to examine whether a linear grading of the adult males, based on their geographic distance from the 'alpha' male, exists among the Arashiyama West troop; (2) if a linear grading of adult males exists, the second objective was to determine the relative importance of using an animal's linear spatial status to explain variations in male sexual behavior and (3) if a linear grading of adult males exists, the third objective was to determine whether a male's linear spatial status is dependent on, or is a function of, his age, rank and/or lineage.

In light of the preceding objectives, the following null hypotheses are proposed:

Hypothesis 1 - Adult male Japanese macaques do not exhibit "spatial status", where spatial status is defined as a linear gradation of the mean distance between each male and the 'alpha' male.

Hypothesis 2 - "Spatial status" has no significant influence on the sexual behavior of male Japanese macaques.

Hypothesis 3 - The variables age, rank and lineage when viewed independently, have no significant influence on a male's "spatial status" or his sexual behavior.

Data Analysis

In order to analyze the focal animal data as well as the locational scans, both sets of data were numerically coded and systematically transcribed onto FORTRAN sheets. The data were keypunched by an operator onto a magnetic tape and were then checked for illogical entries and distribution. Owing to the fact that the type of data collected from scan sampling and focal animal sampling is quite different, it was necessary to run separate statistical tests for both sets of data. For both data sets, the SPSS package (Nie et al., 1975) was employed.

Part 1 - Locational Analysis

The spatial organization of animals is an important aspect in the study of nonhuman primate social behavior. Past studies have shown how the measurement of inter-individual distances in animals can be used as an index of spatial arrangement (e.g., Clark and Evans, 1954; Ehardt-Steward and Bramblett, 1980; Kummer, 1971, 1974). This type of information can yield valuable insight into the dynamics of primate social life.

The first stage of data analysis was designed to examine the spatial organization of the 24 adult males in the troop. Using 115 maps (see Appendix D) which illustrated the position of the 24 focal animals at certain points in time, a grid-map, sectioned into 12.6 meter squares, was superimposed on each. The X and Y coordinates were recorded for every subject and these numbers were transcribed onto FORTRAN sheets. The data were now ready for statistical analysis.

Part 2 - Behavioral Data

Step one in the analysis of the behavioral data was to transcribe the written information from the Focal Animal sheets into numeric form and then onto IBM 80 column FORTRAN sheets. Data were then keypunched onto magnetic tape and SPSS descriptive statistics were used to check for illogical entries and data distribution.

Because the behavioral ethogram in this study consisted of 103 independent units (where several units conjointly characterized a specific social behavior), an effort was made to identify the social behavior and then combine and reduce the number of behavioral units to a more manageable number. The choice of an appropriate behavior unit is generally based on "experience, tradition, logistics and intuition" (Lehner, 1979:63). S.A. Altmann (1965) states that "...categorizing the units of social behavior involves two major problems: when to split and when to lump." He emphasizes the fact that among nonhuman primates there exist natural units of behavior, "thus, the splitting and lumping that one does is, ideally, a reflection of the splitting and lumping that the animals do." Following this line of reasoning then, the lumping of ethogram units necessary for this analysis was based on the detectable function of the behavior. In addition, knowledge of the animal's behavior attained during the preliminary observation period aided in the formation of the functional, higher-level categories of behavior. For example, the behaviors follow, move closer, present hind-quarters, etc., when these interactions occurred between a male and female, and the directions of the behavior were appropriate, were lumped together to form the higher-level category of "Male Courtship Behavior." This process made data analysis not only methodologically more practical, but also conceptually more understandable. A total of twenty higher-level categories of behaviors were formed and incorporated into data analysis (see Table 3).

Statistical Procedures

Part 1 - Locational Data

The MINITAB (Ryan et al., 1980) program package was used to examine the coded locational data. It was possible to calculate for each of the 24 males: (1) their daily distance in meters from the 'alpha' male (and therefore from the center of the troop) and; (2) their total

Table 3 - List of 20 Higher-Level Behavioral Categories

Group 1 - Solitary Behavior (Sexual)

genital touch
masturbate
ejaculate
eat ejaculate

Group 2 - Travel Behavior

locomote
bipedal
climb up
climb down
jump
look for
lope/run

Group 3 - Aggressive Behavior

threat
lunge at
bite
grab
pin and bite

Group 4 - Aggressive Behavior Received

threat received
lunge at received
bite received
grab received

Group 5 - Male Courtship Behavior

follow
sit beside
sit near
huddle
gross body contact
lie beside
move closer
stand beside
approach
glance at
stare
lip quiver
genital inspect
embrace
chase
walk around
yawn
agitated body jerk
bird dog
sexual present

Table 3, continued

Group 6 - Female-Male Advancement Behavior

receive a follow
receive a sit beside
receive a sit near
receive a huddle
receive a gross body contact
receive a lie beside
receive a move closer
receive an approach
receive a stare
receive a lip quiver
receive a genital inspect
receive an embrace
receive a walk around
receive a sexual present
receive a chase
receive an agitated body jerk

Group 7 - Rejection Behavior

move away
leave

Group 8 - Rejection Behavior Received

receive a move away
receive a leave

Group 9 - Male Fearful Behavior

position change--prompted
jump startle--cause unknown
fear grimace

Group 10 - Fearful Behavior Received

receive a fear grimace

Group 11 - Dominance Indicating Behavior

displace

Table 3, continued

Group 12 -- Submissive Behavior

receive a displace

Group 13 -- Male Mounting Behavior

hip touch
restrain
mount
ventral-ventral mount
mount rub
hind legged mount and hold
attempt mount
thrust

Group 14 - Mounting Behavior Received

receive a hip touch
receive a restrain
receive an attempt mount
receive a mount
receive a ventral-ventral mount
receive a mount rub

Group 15 - Female Behavior During Mounting--Received

receive a reach back
receive a look back

Group 16 - Affiliative Behavior

groom solicitation
groom

Group 17 - Affiliative Behavior Received

receive a groom solicitation
receive a groom

Table 3, continued

Group 18 - Non-Sexual Behavior

sit
sit and scan
sit and peer
stand alone
forage
drink
sleep
lie
display
groom self

Group 19 - Male Behavior While Being Mounted

reach back
look back

Group 20 - Male Copulatory Behavior

mount ejaculation

mean distance in meters for the observational period of this study from the 'alpha' male of the troop.

Next, one way analysis of variance (using SPSS) was applied to determine whether the 24 mean distances were heterogeneous. Lastly, the 24 focal animals were ranked according to each male's mean distance from Suma (see Table 4), from the shortest mean distance to the longest mean distance from Suma. This set of mean distances formed the data that were subsequently examined for association with a focal animal's age, dominance rank, lineage and sets of behavior.

It is worth noting that the systematic linear grading of each male's proximity to Suma allowed a more rigorous judgment of which animals constituted the "center" or "core" of the troop and those which constituted the periphery. The array of distances obtained here corroborated impressionistic information provided by the Arashiyama West Institute concerning the spatial organization of the adult males in this troop. That is, the animals labelled "central" by the Arashiyama West staff all appear to have shorter mean distances from Suma than do those animals labelled as "peripheral".

Part 2 - Behavioral Data

Two separate computer files were constructed to analyze the behavioral data collected. In File #1 the absolute frequency that each male was engaged in each of the 20 higher level categories of behavior was calculated, as well as the absolute frequency with which each male was engaged in 24 specific behaviors (see Table 5). Using SPSS, crosstabulations between: (1) Male ID and the 20 higher-level categories and (2) Male ID and 24 specific behaviors (see Table 5) produced the required frequencies.

The following seven behaviors, which occurred for a long enough period of time to render measurement (called states), were defined and incorporated in this and the other file: foraging, locomoting, grooming (direct/receive), sit beside (direct/receive), and sit near. The SPSS subprogram AGGREGATE (Nie et al., 1975) was used to calculate the duration of time spent by each animal in each of the preceding activities. In addition, the total number of times each animal had been recorded to be engaged in each of these activities was obtained, and the minimum and maximum duration values for each state per male were calculated.

A second file consisting of 61 variables was set up to determine if any significant relationships exist between various sociological and biological characteristics of the male (e.g., age, rank and lineage against linear spatial status) and various sexual and non-sexual behaviors. The variables in this file (see Table 6) included: (1) each male's mean distance in meters from

Table 4 - Linear Grading of Adult Males Based on Mean Distance from Suma

Linear Grade Number	Animal Tatoo Number	Mean Distance from Suma (in meters)	Standard Deviation
1	74	64.47	54.01
2	3	69.14	71.50
3	146	75.16	62.84
4	129	79.46	86.09
5	128	89.37	81.94
6	2	95.26	81.78
7	143	101.50	70.25
8	1	112.35	134.18
9	250	113.99	90.56
10	61	117.86	74.17
11	16	155.36	105.54
12	108	157.77	92.17
13	134	158.57	103.69
14	54	162.70	86.07
15	55	168.52	106.32
16	29	182.39	164.01
17	53	204.76	115.78
18	81	218.80	134.80
19	135	224.04	150.75
20	12	244.54	152.22
21	139	252.06	157.16
22	245	300.33	139.86
23	131	354.34	160.12

Table 5 - List of 24 Specific Behaviors

1. follow
2. sit beside (direct)
3. sit beside (receive)
4. approach (direct)
5. approach (receive)
6. leave (direct)
7. leave (receive)
8. masturbate
9. chase
10. display
11. hip touch (direct)
12. hip touch (receive)
13. sit near (direct)
14. sit near (receive)
15. huddle
16. move away (direct)
17. move away (receive
18. move closer (direct)
19. move closer (receive)
20. lip quiver
21. restrain
22. mount rub (receive)
23. attempt mount
24. thrust

Table 6 - Variable List Used in File #2

Mean distance in meters from Suma
Abs. frequency of solitary behavior
Abs. frequency of travel behavior
Abs. frequency of aggressive behavior
Abs. frequency of male courtship behavior
Abs. frequency of female-male advancement behavior
Abs. frequency of rejection behavior
Abs. frequency of rejection behavior received
Abs. frequency of male mounting behavior
Abs. frequency of mounting behavior received
Abs. frequency of male copulatory behavior
Abs. frequency of affiliative behavior
Abs. frequency of affiliative behavior received
Abs. frequency of non-sexual behavior
Abs. frequency of follows
Abs. frequency of sit besides
Abs. frequency of receiving a sit beside
Abs. frequency of approaches
Abs. frequency of receiving an approach
Abs. frequency of leaves
Abs. frequency of receiving a leave
Abs. frequency of masturbation
Abs. frequency of chases
Abs. frequency of displays
Abs. frequency of hip touches
Abs. frequency of receiving a hip touch
Abs. frequency of sit nears
Abs. frequency of receiving a sit near
Abs. frequency of huddles
Abs. frequency of move aways
Abs. frequency of receiving a move away
Abs. frequency of move closers
Abs. frequency of receiving a move closer

Table 6, continued

Abs. frequency of lip quivers
Abs. frequency of restrains
Abs. frequency of receiving a mount rub
Abs. frequency of thrusts
Abs. frequency of attempt mounts
Mean duration of forage
Mean duration of locomote
Mean duration of grooms
Mean duration of grooms received
Mean duration of sit besides
Mean duration of sit besides received
Mean duration of sit nears
Male identification
Age of male
Lineage to which male belonged
Male dominance rank
Linear spatial status
Mother of male present (or absent)
Sister(s) of male present (or absent)
Brother(s) of male present (or absent)

Suma; (2) the absolute frequency with which each male engaged in thirteen higher-level categories of behavior listed below. Since one of the primary focuses of this thesis is on the sexual behavioral variations of male macaques, the higher-level categories pertaining to male-female or female-male sexual interactions were chosen for analysis. Only four higher-level categories of behavior, other than sexual, were chosen to facilitate a comparative analysis between the absolute frequencies of sexual and non-sexual behaviors for each of the 24 males. The thirteen higher-level categories of behavior selected from the twenty in Table 3 were: male courtship behavior, female-male advancement behavior, rejection behavior (direct/receive), male mounting behavior, mounting behavior received, male copulatory behavior, affiliative behavior (direct/receive), solitary behavior, travel behavior, aggressive behavior and non-sexual behavior; (3) the absolute frequency that each male was engaged in 24 specific behaviors (see Table 6); and (4) the mean duration of the previously calculated seven states.

The eight other variables in this file were:

(1) Male ID. This refers to the tatoo number given to each male.

(2) Age of male.

(3) Lineage to which each male belonged. There are eleven different matrilines in this troop. Each lineage was given a number from 1 to 11 and this was entered numerically on the coding sheet to correspond with male ID.

(4) Rank. This was divided in three categories: (1) high, (2) medium and (3) low. These categorizations were defined by and received from the Arashiyama West Institute staff. The staff provided no data on individual ranks of the 24 males.

(5) Linear Spatial Status. This was the position of each male in a hierarchy, where the hierarchy was established by the analysis of the locational data. Each male was given a number from 1-24, where the animal with the number 1 would have the shortest mean distance from Suma and the animal with the number 24 would have the longest mean distance from Suma.

(6) Mommale. This refers to whether the mother of the male was present in the troop. This variable was represented by a score of 1 or 2 denoting a yes/no answer.

(7) Sismale. This refers to the number of females age 4½ or more present in the troop and belonging to the focal animal's immediate family.

(8) Bromale. This refers to the number of males age 5 or more present in the troop and belonging to the focal animal's immediate family.

Two different statistical tests were done with the data in file 2. (1) Pearson correlations: (a) all frequency and duration variables, male ID and age were examined for their association with males' mean distance from Suma; (b) all frequency and duration variables were examined for their association with male age. (2) Oneway Analysis of Variance: (a) the effect of male dominance rank (high, medium, low) on all frequency and duration variables was assessed; (b) the effect of lineage on all frequency and duration variables was determined.

CHAPTER IV

RESULTS

Locational Data

Table 4 contains a list of the 24 focal animals used in this study and their corresponding mean distances in meters from Suma. The mean distances are heterogeneous (F = 6.0, df = 2,21). It is interesting to note that those animals with a mean distance in meters less than 100 are all relatively high ranking, older males, while those males with a mean distance between 100 and 200 meters are, for the most part, medium ranked with ages varying from 7 to 15 years. Those males with a mean distance greater than 200 meters are all relatively low ranking and young individuals.

Clearly, the locational data allow the partitioning of the males in at least three ways. Nothing demands that a twoway classification (e.g. "central/peripheral") be done. However, if this is what one wanted to do then the locational data could be used to set the boundary. For example, if the 200 meter boundary were selected, then the "peripheral" males would all be the young and relatively low ranking males. Such "peripherals" would be like those described by Nishida (1966). On the other hand, were 115 meters selected as the boundary, then the "central" and "peripheral" males would be those currently identified as "central" and "peripheral" by the staff at the Arashiyama West Institute. This grouping tends to conform with the views of Imanishi (1963), who sees the peripheral males as animals of varying rank. Whichever boundary is selected, the choice is arbitrary, and is buffered by no theoretical foundation. This vividly illustrates the problem of definition (e.g. do all researchers agree on what is "peripheral" versus "central"?). In this thesis I have selected 115 meters as the boundary. All males with a mean distance of 115 meters or less are defined as being "central"; all males with a mean distance of over 115 meters are defined as being "peripheral".

Behavioral Data

It was of interest in this study to determine whether an animal's linear spatial status (i.e., the ranked mean distance of each male to the alpha male) could be influenced by biological and sociological variables such as age, rank and lineage. Is an animal's linear spatial status a function of such variables? To answer this question, the behavioral data were analyzed and the association of linear spatial status of each male with his age, rank and lineage, respectively, was assessed.

Because the calculations involved each male's "mean distance from Suma", rather than the spatial status rank of each male, a brief explanation of the ensuing results and interpretation is in order. Foremost, it should be noted that a positive correlation between "mean distance from Suma" and a variable, or a negative correlation between "mean distance from Suma" and a variable DO NOT mean the existence of positive correlation or negative correlation, respectively, of "spatial status" with that variable. This obtains because as "mean distance from Suma" increases, an animal's spatial status actually decreases. Similarly, as "mean distance from Suma" decreases, an animal's spatial status increases. This has the following ramification, as illustrated by example.

Suppose a positive correlation is observed between "mean distance from Suma" and a variable. This means that as distance increases, so the variable also increases. However, expressed in terms of spatial status, the observed correlation is actually negative, for as distance increases and the variable increases, spatial status decreases. Thus, spatial status is actually negatively correlated with the given variable. This distinction between the measure with which correlation analysis was done ("mean distance from Suma" with other variables) and the "spatial status" interpretation should be kept in mind when reading the results listed below.

Age

There is a negative relationship between age and the males' mean distance from Suma ($r = -.74$, $P = .00$). As the age of the male increases, the linear spatial status of the male increases. Thus, it is evident that older males stay closer to Suma and therefore to the center of the troop than younger males do.

Rank

One way analysis of variance revealed that an animal's rank is an important variable in the determination of his spatial proximity. Results indicate that the mean distances from Suma differ significantly among high, medium and low ranking animals ($F = 12.01$; $df = 2,21$; $P = .00$). The Scheffe procedure which determines which subgroups are not significantly associated was employed to test differences between pairs of means. The results reveal that a significant difference in group means exists first, between high and medium ranked animals, and secondly, between high and low ranked animals (high: mean = 81.0 ± 16.0; medium: mean = 158.00 ± 19.21; low: mean = 224.40 ± 27.0). The level of significance selected for this test was set at the .05 level.

Lineage

One way analysis of variance test revealed no significant differences (at the .05 level) among the lineages in their members' mean distances to Suma, and therefore to the center of the troop. The probability, however, of obtaining the observed results by chance was only .07 (F = 2.04; df = 10,13; P = .07). This suggests that a tendency does exist for certain lineages to stay closer to Suma and therefore to the center of the troop. For example, adult male members of the Nose, Syara, Momo and Betta lineages all have mean distances from Suma of less than 120 meters (see Table 7). It is interesting to note that the males in these lineages are all relatively high ranking individuals with an average age of 13 years. The following is a list of each lineage and its corresponding mean distance from Suma.

Table 7 - A list of 10 Lineages and Their Corresponding Mean Distances from Suma

Lineage	Mean Distance in Meters from Suma
Momo	114.00
Nose	114.25
Syara	118.00
Betta	119.00
Pelka	130.00
Rheuse	140.67
Ran	191.33
Matsu	212.00
Petimone	268.00
Shiro	300.00

For a complete list of lineage membership and characteristics, see Appendix A.

Linear Spatial Status

To determine if an animal's linear spatial status can be used to explain differences in male sexual behavior, correlations were run between the mean distances from Suma of each male with 13 higher-level categories of behavior, 24 specific behaviors and the mean duration of seven states. Pearson correlation analysis revealed significant results for 5 of the 13 higher-level behavioral comparisons; 6 of the 24 specific behavior comparisons and 3 of the 7 durational state comparisons (Table 8a and 8b). In greater detail, these results are as follows.

(1) A negative correlation exists between the mean distance from Suma and male courtship behavior (r = -.43, P = .02). Therefore, as males move further away from the center of the troop (i.e., as their linear spatial status decreases), the absolute frequency of male courtship behavior exhibited towards females decreases.

(2) A negative correlation exists between males' mean distance from Suma and frequency of affiliative behavior received from females (r = -.36, P = .04). As males move closer to the center of the troop affiliative behavior (e.g., grooms) from females increases.

(3) A negative correlation exists between mean distance

from Suma and frequency of rejection behavior made by males towards females (r = -.34, P = .05). In terms of spatial status, this means that as the linear spatial status of the male increases (i.e., a shorter distance), the frequency of rejection behavior towards females increases.

(4) A negative correlation exists between males' mean distance from Suma and frequency of rejection behavior received by males from females (r = -.41, P = .04). Therefore, the further males move from the center of the troop, the less rejection behavior they receive from females (e.g., receive a move away, receive a leave).

(5) A negative correlation exists between males' mean distance from Suma and frequency of travel behavior (r = -.40, P = .04). Expressed in terms of spatial status, as linear spatial status increases, the frequency of travel behavior increases. Males who stay closer to the center of the troop exhibit more of what I have called "travel" behavior (e.g., locomote, lope/run) than those males who stay further from the center of the troop.

(6) A negative correlation exists between males' mean distance from Suma and frequency of follow behavior (r = -.50, P = .01). Therefore, the further males move from the center of the troop, the frequency with

which they follow females decreases (i.e., they pursue females less frequently).

(7) A negative correlation exists between males' mean distance from Suma and frequency of chases made by males towards females (r = -.52, P = .00). Therefore, as males move closer to the center of the troop, the frequency of chasing females increases.

(8) A negative correlation exists between males' mean distance from Suma and frequency of approaches made by males toward females (r = -.61, P = .00). Therefore, males which tend to stay closer to the center of the troop approached females more than males which tended to stay further away from the center of the troop.

(9) A negative correlation exists between males' mean distance from Suma and the frequency with which males sat near females (r = -.61, P = .00). In terms of spatial status this means that as linear spatial status increases, the frequency with which males sit near females increases.

(10) A negative correlation exists between males' mean distance from Suma and the frequency with which males moved closer to females (r = -.50, P = .01). Therefore, males which tended to stay closer to the center of the troop moved closer to females more than males which tended to stay further from the center of the

troop.

(11) A negative correlation exists between males' mean distance from Suma and the frequency of lip quivers made by males toward females (r = -.40, P = .03). Therefore, males which stay closer to the center of the troop lip quiver towards females more so than males which stay further away from the center of the troop.

(12) A negative correlation exists between males' mean distance from Suma and the mean duration of sit besides made by a male with a female (r = -.40, P = .03). Therefore, as linear spatial status increases, the mean duration with which males sat beside females increases.

(13) A negative correlation exists between males' mean distance from Suma and mean duration of sit besides received from females towards males (r = -.34, P = .05). Therefore, males which tended to stay closer to the center of the troop received sit besides of a longer duration from females than did males which stayed further away from the center of the troop.

(14) A negative correlation exists between males' mean distance from Suma and mean duration of sit nears made by males with females (r = -.50, P = .01). Therefore, as linear spatial status increases, the amount of time spent by males sitting near females increases.

This first set of results indicate that males which stay relatively closer to the center of the troop (i.e., as linear spatial status increases) interact with females more than those males which stay farther away from the center of the troop. Specifically, as linear spatial status increases, the frequency of the following eleven behaviors increases: male courtship behavior, affiliative behavior (received), rejection behavior (direct/receive), follow behavior, chase, approach, sit near, move closer, lip quiver and travel behavior. It is also evident that males which tended to stay closer to the center of the troop sat near females, sat beside females and received sit besides from females of a longer duration than did males which tended to stay further away from the center of the troop.

A second set of tests were run between the dominance rank of each male and (1) 13 higher-level categories of behavior; (2) 24 specific behaviors; and (3) the mean duration of 7 states. One way analysis of variance tests indicate that the mean frequency of the following behaviors differs significantly among high, medium and low ranked animals: frequency of follows, frequency of approaches and frequency of 'sit nears'. The Scheffe test of homogeneity between subsets revealed that a significant difference in group means for the previously mentioned behaviors exists, firstly between high and medium ranked animals and secondly, between high and low ranked animals. The significant analysis of variance results occurred for the following 3 behaviours: follow behavior, approach behavior, and "sit near" (see Table 9).

Results indicate, therefore, that high ranking males followed, approached and sat near females more than medium or low ranking males did. It is evident that high ranked males tended to pursue females more than lower ranked males did.

It is interesting to note that the frequency of the following behaviors were not affected by the rank of the male: male mounting behavior (F = .06; df = 2,21; P = .94), hip touch (F = .08; df = 2,21; P = .92) and thrusts (F = .08; df = 2,21; P = 92). That is, the particular behaviors that could have reproductive consequences are NOT significantly different among the male dominance categories.

A third set of tests were run which correlated the age of the male with: (1) 13 higher-level behavioral categories; (2) 24 specific behaviors; and (3) the mean duration of 7 states. Pearson correlation analysis revealed significant results for 3 of the 13 higher-level behavioral comparisons; 5 of the 24 specific behavioral comparisons and 1 of the 7 durational state comparisons (see Table 8a and 8b). In greater detail, these are as follows:

(1) A positive correlation exists between age and the

frequency of male courtship behavior (r = .40, P = .03). Therefore, the older the male, the higher the frequency of courtship behavior toward females.

(2) A positive correlation exists between age and the frequency of affiliative behavior received from females toward males (r = .39, P = .03). The older the male the more affiliative behavior shown them from females.

(3) A positive correlation exists between age and the frequency of rejection behavior received from females by males (r = .50, P = .01). Therefore, the older the male, the more rejections (e.g., leaves) from females are received by the male.

(4) A positive correlation exists between age and the frequency of approaches made by males toward females (r = .51, P = .01). Therefore, older males tend to approach females more than younger males do.

(5) A positive correlation exists between age and the frequency of follows made by males towards females (r = .53, P = .00). Therefore, older males tend to follow females more than younger males do.

(6) A positive correlation exists between age and the frequency of leaves received by males from females (r = .50, P = .01). The older the male, therefore, the more leaves from females are received.

(7) A positive correlation exists between age and the

frequency of move aways by males toward females (r = .44, P = .02). Therefore, older males tend to move toward females.

(8) A positive correlation exists between age and the frequency of males sitting near females (r = .51, P = .01). Older males tend to sit near females, while younger males tend not to sit near females.

(9) A positive correlation exists between age and the following mean duration of states: grooms received (r = .40, P = .03), sit beside a female (r = .45, P = .01), sit besides received from a female (r = .50, P = .01), and sit near a female (r = .40, P = .03).

Results from the third set of tests indicate that increasing age in males is associated with a higher frequency of the following 6 behaviors towards females: male courtship behavior, approach, follow, leave, move away and sit near. Increasing age is also associated with a higher frequency of receiving affiliative and rejection behavior from females. The mean duration of the following 4 states was also positively correlated with the age of the male: grooms (received), sit beside (direct/receive), and sit near.

A fourth set of tests were run between the lineage of each male and (1) 13 higher-level categories of behavior, (2) 24 specific behaviors, and (3) the mean duration of 7 states. One way analysis of variance tests revealed that the mean frequencies of various behaviors differ significantly between the lineages. Table 10 is a summary of the _significant_ associations made between behaviors and lineages.

Results indicate that the mean frequencies of the behaviors tested vary significantly for only 4 of the 11 existing matrilines in the Arashiyama West troop. Specifically, Suma followed, approached, sat near, moved closer and left females significantly more than males in other lineages. Suma also received leaves from females more than other males did. Males from the Betta lineage (specifically animals 108 and 129) rejected females and left females more than males in other lineages did. It is also evident that Shiro masturbated more than other males did and that Momo moved away from females, restrained females and sat beside females for a longer duration of time than males in the other lineages.

Table 8a - Summary of Significant^{++} Results Attained From Pearson Correlation Analysis Between Males' Mean Distance From Suma, Male Spatial Status and Age of Each Male With: (1) 13 Higher-Level Categories of Behavior and With (2) 24 Specific Behaviors.

ATTRIBUTES

Behavioral Variables	Males' Mean Distance from 'Alpha' Male		Spatial Status**	Age	
	r	P	Direction of Correlation	r	P
Male courtship behavior	-.43	.02	+	+.40	.03
Affiliative behavior (rec)	-.36	.04	+	+.39	.03
Rejection behavior	-.34	.05	+	NSR*	
Rejection behavior (rec)	-.41	.04	+	+.50	.01
Travel behavior	-.40	.04	+	NSR	
Follow	-.50	.01	+	+.53	.00
Chase	-.52	.00	+	NSR	
Approach	-.61	.00	+	+.51	.01
Sit near	-.61	.00	+	+.51	.01
Move closer	-.50	.01	+	NSR	
Lip quivers	-.40	.03	+	NSR	
Leaves (rec)	NSR		indeterminate	+.50	.01
Move away	NSR		indeterminate	+.44	.02

$^{++}$Only significant results (for at least one test) are shown.

*NSR = non-significant result.

**Spatial Status = ranked mean distances of each male to the 'alpha' male. The animal with the shortest distance has a rank of 1. The direction of the correlation is inferred from the results shown under "Males' Mean Distance from the 'Alpha' Male."

Table 8b - Summary of Pearson Correlation Results Between Males' Mean Distance from Suma, Spatial Status and Age of Each Male and the Mean Duration of 7 States.[++]

Mean Duration of States	Males' Mean Distance from 'Alpha' Male		Spatial Status**	Age	
	r	P	Direction of Correlation	r	P
Mean duration of sit besides	-.40	.03	+	+.45	.01
Mean duration of sit besides (received)	-.34	.05	+	+.50	.01
Mean duration of sit nears	-.50	.01	+	+.40	.03
Mean duration of grooms (received)	NSR*		indeterminate	+.40	.03

[++] Only significant results (for at least one test) are shown.

*NSR = Non-significant result.

**Spatial Status = Ranked mean distances of each male to the 'alpha' male. The direction of the correlation is inferred from the results shown under "Males' Mean Distance from the 'Alpha' Male".

Table 9 - Significant Differences* in Behavior by Dominance Rank

Behavior	Mean Frequencies of Behavior by Rank			Anova		Scheffe's Test		
	High $\bar{X}$ ± SD**	Medium $\bar{X}$ ± SD	Low $\bar{X}$ ± SD	F	df	H-M[+]	H-L[+]	M-L[+]
Follow	17.00 ± 7.00	3.40 ± 1.20	.63 ± .26	5.10	2,21	.02	.02	NS
Approach	15.00 ± 5.00	6.13 ± 1.32	3.00 ± .91	6.00	2,21	.02	.02	NS
Sit Near	29.00 ± 11.00	7.00 ± 1.03	6.00 ± 3.00	4.40	2,21	.03	.03	NS

*All other tests were non-significant (13 higher-level categories, 24 specific behaviors and 7 states were examined by rank).

**Mean frequency of the given behaviors ± standard deviation of that frequency.

[+] H = high rank, M = medium rank, L = low rank

NS = non-significant result

Table 10 - Summary of Results from One Way Analysis of Variance Tests Between Lineages and Behaviors++

BEHAVIOURS	LINEAGES							
	Suma		Betta		Shiro		Momo	
	F	P	F	P	F	P	F	P
Follow	2.30	.05	*NSR		NSR		NSR	
Approach	6.00	.00	NSR		NSR		NSR	
Sit near	7.00	.00	NSR		NSR		NSR	
Move closer	5.00	.01	NSR		NSR		NSR	
Leave (direct)	NSR		4.00	.01	NSR		NSR	
Leave (receive)	3.00	.01	NSR		NSR		NSR	
Move away	NSR		NSR		NSR		5.40	.00
Restrain	NSR		NSR		NSR		12.44	.00
Masturbate	NSR		NSR		4.00	.02	NSR	
Rejection	NSR		4.31	.01	NSR		NSR	
Mean Duration of Sit Beside	NSR		NSR		NSR		3.00	.05

++Only significant results (for at least one test) are shown.

*NSR = non-significant result.

CHAPTER V

DISCUSSION

The major objectives of this study were firstly, to examine whether a linear grading of the adult males based on their geographic distance from the 'alpha' male, exists among the Arashiyama West troop; secondly, if a linear grading of adult males exists, the second objective was to determine the relative importance of using an animal's linear spatial status to explain variations in male sexual behavior; and thirdly, if a linear grading of adult males exists, the third objective was to determine whether a male's linear spatial status is dependent on, or is a function of, his age, rank and/or lineage. In order to meet these objectives, data analysis was divided into several distinct sections and appropriate statistical tests were applied to the data. The discussion to follow is divided systematically to meet the study objectives and theoretically to answer specific research questions.

Spatial Organization of Japanese Macaque Society: Central-Peripheral Tendencies

Although Japanese primatologists have assumed the existence of an innate tendency in *M. fuscata* to structure troops into central and peripheral groupings, at least two primatologists have questioned whether the phenomenon is not an artifact imposed by human intervention. Alexander and Bowers (1967) have hypothesized that Japanese macaque troop structure is simply the direct result of the provisioning methods employed in Japan, i.e., the placement of food in large circles. While this hypothesis may have substance for monkeys in Japan, it is worth noting that (1) provisioning at Arashiyama West does not take place in a circular fashion and that (2) locational data for this study was taken at two different times of the day, neither of which occurred at the time of provisioning. Any evidence for the existence of a central-peripheral tendency in the Arashiyama West troop, then, could not be the consequence of provisioning methods employed.

The quantitative assessment of 'spatial status' conducted on the adult males in the Arashiyama West troop allowed the calculation of the average distance of each male from the 'alpha' male of the troop. The results (as illustrated in Table 4) clearly indicate that the adult males in this troop exhibit 'spatial status', where spatial status is defined as a linear gradation of the distance between each male and the 'alpha' male--hence the first null hypothesis proposed is rejected. Indeed, every sexually mature male in the troop can be positioned along a hypothetical central-peripheral axis. The linear grading of the adult males established in this study supports previously made intuitive, impressionistic, and/or geographic assumptions about the spatial organization in this troop of macaques, as some males are clearly positioned closer to the 'alpha' male than are others. The gradation of distances, however, also shows that the division of males into "central" versus "peripheral" groups, at least for some animals, is done arbitrarily and thereby forces the animals into two artificially constructed groupings. Fedigan's (1976) notion that the claimed central-peripheral structure of Japanese macaque society may be nothing more than a conceptualization used by Japanese primatologists to analyze primate behavior, is certainly supported by the data obtained here.

The linear grading of adult males demonstrated in the Arashiyama West troop brings into question the functional value of the concentric circle theory, whereby certain sub-groups of animals are said to inhabit specific areas of a troop's home range. If one accepts this theory, certain predictions should be possible regarding the distance between sub-groups of animals (e.g., adult peripheral males) and the 'alpha' male of a troop. Specifically, sub-group membership should predict mean distance from the center of the troop. For example, one would expect that the mean distances, over a period of time, of members of specific sub-groups were homogeneous. Clearly, a prediction of this type is invalid when applied to the Arashiyama West macaques, where sub-group membership does not predict mean distance from the center of the troop. For example, adult peripheral males have mean distances from Suma that vary from 117 to 354 meters, with the average mean distance for this sub-group being 192.4 ± 23.0 meters. The size of the standard deviation shows the amount of variability that exists. It is quite obvious that for the sub-group "Adult Peripheral Males", the mean distances from the center of the troop are heterogeneous, not homogeneous over a period of time. Furthermore, labelling a single animal as "peripheral" does not at all indicate how far away it "should be" from the 'alpha' male at any particular point in time. In this study, animals defined by the staff at Arashiyama West as "central" have mean distances that range from 64 meters to 114 meters. One cannot seriously believe that a "central" animal with a mean distance of 114 meters will show vast differences in behavior that set it apart from a "peripheral" animal whose mean distance from the alpha male is 117 meters.

It is of further interest to note that the standard deviations calculated and illustrated in Table 4 clearly indicate that a great deal of variability also exists in the individual mean distances from Suma. The size of the standard deviations for each animal shows the vast amount of existing variation. This serves to re-emphasize the notion that the mean distances from the 'alpha' male of the troop are indeed heterogeneous over time.

These results question seriously the functional value of the concentric circle theory. As Fedigan (1982) suggests, concentric circles are simply a graphic illustration of an abstract concept in social theory, and thus extreme caution should be observed when applying this theory to explain specific aspects of macaque social and spatial organization. While there may be central tendencies for particular behaviors within macaque sub-groups, the behavior of individual animals given the central-peripheral concept, is not likely to be predicted.

Linear Spatial Status and Male Mating Behavior

Given the existence of a linear grading of adult males in the Arashiyama West troop, it remains to be seen whether the grading influences male sexual behavior. The second research objective was designed with this in mind. The analyses done indicate that a male's linear spatial status does not, by itself explain total variation in male sexual behavior.

The data in this thesis show unambiguously that the frequency of the higher-level category of "Male Courtship Behavior" decreases as an animal's mean distance from the 'alpha' male increases. The analysis shows that the frequency of the following 6 specific male courtship behaviors decreased as an animal's distance from the 'alpha' male increased. Namely, males follow, approach, chase, sit near, move closer and lip quiver towards females less frequently as their degree of peripheralization increases (i.e., as linear spatial status decreases). Furthermore, as a male's linear spatial status increases, the amount of time actually spent sitting beside and sitting near females increases. Following this then, it is not surprising that further analysis revealed that peripheral animals receive less affiliative and less rejection behavior from females, simply because they interacted with females for relatively shorter periods of time.

It must be pointed out that although the overall frequency of the higher level category of "Male Courtship Behavior" decreases as an animal's linear spatial status decreases, there are specific courtship and male mounting behaviors which show little correlation with an animal's linear spatial status. For example, results indicate that an animal's linear spatial status did not affect his frequency of directing the following behaviors towards females: sitting beside, huddling, gross body contact, lying beside, standing beside, glance/stare at, genital inspect, and all behaviors included under the higher level category of "Male Mounting Behavior". The data further indicate that although males with a higher degree of centrality (i.e., a shorter mean distance from Suma) seem to be pursuing or courting females more than those animals with a higher degree of peripheralization, there is no significant correlation between an animal's linear spatial status and his frequency of "Male Mounting Behavior" or "Male Copulatory Behavior". Males with a longer mean distance from Suma may therefore be quite actively mounting females and forming consort relationships with females that culminate in ejaculatory mounts.

The type of data collected in this study (i.e. focal animal data) rendered it possible to conduct a very preliminary analysis testing the differences in male behavior based on the rank and age of the interacting female. This was clearly not a research objective, however it was of personal interest to check if the age and rank of the interacting female could further explain variations in male sexual behavior.

The subsequent correlation analysis between the linear spatial status of the male and the higher level category of "Female Advancement Behavior Received" revealed no significant results. On the other hand, analysis of specific "Female Advancement" and "Female Affiliative" behavior towards a male, did indicate that females spent significantly more of their time sitting beside and grooming those males who had a shorter mean distance from Suma. This result suggests that females may prefer central over peripheral males as mating partners, or may prefer to nurture "friendly" relations with centrally located males.

It is beyond the scope of this study to report on female choice of mating partners. Preliminary analysis of the data collected, however, indicates that a significant correlation between an animal's linear spatial status and female solicitation attempts does not clearly exist. That females did tend to sit beside and groom central males for a longer duration of time may well indicate non-sexual behavior. It has been suggested in the literature that grooming is an affiliative, not a sexual behavior conducted between relatives or close friends, and thus grooming is viewed as a poor indicator of sexual attractiveness between animals (e.g., Fedigan, 1982).

I do feel, however, that certain males may be more 'popular' than others, inasmuch as they may possess certain physical characteristics or behavioral attributes which females may find particularly appealing. Japanese macaque males do have elaborate courtship routines which vary from individual to individual, thus it is possible "that female Japanese macaques are attracted to males that perform these displays, in the classic sense that Darwin saw female animals as drawn to males that 'perform the best antics'" (Fedigan, 1982:284).

For example, among the Arashiyama West troop there were two males who were by far the "most popular" during the 1982 mating season. The males in question are brothers, nicknamed Rocky II and Rocky III. Rocky II is 12 years old and a high ranking central male; Rocky III is 8 years old and a medium ranked peripheral male. Both of these males had a following of females which were literally waiting their turn in line to mate with them. It is interesting to note that both Rocky II and Rocky III exhibited a unique behavioral trait during a mount sequence with a female, which I have called a 'back-kick hold'. Perhaps females found this behavior particularly sexually appealing and thus preferred these specific males more so than others. As Fedigan states,

> social perception and motor skills on the part of the males are probably important to the individual rendition of the elaborate weaving, bobbing, whirling, posing display of the courting male. And if we adhere to the tenets of sexual selection, female choice of male partners, and thus male reproductive success, is at least partially based on their display skills (1982:117).

It is evident that specific associations can be made between male mating behavior and linear spatial status and that female choice may have a role in male mating behavior. The latter, however, does not appear to be contingent on male linear spatial status. Female behavior, therefore, can thus be interpreted as something other than "mating behavior" towards males.

The results from this study indicate that a male's linear spatial status is an important variable which can account for some, but definitely not all, of the variation in male sexual behavior. Linear spatial status does have a significant influence on the sexual behavior of male macaques, and thus the second null hypothesis proposed can be rejected. On the other hand, it is possible that other variables such as a male's age, rank and lineage may also influence spatial status. To test whether the "spatial status" concept is independently useful, I also examined the roles played by rank, age and kinship on male mating behavior.

The Influence of Rank, Lineage and Age on Male Mating Behavior Without Consideration of Linear Spatial Status

(a) Rank

Contrary to Altmann's (1962) 'priority of access model', which states that differences in the dominance rank of males can explain all the variance in male reproductive activity, the results from this study indicate that a clear correlation between male dominance rank and mating activity does not exist. Pearson's correlation analysis and the Scheffe test of homogeneity indicate that high ranking males follow, approach and sit near females significantly more than lower ranked males do. There were no other significant results, however, when male rank was correlated against any of the 13 higher-level behavioral categories, or when correlated against the 20 specific sexual behaviors. These results are in accordance with other studies done on Japanese macaques, such as those of Eaton (1976), Enomoto (1974) and Wolfe (1976), where no strong correlations were found between male dominance rank and mating activity.

An interesting suggestion for the lack of correlation between dominance rank and mating activity among Japanese macaques is offered by Enomoto (1981). He suggests that the concentric structure of the troop ceases to function properly during the mating season. He states

> that at this season, each male follows estrous females somewhere around the troop. The females do not intensively follow higher ranked males, which is in contrast to the situation in the non-mating season.... Ultimately this brings the wall which separates the central part of the troop from its periphery under the pressure of higher ranked males into collapse in the mating season. Even males of lower rank can walk among the females with their tails raised and testes lowered into the scrotum, and they can chase some females (Enomoto, 1981:20-21).

This suggestion, however, remains questionable, in light of the fact that data for this study was collected during the mating season and there was no apparent "collapse" of "normal" troop structure. The existence of male 'spatial status' persisted for the duration of this study that encompassed the entire mating season.

On the other hand, it has been reported by Tokuda (1961-62) and Stephenson (1975), that a male's dominance rank can be correlated with mating behavior. The discrepancy between this finding and those described in this thesis suggests that factors other than the dominance rank of males (e.g., age and lineage which are in some cases correlated with rank) actually exert an effect on the frequency of male sexual behavior (Enomoto, 1981). It is worth noting that varying results between studies of different investigators probably "serve to emphasize the plasticity of individual and group behavior that characterize all primates" (Eaton, 1976:295).

Why higher ranked males do not maximize their opportunity for mating is problematic. It is suggested that such males either do not want to, or are not able to maximize the advantages conferred upon them strictly on the basis of their rank. As Chapais (1983) found, it was not uncommon for high ranking males to be unsuccessful in their attempts to consort with estrous females who were already being consorted by lower-ranked males. The females would appear to be uninterested in the advances made by the higher-ranked male and would not allow him to mount her. This implies that females are choosing their mate partners. However, the basis on which this choice is being made remains unknown.

Results from this study indicate that male dominance rank, when viewed as an isolated variable, cannot explain all the variance in male reproductive activity. The three single behaviors exhibited more commonly by high ranking males may just be "friendly" behaviors, and should not be imbued with more importance than the 20 specific sexual behaviors that showed no association with male rank. Lastly, the outcome in this study is not likely to be an artifact arising from the way in which male rank was assigned (males grouped into "high, medium and low" by the Arashiyama West Institute staff), for similar findings have been found by several other investigators (e.g., Eaton, 1976; Enomoto, 1974; and Wolfe, 1976).

(b) Lineage

Another factor that may influence a male's 'spatial status' is his membership in a kin group. It has been well documented in the literature that a Japanese macaque society is structured around sets of matrilineal kin groups, and that an animal's rank is established early in life, primarily on the basis of his mother's rank (Fedigan, 1982; Nishida, 1966; Tokuda, 1961). The Arashiyama West troop is comprised of eleven different matrilines and thus analysis was undertaken to determine if lineage membership can account for any of the variability in male sexual behavior (e.g., do males in certain lineages mount females more frequently or exhibit courtship behavior towards females more than males in other lineages?).

Results from one way analysis of variance tests revealed that a relatively small amount of variation does exist between the lineages in the frequency of "Male Courtship Behavior" exhibited by males towards females. Suma, the 'alpha' male of the troop, followed, approached, sat near and moved closer to females significantly more than males in the other lineages. Suma is the only male in this matriline and he often monopolized the space around the specific females and thus deterred them from forming consort relations with any other males. Although it appears that Suma pursued estrous females more frequently, it should be noted that this does not mean that Suma attained a higher rate of reproductive success. Suma also received leaves from females significantly more than other males did.

Of the 11 matrilines in the Arashiyama West troop, one does not stand out from the others in the behavior of its adult males. In the Betta lineage, males (specifically animals 108 and 129) rejected females and left females more than males in the other lineages. Because no other significant differences in behavior were seen, it is difficult to account for the behavioral variation present in this lineage.

It must be concluded that although some behavioral variation can be seen between the lineages, the results attained from the lineage comparisons are basically inconclusive and have little explanatory value.

(c) Age

The last factor that may influence 'spatial status' and therefore, mating behavior, is age. Hanby and Brown (1974) suggest that learning and social experience are influential factors towards the attainment of behavioral sexual maturity. The suggestion is that older males show a refinement in their courtship behaviors toward females and that more elaborate courting behaviors are indicative of older males who have learned them from previous experience.

The results from this study indicate that the age of the male appears to be the most influential biological factor, which accounts for a great deal of the variability in male courtship behavior. Pearson's Correlation analysis indicates that age is positively correlated with the higher level category of "Male Courtship Behavior" and more specifically with the following individual behaviors: approach, follow, sit near, move away, sit beside and leaves (received). Furthermore, age was positively correlated with the two higher level categories of "Affiliative" and "Rejection" behavior received from females towards males, as well as with the higher level category of "Aggressive" behavior. Not only are older males 'courting' females with a higher frequency, they are also spending significantly more of their time in close proximity with females. The age of the male was positively correlated with the mean duration of time spent by males sitting beside, sitting near and receiving a groom from a female.

It is interesting to note that even though older males exhibit a higher frequency of "Courtship" behavior toward females than younger males, they are also receiving more rejection behavior from females. The relationship between male age and rejection behavior received from females could be due to the fact that females are generally pursued more by older males than by younger males. It follows then, that an increase in the frequency of advances received by females from older males could explain the latter correlation.

Results from this study indicate that the variables age, to a limited extent, lineage, and least of all, rank, influence male sexual behavior. Accordingly, it is necessary to examine the combined effects of all these variables, as well as spatial status, to gain a holistic understanding of the dynamics behind male sexual behavior.

Linear Spatial Status as a Function of Rank, Age and Lineage

The third research objective was designed to determine whether an animal's age, rank and/or lineage can be used as indicators to predict an animal's 'spatial status' within a troop; and furthermore, whether a male's linear spatial status is a function of such variables.

The literature on the social structure of Japanese monkeys suggests that control of the multi-male and multi-female troop is carried out by a small group of high ranking, mature leader males (e.g., Sugiyama, 1976). It also suggests that after a period of peripheral life, males who are sons of higher-ranked females leave the periphery of the troop and return to the center part to attain a leadership position (Sugiyama, 1976). Whether sons of higher-ranked females show a decreased tendency for peripheralization and therefore a higher degree of centrality, however, needs to be demonstrated.

In their earlier consideration of some of these issues, Sugiyama and Oshsawa (1975) and Koyama (1967) concluded that peripheralization occurs regardless of a male's rank or the rank of his mother. The authors found that sons of high ranking females, as well as those of low ranking females, peripheralize from the center of the troop and that "the rank of the male's mother was related neither to his separate movement from the natal troop, nor to his moving into the periphery of the troop" (Sugiyama, 1976:269).

This line of reasoning suggests that male dominance rank <u>does not</u> directly affect an animal's <u>degree</u> of centrality or peripherality (and thus his linear spatial status) in a troop. This, however, is not the case among the Arashiyama West macaques. Indeed, in the majority of Japanese macaque societies, the central part of the troop is made up of older, higher ranked males, who are in fact sons of high ranking females. This indicates that maternal dominance rank can influence an animal's spatial proximity within the troop.

The mechanism whereby this influence develops has been suggested by Imanishi (1957). He noted that offspring of higher ranked females, who have been brought up in the center of the troop and could thus observe the behavior of the leader males at close quarters, become able to identify and comprehend the behavioral traits of leader males. Even though they spend their youth at the periphery of the troop, only such males can succeed in returning to the central part and become high ranking leader males themselves when they mature.

Following this then, it seems plausible to assert that a male's affiliation with the center part of the troop does affect his capabilities to become a leader male himself and that such affiliations will ultimately reinforce his dominance rank within the troop.

It is apparent that associations drawn between a male's rank and his linear spatial status do not indicate causality. One cannot, on the basis of the type of data collected in this thesis, decide whether male dominance rank determines an animal's linear spatial status, or if linear spatial status determines dominance rank. Material in the literature suggests, however, that maternal dominance rank plays a role in subsequent adult filial dominance rank, and that the latter will influence linear spatial status in adulthood.

Of greater importance than dominance rank is the <u>age</u> of the males. Age is known to be an important biological variable and has been shown to have a great deal of influence in establishing a male's linear spatial status. This variable has also been employed by numerous researchers in their discussions of the social structure in Japanese macaque troops (e.g., the concentric circle theory differentiates central and peripheral group membership primarily on the basis of age and dominance rank).

The linear grading of adult males proposed in this study illustrates that older males stay relatively closer to the center of the troop than younger males do.

Analysis reveals that a direct correlation exists between age and linear spatial status, thus substantiating the notion that older males tend to form the central part of a Japanese macaque troop.

Deviations from this pattern do exist. For example, among the Arashiyama West troop the age composition of those males with a high degree of peripheralization (i.e., a mean distance from Suma over 115 meters) varies from 7 to 15 years of age. This indicates that age, when viewed as an independent variable, does not necessarily determine, nor can it predict, a male's linear spatial status, although it does significantly influence it.

A male's maternal lineage is a third variable which also has a powerful, though not quite statistically significant, effect on a male's linear spatial status. Japanese primatologists have reported that within a Japanese macaque troop whole matrilineages may be ranked as being higher or lower in dominance than others. Other studies have shown that uterine groups are made up of monkeys who often share characteristics such as specific central-peripheral tendencies, certain rank and certain behavioral similarities (e.g., Fedigan, 1976). Koyama (1967) found that the ranks of troop members are strictly fixed by the ranks of their families, and that it is common for certain lineages to cohabit specific areas of the troop's home range.

Among the Arashiyama West troop a geographic distinction could be made of the central and peripheral parts of the troop based on lineage membership. For example, it was common for four of the existing eleven matrilines to occupy the geographic center of the troop (namely Nose, Momo, Suma and Betta), while the remaining seven lineages generally occupied the outermost or peripheral region (Namely Wania, Petimone, Matsu, Ran, Blanche, Syara and Shiro). It is of interest to note that both the males and females of the former mentioned lineages are all relatively high ranking animals, while those belonging to the latter lineages are relatively low ranking animals.

Results of this study indicate that a relationship can be drawn between dominance rank and age; secondly between lineage, dominance rank and linear spatial status; and thirdly between lineage, dominance rank, age and linear spatial status. Therefore, it is concluded that a male's linear spatial status is a likely function of the combined effects of age, rank and lineage, as well as being indirectly dependent on the isolated effects of any one of the aforementioned variables. In light of the results attained in this study, the third null hypothesis proposed (namely, that the variables age, rank and lineage when viewed independently, have no significant influence on a male's spatial status or sexual behavior) must be rejected.

As illustrated in Table 11, it is clear that a number of the predictors, specifically age, rank, lineage and linear spatial status, are concordant, for each has significant associations with specific sexual behaviors. For example, age, rank and linear spatial status each influence the frequency of males exhibiting the following three behaviors toward females: follow, approach and sit near. The only lineage to be included in this combination of predictors is the single-member matriline of Suma. The latter animal, however, is the 'alpha' male and without other males in his lineage, it is impossible to ascertain whether lineage *per se*--rather than the spatial status of the 'alpha' male--accounts for the lineage association.

A second significant association can be drawn between the predictors age and linear spatial status with the higher level category of "Male Courtship Behavior", as well as with the frequency of affiliative behavior received and rejection behavior received by males from females.

It is interesting to note that the following pairs of predictors show no significant associations with any of the 16 behavioral units listed in Table 11: rank and age, rank and lineage, or rank and linear spatial status. In

Table 11 - A Summary of the Significant Associations Between the Precitors Age, Rank, Lineage and Linear Spatial Status and 16 Behavioral Units. (The shaded areas represent significant associations with the specific behavioral unit and the unshaded areas represent an absence of association.)

Behavior	Age	Rank (High)	Lineage	Linear Spatial Status
Male courtship behavior	●			●
Affiliative behavior received	●			●
Rejection behavior			● Betta	●
Rejection behavior received	●			●
Travel behavior				●
Follow behavior	●	●	● Suma	●
Chase				●
Restrain			● Momo	
Approach	●	●	● Suma	●
Masturbate			● Shiro	
Sit near	●	●	● Suma	●
Lip quiver				●
Move closer			● Suma	●
Leave			● Betta	
Leave (receive)	●		● Suma	
Move away	●		● Momo	

addition, the combination of age, rank and lineage show no significant association with the following behaviors: travel, chase and lip quiver.

Special attention must be drawn to the apparent non-significant influence of dominance rank on mating behavior. When viewed as an isolated variable, dominance rank has no significant influence on the following 13 behaviors: male courtship behavior, affiliative behavior (received), rejection behavior (direct/receive), travel, chase, 'move closer', lip quiver, leave (direct/receive), move away, restrain and masturbate. Dominance rank is significantly associated with the following behaviors only when in combination with the predictors age, lineage and linear spatial status: follow behavior, approach behavior and 'sit near'. The lack of significant associations between dominance rank and mating activity substantiates the notion that rank, when viewed as an independent variable, is a poor predictor of male mating behavior.

Contrary to this, it is evident that the predictors age and linear spatial status, when examined for either their joint or isolated associations with the behavioral units, account for the highest number of significant associations with mating activity. When viewed as an isolated variable, age is significantly associated with 8 of the 16 listed behaviors, while linear spatial status is significantly associated with 11 of the 16 behaviors. It is therefore concluded that an animal's age and linear spatial status are the predictors with the most significant influence on male mating behavior.

Not only is a male's linear spatial status an important variable in the study of male sexual behavior, but it is also a useful index in the study of nonhuman primate social structure. For example, once an animal's linear spatial status is determined, it may be possible to postulate an animal's age and rank when these variables are not known. Results from this study clearly indicate that a significant correlation exists between linear spatial status and age and probably also between linear spatial status and dominance rank, for animals with the highest spatial status are the high ranked animals. Hence, the location of males within a troop is a useful key to understanding the dynamics behind Japanese macaque social organization.

One suggestion which emerges from this study is that the term "spatial status" be considered a sociological label which incorporates the cumulative effects of age, dominance rank and lineage to measure an animal's degree of 'sociability' within a troop. By viewing "spatial status" as a label (as Fedigan briefly does in her 1976 study), a great deal of the known variability in male sociosexual behavior (which is influenced by a male's age, rank and lineage) could be accounted for. This is not to say that all behavioral interactions which occur in Japanese macaque troops can be explained by this approach. Using the term "spatial status" as a label should be viewed as a means to an end in the hope of gaining a better understanding of macaque social life and more specifically, help gain a deeper insight into nonhuman primate sexual behavior.

Linear Spatial Status: An Adaptation or an Exaptation?

Adaptation has been defined and recognized by two different criteria: historical genesis, which refers to features built by natural selection for their present role; and current utility, which refers to features presently enhancing fitness, regardless of how they have arisen (Gould and Vrba, 1981). Can the 'spatial status' concept and/or the process of peripheralization be viewed as adaptations which have evolved through the process of natural selection to perform specific roles or tasks? Or, to borrow a term from Gould and Vrba (1981), should the aforementioned features be viewed as "exaptations" in that they are features which exist today but "were not built by natural selection for their current role" (Gould and Vrba, 1981:6)?

The term 'exaptation' was introduced by Stephen J. Gould primarily because he felt that people "have tended to view natural selection as so dominant among evolutionary mechanisms that historical process and current product become one" (1981:4). Thus, in an attempt to clarify such blurred interpretations of evolutionary theory, Gould suggests that adaptations be restricted, as Darwin suggested, to features built by selection for their current role, and that features which now enhance fitness, but were not built by natural selection for their current role, be called "exaptations" (1981:4). Gould's operational definition does not downplay the role which adaptation plays in the conceptual framework of evolutionary theory. It does, however, offer an insightful alternative to discuss how existing characters may have evolved because they were fit for their current role, but not specifically designed for it, and are therefore not pushed toward fitness (Gould, 1981).

The central thesis in Gould's argument is summarized in the following statement: "adaptations have functions; exaptations have effects" (1981:6). Specifically, Gould argues that the operation of an adaptation is its function, and that the operation of an exaptation should be labelled an "effect".

Many researchers have asserted that the function and/or proximate cause of peripheralization is 'inbreeding avoidance', and that male emigration promotes outbreeding (e.g., Koyama, 1974; Imanishi, 1960). Peripheralization may indeed promote the transfer of new genetic material from one troop to another, thus facilitating genetic variability in the species. It is important to stress, however, that outbreeding is a result of peripheralization, and should not be viewed as a directed, nor intended consequence of it.

Similarly, inbreeding avoidance cannot be viewed as a factor which drives males away from their natal troop; again it may be a result, not a cause of peripheralization. As Fedigan states,

> the existence of a psychological incest avoidance mechanism...in nonhuman primates, cannot be proven using only the data of male emigration of group transfers, unless it can be documented that an inhibition against mating or an unwillingness to mate with matrilineal kin is the proximate cause of male emigration (1982:131; emphasis added).

Among the Arashiyama West troop the somewhat 'natural' tendency for males to emigrate to neighboring troops is prevented by the fact that the troop is presently isolated from other groups of nonhuman primates. If one accepts the hypothesis that male emigration functions as an incest avoiding mechanism, then it would follow that there would be an increase in the amount of inbreeding among this troop. In light of the data collected by

Fedigan and Gouzoules (1978) on consort relations of the Arashiyama West troop, this hypothesis must be rejected. The authors have been collecting consort and mating data on this troop for the past five years and report that

> out of more than 1000 matings, we have *never* observed a mother-son copulation, only one brother-sister mating, and one grandmother-grandson mating. Among the Arashiyama West troop almost all males remain in the natal troop, so that the opportunities for mother-son and within-matriline matings are constantly increasing. In spite of this, *cases of within-family mating continue to be rare to non-existent* (cited in Fedigan 1982:131; emphasis added).

What is apparent is that the exact function of peripheralization among Japanese macaques, and more specifically, the linear grading of adult males according to their mean distance from the 'alpha' male, among the Arashiyama West troop, remains undetermined.

Although it is evident that males are geographically positioning themselves in a linear fashion, it is important to stress that there exists a great deal of inherent variability and thus it becomes clear that the spatial organization characteristic of the Arashiyama West troop is not a rigid structure. Whether the 'spatial status' concept is an adaptation or has any adaptive significance is difficult to determine at this time. It is questionable whether the linear grading of males present in this troop of macaques has evolved through the process of natural selection to promote 'fitness' in the males of this species. For example, it is difficult to ascertain whether an animal's chance of survival or his reproductive success are enhanced by the existence of a linear gradation.

At the outset of this study, it was hypothesized that only those males which stayed relatively closer to the 'alpha' male of the troop could maximize their reproductive success by forming successful consort relations with estrous females--thus suggesting that 'spatial status' could promote 'fitness' in males with a shorter mean distance from the 'alpha' male. This hypothesis suggests that males with a relatively short mean distance from Suma will mate more often with estrous females than will males with a longer mean distance from Suma. Through the course of this study, it has become evident that one cannot, on the basis of correlation results, prove that a reproductive advantage is incurred by males with a shorter mean distance from the 'alpha' male. It would be incorrect to infer that a male's 'spatial status' gives him 'priority of access' to estrous females, if by the latter phrase a higher successful copulatory frequency is implied.

The results from this study did indicate that linear spatial status was significantly correlated with the higher level category of "Male Courtship Behavior" (i.e., as linear spatial status increases, the frequency of "Male Courtship Behavior" increases), and a male's linear spatial status did have a significant effect on the frequency of certain male sexual and non-sexual behaviors.

However, male spatial status was not significantly associated with "Male Mounting Behavior", or "Male Copulatory Behavior". This means that although spatial status does indeed influence males' proximity to and interactions with females, spatial status does not influence the likelihood of increased male reproduction, since the key behaviors involved with possible reproduction (mounting behavior, copulatory behavior) are not associated with it (i.e., with spatial status). Such results do not suggest that spatial status would be associated with fertility fitness differences. Hence, linear gradation of male distances from the alpha male is not likely to be a pattern that has been, or is being "selected for" through differential fertility.

On the other hand, it is important to stress that in order to determine rigorously whether 'spatial status' has any adaptive significance, it would be necessary to establish individual male fertility rates and correlate these with 'spatial status'. A more specific question is whether males with a shorter mean distance from Suma have a higher rate of reproductive success than do males with a longer mean distance from Suma. This question cannot be answered with the data in this thesis. Indeed, the available literature on Japanese macaques cannot provide an answer, for a true measure of reproductive success of nonhuman primates requires accurate identification of fathers. Information on biological paternity in monkeys is simply not available and as Fedigan (1982) states,

> since it is not possible to administer biological tests of paternity (biochemical blood protein analyses) in most of the multi-male, multi-female groups studied, researchers have been forced to rely on the indirect evidence of mating activities to infer male parentage (1982:280; emphasis added).

A less reliable method of measuring male reproductive success is the measurement of ejaculation frequencies. This method has beem employed by researchers (e.g., Eaton, 1974; Hanby et al, 1971) as an alternative to biological tests of paternity. However, one major problem with the measurement of ejaculation frequencies is that "female primates may mate in the nonovulatory phases of their cycles" (Fedigan, 1982:280), and therefore every ejaculation does not necessarily result in fertilization. The problem is compounded in Japanese macaques, for in the females of this species there are no clear external signs that correlate internal ovulatory events (i.e., the perineum or face of the female does not act as an indicator of ovulation), as occurs in some other monkey species (e.g., Papio anubis). The issue of whether spatial status constitutes an exaptation or adaptation, then, remains open, although the findings in this thesis favour the notion of exaptation.

Clearly, future research is needed to shed more light on the role of male 'spatial status' as well as on the adaptive significance if any, of the linear gradation of males. A direction for future research could be to seek alternative explanations for the existence of the peripheralization tendency. A longitudinal study on the complete life history of male Japanese monkeys combined with new and improved methods of paternity testing, would yield valuable insight into the social, biological, and evolutionary functions of nonhuman primate spatial and social structure. A study of this type would also offer valuable information on the role and effect which kinship has on nonhuman primate mating patterns.

CHAPTER V

SUMMARY

The present study offers an objective method of measuring the central-peripheral tendency in a Japanese macaque troop. Calculating an animal's mean distance in meters from the 'alpha' male of a troop allows a hierarchical grading of animals to be formed which clearly illustrates a troop's spatial organization. This method was applied to the Arashiyama West troop of Japanese macaques and results indicate without a doubt that the adult males in this troop can be spatially arranged along a theoretical central-peripheral axis. The resultant linear grading, when divided into two at the 115 meter mark from the 'alpha' male, identifies 'central' and 'peripheral' male groups that corroborate previously made intuitive distinctions concerning the spatial status of sexually mature males in this troop.

Defining 'spatial status' as a gradation of the distance between each male and the 'alpha' male where the shortest mean distance corresponds to the highest spatial status, this study examines the influence which age, dominance rank, and lineage have on determining a male's 'spatial status' within a troop. The isolated and cumulative effects of the aforementioned variables are als-examined to explain variations in male sexual behavior.

Results from this study indicate that a male's 'spatial status' is influenced directly by the combined effects of age, rank and lineage, as well as being indirectly influenced by the isolated effects of any one of the previously mentioned variables.

Furthermore, the results indicate that a male's 'spatial status' does significantly influence the frequency of courtship behavior exhibited by males toward females. A positive correlation was found to exist between linear spatial status and "male courtship behavior", thus indicating that as a male's degree of centralization increases, the frequency of courtship behavior exhibited towards females increases.

The frequency of "male courtship behavior" or "male copulatory behavior" (mount ejaculation) did not differ among the three male dominance ranks, nor was "male copulatory behavior" correlated with spatial status. Therefore, the hypothesis made that only high ranked, central males have reproductively meaningful access to central females (e.g., Altmann, 1962) must be rejected.

The results indicate the a male's age and his 'spatial status' explain the most variability in male mating activity. In this study, testing the maternal lineage of the male produced inconclusive results, although some behavioral variation between the lineages is documented.

Two major suggestions are proposed in this study. Firstly, the term 'spatial status' should be considered a sociological label; one which incorporates the interacting effects of age, rank and lineage and which can be used to describe the dynamics of Japanese macaque social life. Secondly, the process of peripheralization and the existence of adult male 'spatial status', both of which are present in macaque troops, be viewed as probable "exaptations" (as opposed to "adaptations"), that probably did not evolve through the process of natural selection to promote "fitness".

APPENDIX A

Tatoo #	Animal Name	Numerical Lineage Code	Rank: High/Med/Low	Spatial Status: Cent/Per.	Linear Spatial Grading From Alpha Male	Is Mother of Male Present in Troop?	# of Females in Focal Animal's Immed. Family	# Males in Focal Animal's Immed. Family	Mean Distance from Alpha Male (in meters)	Age	Comments
1	Rh 6271	1	H	C	8	No	1	0	112.32	12	
2	P 70	2	M	C	6	No	3	1	95.26	13	
3	N 6272	3	H	C	2	Yes	1	0	69.14	11	
12	Rh58636975	1	M	P	20	Yes	0	0	244.54	8	
16	P 6573	2	H	P	11	Yes	1	0	155.36	10	
28	Suma'64	4	H	C	--	No	0	0	-	18	Alpha male
29	Pet 6470	5	L	P	16	Yes	2	0	182.39	13	
53	Mat 586376	6	L	P	17	No	3	0	204.76	7	
54	Ra 76	7	M	P	14	Yes	0	1	162.70	7	
55	Wa 70	2	L	P	15	Yes	6	0	168.52	13	
61	Sy 67	8	M	P	10	No	0	0	117.86	16	
74	Ro 6370	1	H	C	1	Yes	1	0	64.47	13	
81	Mat 616776	6	L	P	18	No	1	0	218.80	7	
108	B 586475	9	M	P	12	Yes	2	1	157.77	8	
128	Me 65	3	H	C	5	Yes	2	1	89.37	18	
129	B 586471	9	H	C	4	Yes	2	1	79.46	12	Second ranked male
131	Pet 6175	5	L	P	23	No	2	0	354.34	8	
134	Ra 68	7	M	P	13	Yes	0	1	158.57	15	
135	Me 6776	3	M	P	19	Yes	1	0	224.04	7	
139	Bl 6777	7	L	P	21	Yes	0	0	252.06		
143	P 68	2	M	C	7	No	3	1	101.50	15	
146	Me 69	3	H	C	3	Yes	2	1	75.16	14	
245	Sh 6477	10	L	P	22	No	0	0	300.33	6	
250	Momo'64	11	L	C	9	No	0	0	113.99	18	

APPENDIX B. Example of Focal Animal Data Sheet

Subject: 28

Date: Nov. 1, 1982

Time: 0900 hrs.

Number of Focal Session on Subject 3

Time	Behavior	Direction	Interacting Animal	Comments
0900:00	groom	→	7	Female
3:50	sit beside	→	7	
5:00	leave	→	7	
5:01	locomote			
10:00	forage			
11:15	sit			
12:00	approach	→	117-female	
12:30	sit beside	→	117	

APPENDIX C. Behavioral units recorded and defined throughout this study (*denotes definition was taken from Fedigan (1976) Ethogram).

1. Forage: the active search for food which is followed by the chewing and swallowing of the food item.
2. Locomote: to move across the ground at a walking speed in a quadrupedal fashion.
3. Follow-direct/receive: to travel directly behind and in the path of another monkey. This behavior is usually accompanied by the leading animal looking backwards at the animal following him/her.
4. Approach-direct/receive: a direct advance made by one monkey towards another with is generally followed by a social interaction.
5. Lope/run: quadrupedal locomotion made at a swinging stride.
6. Chase-direct/receive: the pursuit of one monkey by another, usually accompanied by distinct vocalizations.
7. *Climb-up/down: the act of ascension or decension using both the hands and the feet.
8. Jump: a monkey springs/bounds from a tree or structure onto the ground, or from tree to tree.
9. Bipedal: an attentive stance made on a monkey's two hind limbs.
10. Bird dog: a frozen stance suddenly performed by males while locomoting. The tail is usually in an upright position. This behavior usually lasts from 3-5 seconds.
11. Stand alone: four-legged stance, usually a transitional behavior between movement patterns.
12. Stand and scan: four-legged stance where the monkey is stationary and visually examining the area around him.
13. Stand beside-direct/receive: four-legged stance, made in slight body contact with another animal. This behavior is frequently exhibited after leading and following and it appears to be a restful affiliative gesture.

14. Drink: the consumption of water from either of the waterholes or from puddles.

15. *Sit or lie alone: this is an "inactive" behavioral category. It is recorded when the subject is in a sitting or prone posture, and not performing any of the other behaviors in this ethogram.

16. Sit and scan: the subject is in a sitting posture and usually examining the area around him/her.

17. Sit and peer: the subject is in a sitting posture and is intensely staring at another animal.

18. Sit beside-direct/receive: sitting in slight body contact with another animal where the fur is touching. This behavior was recorded generally after a direct advance was made by one monkey towards another.

19. Sit near-direct/receive: animals sitting more than one meter apart. This behavior was only recorded when it was obvious that a male approached and sat near a female, or vice versa. No male-male sit nears were recorded.

20. Huddle-direct/receive: to sit in extreme bodily contact with another monkey. The monkeys appear to be holding/clasping each other in a ventral-dorsal position. Usually the animal in the rear initiates this positioning.

21. Gross body contact/direct/receive: any non-ventral close body contact made between two monkeys, e.g., a male sitting against the side of a female.

22. Embrace: a close ventral-ventral sitting position between two monkeys accompanied by a light-hold.

23. Lie beside: the subject is in a prone position lying in slight body contact to another monkey with fur touching.

24. *Sleep: the subject is either in a sitting or lying posture with his eyes closed and is assumed to be asleep.

25. *Object manipulation: the continual handling of a small object (e.g., a twig) which is not a food item.

26. *Groom solicitation-direct/receive: the presentation made by one monkey towards another with a portion of its body (e.g., chest, back).

27. Groom-direct/receive: the picking, cleaning and/or spreading of the fur or skin made by one monkey to another.

28. Groom-self: the subject picks and cleans his own fur.

29. Change position: a voluntary change in position made by a stationary animal (e.g., an animal changes position while lying down by rolling over).

30. Glance at/look at: an instantaneous look made by one monkey towards another.

31. Stare-direct/receive: an animal looks intensively at another animal. This is a prolonged and deliberate behavior.

32. Lip quiver-direct/receive: a rather rapid up and down movement of the lips over the teeth with the lips slightly pouted. This appears to be a reassurance signal used in social situations in which there might be some tension.

33. *Fear grimace-direct/receive: a submissive visual signal where the lips retract from the teeth. The teeth are tightly clenched together.

34. *Visual and vocal threat-direct/receive: consists of the following agonistic signals: stare, lid, gape and growl. The components are rapid and flexible in combination and sequence, thus they are combined into this "threat unit".

35. *Displace-direct/receive: one monkey moves toward another who immediately moves out of the former's way. This behavior is usually a clear indication of relative dominance status.

36. *Lunge-direct/receive: a plunge towards an opponent in an agonistic encounter, followed by quick retreat.

37. *Bite-direct/receive: to seize another animal with the teeth.

38. Pin and bite-direct/receive: to aggressively take hold of another monkey's body and seize a part of it with the teeth.

39. Grab-direct/receive: to take hold of another animal's body and squeezing, usually to the point of pain.

40. *Jump startle (A): a sudden explosive movement of the body in place, occurring when a monkey is caught unaware, for example, when another monkey is not heard to approach, but is suddenly seen at close range.

41. Leave-direct/receive: an animal breaks contact with another animal by increasing the distance between them, with body turned away.

42. Walk around-direct/receive: an animal will approach and make a circle around another animal and then either walk away or sit beside the animal. This behavior is generally seen by males toward females.

43. Look back (travel): while locomoting, a monkey turns its head and appears to be looking at something in his wake.

44. *Look back (sexual)-direct/receive: a mounted monkey twists its head and body around in order to make visual contact with the mounter.

45. *Sex present-direct/receive: a gesture of orienting the hind quarters toward another while sitting with the posterior raised slightly off the ground.

46. *Display: a vigorous locomotor pattern which calls attention to the actor. A display usually involves hearty shaking of a large flexible item in the environment, such as branches, poles, etc. Often accompanied by grunting vocalizations.

47. Yawn: the opening of the mouth in the shape of an enlarged oval, followed by the corners of the mouth being pulled back so that the teeth and gums are exposed. This is observed frequently in the copulatory sequence.

48. Move away-direct/receive: a monkey slightly edges away from another monkey, but is still sitting near it.

49. Move closer-direct/receive: a monkey increases its proximity to another by slightly edging toward it. This behavior is less obvious and direct than an approach.

50. Genital inspect-direct/receive: a monkey manipulates the genitals of another monkey for over 3 seconds.

51. Genital touch-direct/receive: an instantaneous touching/grasping of a monkey's genitals made by another monkey for less than 3 seconds.

52. *Masturbate: self-manipulation of the genitals.

53. Ejaculation: the sudden, spontaneous discharging of semen resulting from male masturbation.

54. Eat ejaculate: this is a behavior exhibited by males whereby they will pick ejaculate from their genitals and eat it.

55. Hip touch-direct/receive: a gesture preliminary to a mount in which the actor pulls upward on the pelvis of the recipient. This is apparently an attempt to get the recipient into the proper position for mounting.

56. Restrain-direct/receive: a gesture of holding an animal by the foot, hand or tail. This is often exhibited by males toward females in a copulatory sequence.

57. Mount-direct/receive: one monkey stands up against the back of another, braces its feet on this animal's calves and its hands on its back.

58. Ventral-ventral mount-direct/receive: one animal ventrally embraces and exerts its body weight on another. The male displays pelvic thrusts, but it is not clear whether he inserts his penis into the female's vagina. The male does not ejaculate in this posture.

59. Mount rub-direct/receive: a mount with noticeable rubbing of the genitalia, but no penetration is made.

60. Hind-legged mount and hold: a rapid behavior exhibited by certain males toward females during a copulatory sequence. The male turns his back to the female, places his feet on her calves and remains in this position from 5 to 10 seconds. He then dismounts and the copulatory sequence resumes.

61. *Thrust-direct/receive: forward-backward movement of the pelvis by the mounter. Performed both in the presence and absence of intromission.

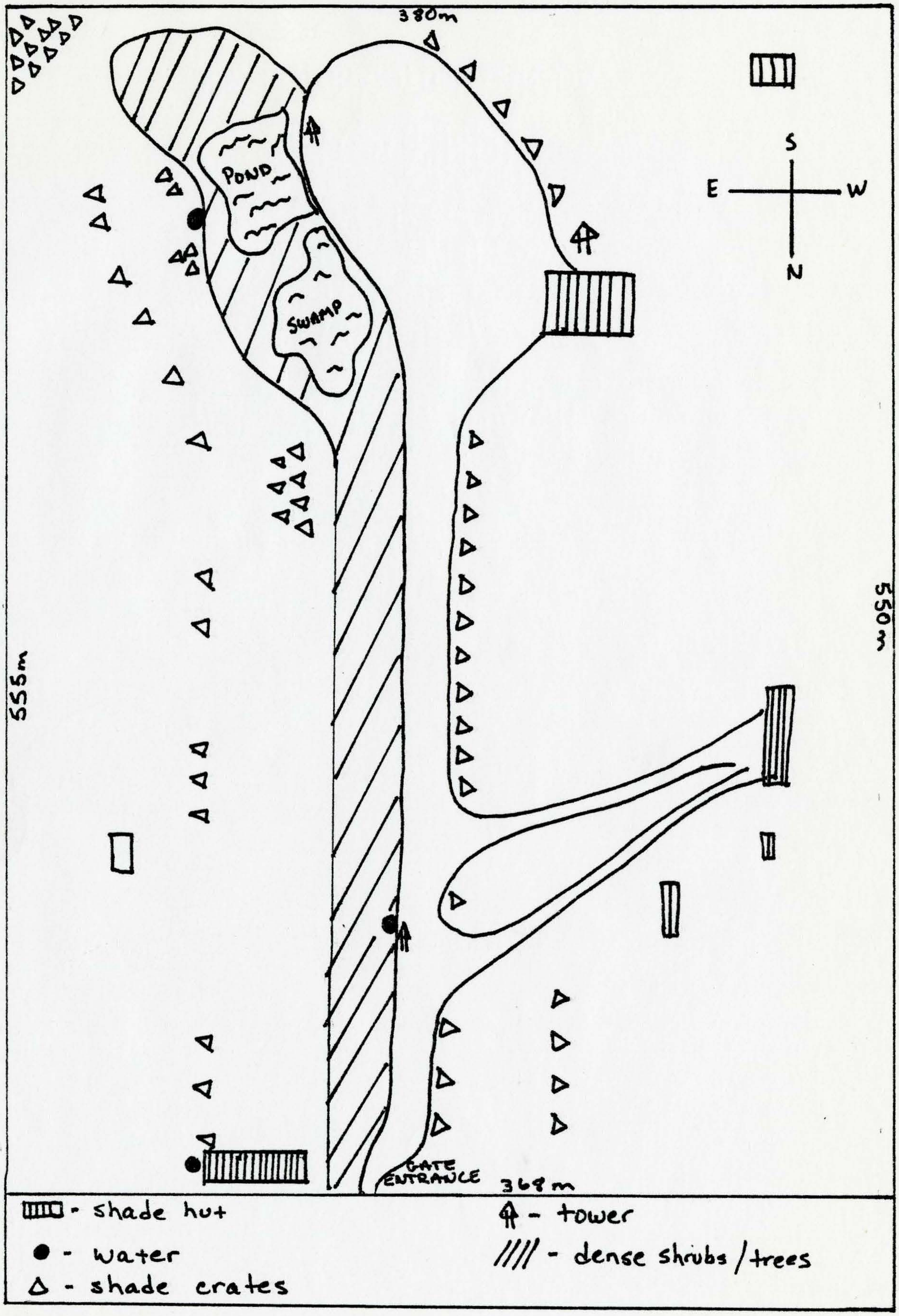
62. Mount ejaculate: the spontaneous discharging of semen by the male during the last mount in the copulatory sequence.

63. Attempt mount-direct/receive: an unsuccessful mount made by one animal towards another.

64. *Agitated body jerk-direct/receive: a rapid, repeated twitching of the entire body when individuals are frustrated in their attempts at some type of social interaction. Body jerks are often given by courting males when females to not act receptive.

65. *Reach back-direct/receive: a mounted monkey reaches back and grasps the leg or other body part of the mounter.

APPENDIX D. Arashiyama West Enclosure, Dilly, Texas



REFERENCES CITED

Alexander, B.K. and Bowers, J.M.
1967 The social structure of the Oregon troop of Japanese macaques. Primates 8:33-40.

Altmann, S.A.
1962 A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Annual New York Academy of Science 102:338-435.

1965 Cited in P. Lehner, *Handbook of Ethological Methods*. New York: Garland Press, 1979, p. 63.

Baxter, M.J. and Fedigan, L.M.
1979 Grooming and consort partner selection in a troop of Japanese monkeys (*Macaca fuscata*). Arch. Sexual Behavior 8:445-458.

Bernstein, I.S.
1970 Primate Status Hierarchies. In: *Primate Behavior: Developments in Field and Laboratory Research*, I. Bernstein, ed. New York:

1976 Dominance, aggression and reproduction in primate societies. J. Theor. Biol. 60:459-472.

Bernstein, I.S. and Gordon, T.P.
1974 The function of aggression in primate societies. J. Theor. Biol. 60:459-472.

Boelkins, R.C.
1967 Determination of dominance hierarchies in monkeys. Psychoneurological Science 7:317-318.

Bramblett, C.
1976 *Patterns of Primate Behavior*. Palo Alto: Mayfield Press.

Bullard, J.
1983 Mount-eliciting behaviors of consorting female Japanese macaques. Paper delivered at the Canadian Association of Physical Anthropologists Meetings, October, 1983. Montreal, Canada.

Carpenter, C.R.
1942 Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). J. Comp. Psych. 33:113-162.

Casey, D.E. and Clark, T.E.
1976 Some spacing relations among the central males of a transplated troop of Japanese macaques (Arashiyama West). Primates 17: 433-450.

Chapais, B.
1983 Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. Behav. Ecol. Sociobiol. 12:215-228.

Clark, P.J. and Evans, F.C.
1954 Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35:445.

Conoway, C.H. and Koford, C.B.
1965 Estrous cycles and mating behavior in a free-ranging band of rhesus monkeys. Journal of Mammology 45:577-588.

Darwin, C.
1859 On the Origin of Species. London: J. Murray.

Davenport, R.K. and Rogers, C.M.
1978 Intellectual performance of differentially reared chimpanzees. I. Delayed response. Amer. J. Ment. Defic. 72:674-680.

Drickamer, L.C.
1974 Social rank, observability and sexual behavior of rhesus monkeys (Macaca mulatta). J. Reprod. Fert. 37:117-120.

1974 Quantitative observation of behavior in free-ranging Macaca mulatta: methodology and aggression. Behavior 55:202-236.

Drickamer, L.C. and Vessey, S.H.
1973 Group changing in free-ranging male rhesus monkeys. Primates 14:359-368.

Eaton, G.
1974 Male dominance and aggression in Japanese macaque reproduction. In: Reproductive Behavior, W. Montagna, ed. New York: Plenum Press, pp. 287-297.

1976 The social order of Japanese macaques. Scientific American 235:96-106.

Eaton, G.
1978 Longitudinal studies of sexual behavior in the Oregon troop of Japanese macaques. In: Sex and Behavior, Status and Prospectus, J.E. Gill, D.A. Dewsbury and B.D. Sachs, eds. New York: Plenum Press.

Ehardt-Steward, C. and Bramblett, C.A.
1980 The structure of social space among a captive group of vervet monkeys. Folia Primatol. 34: 214-238.

Emory, G.R.
1975 Comparison of spatial and orientational relationships as manifestations of divergent modes of social organization in captive groups of M. sphinx and T. gelada. Folia Primat. 24:293-314.

Enomoto, T.
1974 The sexual behavior of Japanese monkeys. J. Human Evol. 3:351-372.

1978 On social preference in sexual behavior of Japanese monkeys. J. Human Evol. 7:283-293.

1981 Male aggression and the sexual behavior of Japanese monkeys. Primates 22(1):15-23.

Fedigan, L.M.
1976 A study of roles in the Arashiyama West troop of Japanese macaques (Macaca fuscata). Contributions to Primatology 9. Basel: S. Karger.

1982 Primate Paradigms. Montreal: Eden Press.

Fedigan, L.M. and Gouzoulez, H.
1978 The consort relationship in a troop of Japanese monkeys. In: Recent Advances in Primatology, Vol. 1: Behavior. D. Chivers, ed. London: Academic Press, pp. 493-495.

Gartlan, I.S.
1968 Structure and function in primate society. Folia. Primat. 8:89-120.

Gould, S.J. and Vrba, E.S.
1981 Exaptation--a missing term in the science of form. Paleobiology 8(1):4-15.

Hall, K.R.
1967 Social interactions of the adult male and adult females of a patas monkey group. In: Social Communication Among Primates, S.A. Altmann, ed. Chicago: University of Chicago Press, pp. 261-280.

Hanby, J.P. and Brown, C.E.
1974 The development of sociosexual behaviors in Japanese macaques. Behavior 49(1-2):152-196.

Hanby, J.P., Robertson, L.T. and Phoenix, C.H.
1971 The sexual behavior of a confined troop of Japanese macaques. Folia Primatol. 16:123-143.

Harlow, H.F.
1962 The heterosexual affectional system in monkeys. Am. Psych. 17:1-9.

Hausfater, G.
1975 Dominance and reproduction in baboons. In: Contributions to Primatology, 7. Basel: S. Karger.

Hinde, R.A.
1978 Dominance and roles--two concepts with dual meanings. J. Social Biol. Structure, 1:27-38.

Holt, N.
1980 Social Dominance in a Group of Captive Mandrills (Mandrillus sphinx): An Analysis of Behaviour Indices. Unpublished Masters Thesis, McMaster University.

Imanishi, K.
1957 Social behavior in Japanese monkeys (Macaca fuscata). Psychologia 1:47-54.

1960 Social organization of subhuman primates in their natural habitat. Cur. Anthrop. 1: 390-405.

1963 Social behavior in Japanese monkeys (Macaca fuscata). In: C.H. Southwick, ed., Primate Social Behavior. Princeton: Van Nostrand, pp. 68-81.

1965 Identification: a process of socialization in the subhuman society of Macaca fuscata. In: Japanese Monkeys, K. Imanishi and S. Altmann, eds. Atlanta: Emory University Press, pp. 30-51.

Itani, J.
1954 Japanese monkeys in Takasakiyama. Cited in Sugiyama, Y. Life History of Male Japanese Monkeys. In: *Advances in the Study of Behavior* (7), 1976, p. 225.

Itoigawa, N.
1974 Variables in male leaving a group of Japanese monkeys. In: *Proc. Symp. 5th Cong. Prim. Soc.*, S. Kondo, M. Kawai, A. Ehara and S. Kamura, eds. Tokyo, Japan: Japan Science Press, pp. 233-245.

Kaufman, I.C.
1965 A three year study of mating behavior in a free-ranging band of rhesus monkeys. Ecology *46*:500-512.

Kawamura, S.
1958 A study on the rank system of Japanese monkeys. *Primates* *1*:149-156.

Koyama, N.
1967 On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates *8*:189-216.

1974 Division of the Arashiyama troop--its mechanism and blood relationship. Anima. *11*:31-36.

Kummer, H.
1971 *Primate Societies. Group Techniques of Ecological Adaptation.* Chicago: Aldine-Atherton.

1974 Distribution of interindividual distances in Patas monkeys and Gelada baboons. Folia Primatol. *21*:153-160.

Lancaster, J.B.
1973 In praise of the achieving female monkey. Psych. Today, 30-36.

Lehner, P.
1979 *Handbook of Ethological Methods.* New York: Garland Press.

Loy, J.
1971 Estrous behavior of free-ranging rhesus monkeys (*Macaca mulatta*). Primates *12*:1-31.

Mason, M.
1961 The effects of social restriction on the behavior of rhesus monkeys: 1. Free social behavior. J. Comp. Physiol. Psychol. 53:582-589.

Missakia, E.
1969 Reproductive behavior of socially deprived adult male rhesus monkeys (*Macaca mulatta*). J. Comp. Physiol. Psychol. 69:403-407.

Nie, N., et al.
1975 *Statistical Package for the Social Sciences*. 2nd ed. New York: McGraw Hill.

Nishida, T.
1966 A sociological study of solitary male monkeys. Primates 7:141-204.

1970 Social behavior and relationships among wild chimpanzees of the Mahali mountains. Primates 11:47-87.

Norikoshi, K. and Koyama, N.
1975 Group shifting and social organization among Japanese monkeys. In: *Proc. Symp. 5th Cong. Int. Primat. Soc.*, S. Kondo, M. Kawai, A. Ehara, S. Kawamura, eds. Tokyo, Japan: Japan Science Press, 43-61.

Reisen, A.H.
1971 Chimpanzee visual perception. In: G.H. Bourne, ed., *The Chimpanzee*, Vol. 2. Basel: Karger.

Rowell, T.E.
1966 Hierarchy in the organization of a captive baboon group. Animal Behavior 14:430-443.

1974 The concept of dominance. Behav. Biol. 11: 131-154.

Ryan, T., et al.
1980 *Minitab: Reference Manual*. McMaster University Printing.

Schjelderup-Ebbe, T.
1922 Contributions to the social psychology of the domestic chicken. In: *Social Hierarchy and Dominance*. M.W. Schein, ed. Pennsylvania: Halsted Press, pp. 35-49.

Seyfarth, R.M.
1977 A model of social grooming among adult female monkeys. J. Theor. Biol. 65:671-698.

Shively, C., Clark, S., King, N., Schapiro, S. and G. Mitchell
1982 Patterns of sexual behavior in male macaques. A.J. Primatol. 2:373-384.

Stephenson, G.R.
1973 Cited in L.M. Fedigan. Primate Paradigms, 1982. Montreal: Eden Press, p. 117.

1975 Social structure of mating activity in Japanese macaques. In: Proc. Symp. 5th Congress Int. Primat. Soc., S. Kondo, M. Kawai, A. Ehara, S. Kawamura, eds. Tokyo, Japan: Japan Science Press, pp. 63-115.

Sugawara, K.
1980 The structure of social encounters among solitary males of Japanese monkeys. Quart. Anthrop. 11:3-70.

Sugiyama, Y.
1976 Life history of male Japanese monkeys. In: Advances in the Study of Behavior, Vol. 7. J.S. Rosenblatt, R.A. Hinde, E. Shaw and C. Beer, eds. New York: Academic Press, pp. 255-285.

Sugiyama, Y. and Oshsawa, H.
1975 Life history of male Japanese macaques at Ryozenyama. In: Contemporary Primatology, S. Kondo, A. Ehara and M. Kawai, eds. Karger: Basel, pp. 407-410.

Takahata, Y.
1981 The Socio-Sexual Behavior of Japanese monkeys. Z. Tierpsychol. 59:89-108.

Tokuda, E.K.
1958 The monkeys in Koshima Islet--Their sexual behavior. Cited in T. Enomoto, Male aggression and the sexual behavior of Japanese monkeys. 1981 Primates 22:21.

1961 A study on the sexual behaviors in the Japanese monkey troop. Primates 3(2):1-40.

Williams, G.
1966 Adaptation and Natural Selection. Princeton, New Jersey: Princeton University Press.

Wilson, A.P.
1968 Cited in S. Bernstein, Dominance, aggression and reproduction in primate societies. In: J. Theor. Biol. (1976) 60:467.

Wolfe, L.
1976 The Sexual Behavior of the Arashiyama West Troop of Japanese Macaques. Doctoral Dissertation, University of Oregon.

Yamada, M.
1966 Five natural troops of Japanese monkeys in Shodoshima Island. Primates 7:315-361.

1971 Five natural troops of Japanese monkeys in Shodoshima Island, II. A comparison of social structure. Primates 12:81-104.