THE COURTSHIP BEHAVIOUR OF FEMALE JAPANESE MONKEYS

THE COURTSHIP BEHAVIOUR
OF
FEMALE JAPANESE MONKEYS

By

MARY SUSAN MCDONALD, B.A.

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

McMaster University
October 1983

MASTER OF ARTS (1983)
(Anthropology)

McMASTER UNIVERSITY
Hamilton, Ontario

TITLE: The Courtship Behaviour of Female Japanese Monkeys

AUTHOR: Mary S. McDonald, B.A.

SUPERVISOR: Dr. Shelley Saunders

LENGTH: vii, 79

Abstract

The non-copulatory estrous behaviour of semi-free ranging female Japanese monkeys was observed for 3 months, in order to investigate the role of the female in the establishment of mating pairs. It was concluded that the females play a very active role in the formation of mating pairs, showing three times more solicitation behaviour than males. They also reject more than 30% of the advances they do receive. This is interpretated as an indication of selectivity in the choice of sexual partners. The behaviour of the female in this courtship context is described, with emphasis on proceptive or solicitation behaviour. The data were tested for behavioural differences based on the female's age, rank, parity, number of offspring and the presence of an infant, and for differences based on the age, rank and spatial status of the interacting male. Age of the female had the greatest effect on behaviour, with older females behaving in a more calm, sophisticated manner when soliciting a male. Age was also the most significant male variable, with females showing more rejection to younger males. Other than age related findings it must be concluded that these sociological characteristics of the animals are not predictive of the females' courtship behaviour. A number of alternate lines of inquiry for future research are suggested. They include an investigation of the hormonal basis of estrous behaviour, a multivariate analysis, and a sequential analysis of behaviour.

Acknowledgments

I would like to express my sincere appreciation and thanks to Dr. Linda Fedigan, for introducing me to and providing the opportunity for, research on free ranging animals, and for her continued guidance and support throughout the course of this project. I also wish to thank Dr. Larry Fedigan for the many instructive discussions. For further advice and suggestions I am grateful to Dr. Shelley Saunders and Dr. Ed Glanville.

The computer analysis was carried out at the University of Alberta, and I thank the Department of Anthropology for allowing me to use their facilities. To Colin Chapman I am greatly indebted for generously donating his time and effort in the analysis of the data. The 'intuitive insights' provided by Jeff Bullard are also appreciated.

To Lou Griffin, manager of Arashiyama West Institute, I owe a great many thanks, for her patience and encouragement in teaching me to identify the animals, and for the many practical, academic, intellectual and emotional discussions that were so helpful throughout the course of the field work. I would also like to acknowledge Ola Urban and the other A.W.I. researchers with whom I shared the field experience.

My sincere thanks go to Dr. David Counts for repeatedly helping me cut through 'red tape', and to Rosita Jordan for her accurate typing of this thesis.

To my family I will always be grateful, for their constant encouragement and support.

The financial assistance provided by the Yates Fund and by Dr. Fedigan's NSERC grant (#A7723) is gratefully acknowledged.

CONTENTS

LIST OF TABLES

CHAPTER ONE

INTRODUCTION

Research Question

In an attempt to explain the existence of secondary sexual characters, Darwin developed the theory of sexual selection. According to this theory, certain features of dimorphism are selected because they increase the individual's reproductive success, not because they make the individual more likely to survive. The theory of sexual selection is usually divided into two processes: epigamic selection, which is interactions between the sexes (usually female choice) and intra-sexual selection, which is interactions within one sex (usually male competition). There has been a great deal of controversy over the relationship between these two forces, and over the issue of whether it is males or females that are the "creative force in sexual selection" (Fedigan, 1982). Most discussions of sexual selection in mammals stress the importance of intrasexual selection; aggressive male behaviour is seen as more important than female choice (Ralls, 1977). The idea that females automatically choose the winners of male-male competition is extremely common, yet as Fedigan (1982) points out, if females must choose the already victorious males, then they really have no choice at all. Not surprisingly, another pervasive notion is that the females are essentially passive, simply accepting male sexual initiations. This concept, however, seriously misrepresents the normal mating sequence and encourages a biased concept of feminine sexuality (Beach, 1976).

Until recently, the subject of female choice has been largely overlooked in primate research. The Japanese macaque (Macaca fuscata) is one of the most popular species in behavioural research and there has been a significant amount of work done on Japanese monkey sexual behaviour. However, few studies have addressed the issue of female choice, despite the fact that reports of male-male competition are rare, and reports of females exercising choice of partners is common (Tokuda 1961-2; Wolfe, 1979; Enomoto, 1974). The most popular issue under investigation is the relationship between male dominance rank and mating success, and the results of these investigations are mixed. A positive correlation between male rank and mating success in macaques has been reported by Tokuda (1961-2), but Drickamer (1974) and Eaton (1974) reported no correlation. Other studies had mixed results (Hanby et. al., 1971; Fedigan and Gouzoules, 1978). Furthermore, such research is often done from the perspective that high rank in males means greater access to estrous females, rather than from the perspective that the female's choice of partners may reflect a preference for males of higher status. A few studies have attempted to determine other variables that might affect partner choice. Baxter and Fedigan (1979) demonstrated that animals avoid mating with close kin or yearlong grooming partners. Enomoto (1974) reported that age is a factor in partner choice, for example young females were less likely to receive male sexual advances than were older females.

Recent years have shown an increased awareness of the importance of female choice, and some studies try to correlate various male behaviours and mating success. For example, Modahl and Eaton (1977) and Wolfe (1981) have shown a correlation between male displays and mating success (as measured by ejaculation frequency). Enomoto (1981) reports a correlation between aggressive behaviour toward the female, such as chasing, and mating success. Presumably these studies say something about the factors that influence female choice as a mechanism of sexual selection, however, the evidence is indirect - inferred by male behaviour and mating success. The authors themselves recognize that the data offer only preliminary support (Modahl and Eaton, 1977) and that the females' reactions to the displays must be defined (Enomoto, 1981).

Notably absent from the literature are studies which focus on female behaviour during the mating season - specifically female behaviour prior to the actual consort and mating. Clearly, studies such as these are essential to to our understanding of pair formation. Wolfe (1979) has reported on the behavioural patterns of estrous females at Arashiyama West, however, this study is largely concerned with actual mating behaviour. Courtship behaviour is also important because courtship helps to construct the male-female bond that is necessary for a successful consort. A true understanding of female choice would necessarily involve focusing on the behaviour of the females that precedes and/or leads to a consort pairing. Both proceptive (initiative) behaviours by the females as well as reactions to the behaviours of males (receptive and non-receptive behaviours) are important indicators of female choice.

The following is a study of the courtship behaviour of female Japanese monkeys. The objectives of this report will be to 1) describe the repertoire of female courtship behaviour in Macaca fuscata; 2) to compare females on the basis of age/parity, rank, number of offspring, and presence of a recent infant to test for differences in courtship patterns; and 3) to relate female courtship behaviour to the characteristics of the interacting males.

Definitions

Estrus was identified behaviourally quite simply as the "female motivation (proceptivity) and/or willingness (receptivity) to mate" (Fedigan 1982:140). This behavioural state was often accompanied by a reddening of the face and perineum. Identification of estrous females was aided by this physical change but was not dependent on it. Any behaviour displayed by an estrous female was classified as estrous behaviour. Only estrous behaviour was recorded and analysed in this study.

The behaviour of an estrous female was further classified into copulatory and non-copulatory stages. The non-copulatory behaviour sequences were considered to be courtship sequences, regardless of whether the female was soliciting or rejecting a male. Courtship in this study is any behaviour received or directed by an estrous female who is not engaged in a mount sequence. It is assumed that these females, readily identifiable by the nature of their behaviour (sexually motivated), are ultimately working toward the establishment of a mount sequence.

Females who were obviously uninterested (sexually) in any males would not have been displaying the kind of estrous behaviour necessary for them to have been chosen as subjects, so while rejection behaviour is present in the study, it is much less common (and of less interest) than active solicitation. This definition of courtship is in line with Desmond's definition of courtship as "the heterosexual reproductive communication system leading up to the consummatory sexual act" and the term includes "both pair formation behaviour and pre-copulatory behaviour" (Morris 1956:12). Only this non-copulatory estrous behaviour, the courtship behaviour, was analysed in this report.

A variety of behavioural patterns were observed in the context of courtship. Beach (1976) introduced the term proceptivity, which generally refers to female sexual initiative behaviours. It is not possible, at least in the field situation, to know which animal initiated a sexual interaction. As Eaton (1978) pointed out, what appears to be a female initiation may have been preceded by a courtship behaviour by the male over a week ago. It is possible however to delineate behaviours which are performed by the female and are clearly intended to establish a pair formation or copulation, regardless of which partner actually initiated the interaction. These behaviours will be referred to as proceptive or solicitation behaviours. Other behaviours which occur in the courtship or non-copulatory estrus stage include advances received, rejection behaviour, fear indicators and affiliative behaviours.

In Japanese monkeys, the act of copulation involves a series of mounts. Generally the male mounts, thrusts a few times, dismounts, waits a short while and repeats the mount. Only after a number of mounts does the male reach ejaculation. Michael and Zumpe (1971) have noted that series mounters also tend to form mating pairs known as 'consorts', and this is true of Japanese monkeys. The term consort bond was first introduced and defined by Carpenter

(1942). Just as it is impossible to know which partner initiated a sexual interaction, it is also often impossible to know whether a given pair are just entering a consort or whether they are simply between copulations within a consort. In order to avoid making faulty assumptions, no distinction was made between pre- and post-copulation or between established consorts and newly forming ones.

Related Studies

Various relevant studies of Japanese monkey sexual behaviour have been mentioned in the outline of the research question. In this section I will present an overview of some of the other studies which deal with sexual behaviour in a number of macaque species.

Rhesus macaques (*Macaca mulatta*) are possibly the most commonly studied of the non-human primates. An early study by Carpenter(1942) on the sexual behaviour of free-ranging rhesus monkeys contributed extensive descriptions of the behavioural characteristics of estrus, the nature of mating pairs,and female selectivity,as part of the mating behaviour of the species. Pheonix (1978) compared the sexual behaviour of wild- and laboratory-born male rhesus monkeys and reported that the level of sexual adequacy was much lower in the laboratory animals. Herbert(1968) studied the sexual preference of adult male rhesus monkeys and found that there were quantitative differences in the males' behaviour with different females, and that this difference was based on differential preference by the male. The authors relate these findings to the influence of ovarian hormones.

The sexual initiating behaviour in female rhesus monkeys under laboratory conditions have been described by Michael and Zumpe (1970). After comparing intact and ovarectomized females they suggested that 'hand-reaches', 'head-ducks' and 'head-bobs' provide an indication of the females' motivational state. Differences between the females based on sociological variables were not investigated. These authors later investigated female bisexual behaviour based on male and female hormonal status. They concluded that female bisexuality increased when heterosexual activity was minimal, and that female initiative behaviour was likely to result when male initiative behaviour ceased (Michael, Wilson, and Zumpe 1974).

An operant conditioning situation was used by Michael, Bonsall and Zumpe (1978) to study the formation and dissolution of consort bonds in rhesus monkeys. They concluded that females preferred males that spent more time grooming, ejaculated more frequently, and elicited fewer submissive behaviour patterns. Social dominance is reported to affect behaviour in rhesus monkeys, although sexual competition among females is not at the basis of rank differences in copulatory behaviour (Wilson, 1981).

The author suggested that higher ranking animals initiate copulatory series.

Czaja and Bielert(1975) tested the behavioural differences between female rhesus monkeys in relation to the stage of the menstrual cycle; they found that the amount of time spent in proximity to the male peaked at the time of likely ovulation, as did the frequency of some female solicitations. This suggests that in rhesus monkeys, the female's sexual motivation may be controlled by internal hormonal action. A study by Cochran(1979) on proceptive patterns of behaviour and the menstrual cycle support this finding. Sexual presentations however, which are generally used as a good indication of a female's willingness or desire to copulate, did not correspond to the stage of the menstrual cycle(Czaja and Bielert, 1975).

The question of mating strategies is considered by Wilson, Gordon and Chikazawa(1982) in their investigation of female mating relationships in rhesus monkeys. Rhesus females typically mate with several different males, and this study revealed that successive copulatory series on the same day more often involved a new male. Partners which tended to stay together were significantly more often higher ranking animals, and the interval between copulations was higher than for females who were involved with a different male.

Other descriptions of rhesus mating behaviour can be found in Altmann(1962), Conway and Koford(1964), Kaufman(1965), and Southwick, Beg and Siddigi(1965).

Chevalier-Skolnikoff(1975) reported on the heterosexual copulatory behaviour of stumptail macaques (*Macaca arctoides*) and compared a variety of behavioural patterns to other macaque species. This paper generally deals with copulatory behaviour although she also compares the perceived 'solicitor' (male or female) across species. For descriptions of stumptail sexual behaviour see also Lemmon and Oakes(1967), Blurton-Jones and Trollope(1968), and Trollope and Blurton-Jones (1970).

Less commonly studied are the pigtailed macaques (*Macaca nemestrina*) and the barbary macaques (*Macaca sylvanus*). Tokuda, Simons, and Jenson(1968) reported on the patterns of estrous cycles and sexual behaviour in pigtailed macaques, comparing the sexual behaviour and sexual swelling to that of Japanese monkeys. One interesting behavioural difference noted was that in Japanese monkeys, interference of mounting by an intruding male will usually result in the female of the pair being attacked by her partner (if he is a leader or a more dominant male). In pigtails the intruding male received the aggression. This tendency for the female to receive more aggression during sexual interactions in Japanese monkeys may have interesting implications for the female's motivation and receptivity regarding pair formation.

Taub(1980) looked at Barbary macaque female mating strategies and argued that female Barbary monkeys play an active role in the initiation of sexual behaviour.

Japanese monkeys are one of the most popular species for the study of sexual behaviour. A longitudinal study at the Oregon Regional Primate Centre has approached the subject from a variety of perspectives, and has yielded an number of descriptions of Japanese macaque reproductive behaviour. Hanby, Robertson and Pheonix(1971) made a number of interesting observations. For example, low ranking males were said to mount more frequently, yet dominant males ejaculated more frequently. Middle aged females were very sexually active as opposed to females with recent infants who were least active. These authors also suggest that much of mating season activity is social rather than reproductive in nature. In a study on the development of sociosexual behaviours in Japanese monkeys, Hanby and Brown(1974) noted the importance of social experience in the development and integration of sexual postures, thrusting, intromission, and ejaculation. They did not discuss the development of pair formation behaviours. Wolfe(1978) also investigated the relation between age and sexual behaviour, and pointed out the importance of learning in the attainment of sexual maturity. She dealt specifically with copulation behaviour.

A longitudinal study by Eaton(1978) investigated the mechanisms that regulate social and sexual behaviour and suggested for example, that male rank (as determined by aggressive interaction) is not correlated with mating success, as opposed to displays, which serve a courtship function, and do correlate with mating success. For a further discussion of female choice and male display behaviour see Modahl and Eaton(1977).

Lengthy descriptions of Japanese monkey sexual behaviour in Japan are provided by Tokuda(1961-62) and Enomoto(1974). Enomoto provides a catalogue of 46 sexual behaviours. He relates the patterns of sexual behaviour to age, rank, and for females, the presence of an infant, and found for example that the absence of an infant allowed a female to direct and receive more positive sexual behaviour. Enomoto(1978) has also looked at social preference in Japanese monkeys and he observed that grooming pairs and matrilineally related pairs showed little sexual interaction. This is consistent with the findings of Baxter and Fedigan(1979) for the Arashiyama West troop. Male aggression is also reported to affect social preference(Enomoto, 1981).

Fedigan and Gouzoules(1978) investigated partner choice in Japanese monkeys by recording all pairs of animals observed consorting over three breeding seasons and testing for evidence of choice based on age, rank, year round affinitive bonds and kinship bonds. They suggested that female consort behaviour and partner choice might be cyclical, depending on the presence of recent offspring. Stephenson (1974) described the mating activity of a number of Japanese macaque troops with respect to social classes of males and estimated conception of the females. He also considered Japanese macaque courtship behaviour (1973). He dealt with courtship as a communication pattern which serves to mediate interactions among individuals, and his interest was in the cultural variability in five specific courtship patterns.

Japanese monkey reproduction has also been analyzed from a physiological perspective. Takahata (1980) provided physiological data on estrus periods and related female age and rank to sexual activity. Nigi (1975) has researched conception, gestation and the nature of the menstrual cycle.

Studies of macaque sexual behaviour are numerous; many deal with the issues of partner choice and with the variables that might affect sexual behaviour patterns. The present study differs from all previous studies by focusing on pair formation and the role of the female. This approach differs from that of previous research, while attempting to answer similar kinds of questions.

CHAPTER TWO

MATERIALS AND METHODS

The Study Troop

The Arashiyama West troop of Japanese monkeys are located in a 50 acre enclosure on a ranch near the town of Dilley in south Texas. In 1972 this natural troop was transported intact from Kyoto, Japan, where they had been provisioned and studied since 1954. In 1966 the original Arashiyama troop fissioned into two troops which were then identified as Arashiyama A and Ariashiyama B. The Arashiyama A troop ranged more and more into the suburbs of Kyoto where they became a nuisance and had to be moved. The first relocation was to a 108 acre enclosure on a ranch outside of Laredo, Texas. The troop was at this time renamed Arashiyama West. In 1980 they were again relocated to the present site.

The original 150 member Arashiyama West troop has grown to number more than 300 individuals. All age/sex classes are represented, and complete maternal geneologies, life histories and dominance relations are known. Each individual is identifiable by a facial tattoo.

The environment of the ranch is hot, dry, flat and characterised by thorn brush. The enclosure is surrounded by an electrified fence. This area is bordered on the east and west sides by large fields of native and planted grasses. The two fields are separated by a 20 ft wide seasonally wet gully containing dense brush. This gully runs the length of the enclosure from north to south. The brushline meets two large artificially maintained waterholes surrounded by large trees at the south end. The canopy around the waterhole is 5-6 meters, dropping to no more than 2 meters in the brush area. Various man-made shade and climbing structures are scattered throughout the enclosure. The monkeys share the enclosed area with snakes, lizards, mice, rabbits, ground squirrels, turtles, geese, four vervet monkeys, and a variety of birds (see Appendix 1).

The animals are provisioned once a day with grain, cattle cubes, peanuts and produce. They also forage on natural flora. Other than provisioning, the animals exist with a minimum of human intervention. They are habituated to the continual presence of at least one behavioural researcher.

Data Collection

The study was conducted during the 1982 mating season, from the beginning of October to the end of December. Six weeks prior to the mating season were spent learning the animals and practicing focal animal sessions. Sexual activity was slow for more than a month so most of the data were collected during November and December. The total number of observation hours spent in the field was approximately 700 during which 140 hours of focal animal data were collected.

All adult females were classifed into groups based on age, parity, rank, presence of an infant and number of offspring. An attempt was made to sample evenly from the following fifteen categories:

1. High Ranking - Young Nulliparous
2. High Ranking - Primiparous - with infant
3. High Ranking - Primiparous - without infant
4. High Ranking - Mature Multiparous - with infant
5. High Ranking - Mature Multiparous - without infant
6. Middle Ranking - Young Nulliparous
7. Middle Ranking - Primiparous - with infant
8. Middle Ranking - Primiparous - without infant
9. Middle Ranking - Mature Multiparous - with infant
10. Middle Ranking - Mature Multiparous - without infant
11. Low Ranking - Young Nulliparous
12. Low Ranking - Primiparous - with infant
13. Low Ranking - Primiparous - without infant
14. Low Ranking - Mature Multiparous - with infant
15. Low Ranking - Mature Multiparous - without infant

The actual choice of focal animals was determined in large part by which females came into estrus during the season, and the unpredictable nature of estrous behaviour made it impossible to sample equally from each of the above categories. At least 5 hours of data were obtained on as many females as possible.

Focal animal data sheets were used and thus the frequency, duration, sequence, direction and recipient of behaviour was recorded. Focal animal sessions were one hour in length (see Appendix 2).

The ethogram was designed to include any possible behaviour, however sexual behaviours predominate. Both male and female behaviours are listed since behaviour directed at a female by a male is included in the focal data.

Ethogram

States: states are arranged hierarchically and are mutually exclusive. Onset time of each consecutive event is recorded throughout the test session.

1. Follow - direct/receive - animal moves in same direction as preceeding animal. May repeatedly look in the direction of the preceeding animal.

2. Flee - animal moves away from pursuing animal. May include walking or running away from that animal. Animal may look in the direction of the pursuing animal.

3. Forage - animal may be sitting, standing, or moving, or a combination of the above while actively searching for and eating food.

4. Walk - quadrupedal locomotion at a casual walking speed.

5. Run - quadrupedal locomotion at a trotting or running speed.

6. Groom - direct/receive - one monkey inspects and cleans the fur of another. This is done with a gently rhythmical pattern of fur separation, scratching at the skin, and stroking pulls of the fur.

7. Self groom - animal grooms self for a duration greater than one second.

8. Sit - a general inactive category; animal may be resting or casually observing. It is recorded when the subject is not performing any other of the behaviors in this ethogram.

9. Sit beside - direct/receive - sitting in slight body contact with another animal.

10. Sit near - direct/receive - animal sitting close, but no body or fur contact. Usually more than one meter apart. Animal may be facing or have back to other animal.

11. Ventral sit against - direct/receive - a stylized position in which the animals are sitting facing the same direction such that there is ventral-dorsal contact. Usually the animal in the rear initiates the positioning.

12. Embrace - two animals sit very close together (ventral/ventral) often lightly holding each other.

Events: A single or transitory action. May be repeated consecutively. Ordered hierarchically, and most are mutually exclusive. May be coincident with states.

13. Approach - direct/receive - a direct advance by one monkey towards another. If the animal being approached is not stationary, it shall be recorded as a follow.

14. Increase proximity - direct/receive - a move by one animal which increases the proximity to another who is sitting nearby. Less obvious and direct than an approach, usually does not involve a move of more than two feet. Performed by estrous females who appear to be soliciting sexual attention from a male.

15. Decrease proximity - direct/receive - a move by one animal which decreases the proximity to another who is sitting nearby. Less obvious and direct than a leave, usually does not involve a move of more than two feet.

16. Leave - direct/receive - animal breaks contact with another animal; or moves away from that animal.

17. Response move - animal sitting in proximity to another jumps or moves quickly in response to some movement by the nearby animal. Performing animal appears startled and/or afraid of attack. Performed when an animal first catches sight of another. The animal does not flee but may fear grimace.

18. Stare - animal looks directly and intensively into the eyes of another animal. Often the head is lowered and the look is prolonged.

19. Lip quiver - direct/receive - a rapid up and down movement of the lips slightly pouted. This facial expression is believed to function as a distance decreaser in a variety of contexts, including courtship.

20. Fear grimace - direct/receive - a submissive visual signal in which the lips are retracted from the teeth with the teeth clenched.

21. Genital inspect - direct/receive - animal looks at the genitals of another animal. Often occurs just before mount series or between mounts.

22. Groom solicitation - direct/receive - a monkey presents a portion of its body (chest, back, etc.) to another monkey at very close range.

23. Manipulate nipples - females squeezes own nipples into her mouth. Appears to be drinking drops of milk.

24. 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.

25. Displace - direct/receive - one monkey moves toward another who immediately moves out of the former's way. Frequently the displacer will sit down or stand in the exact location the displaced has just vacated. Usually a very clear indication of relative dominance status.

26. Lunge - direct/receive - a lunge forward toward another animal followed by a quick retreat. No contact is made.

27. Chase - direct/receive - one animal pursues another, but does not appear serious or aggressive. A lopping along

that looks more ritualized than an aggressive chase. This usually terminates when the pursued individual ceased to flee. Chaser and chasee may sit down together afterwards.

28. Aggressive chase - direct/receive - to pursue another monkey with accompanying agonistic signals indicating the intent is to do harm or drive away the chased individual. This often terminates in contact aggression unless the pursued individual escapes.

29. Grab - animal reaches out and slaps or pulls the fur of another with accompanying threat signals.

30. Bite - direct/receive - to seize another with the teeth.

31. Pin and bite - direct/receive - appears more serious and aggressive than bite. Animal may hold other animal down while biting (sometimes repeatedly and/or shaking head while biting).

32. Walk by - direct/receive - an animal approaches but walks past another animal at a short distance. Often fur will touch.

33. Walk past - direct/receive - animal walks in front of a significant other (usually one with whom it has been interacting) but at a distance greater than one meter.

34. Walk around - direct/receive - animal walks completely around another with fur touching. Often results in the two animals sitting in contact.

35. Whirl-pivot - animal whirls around so that the hindquarters are presented to the face of the other animal. Often appears as if the animal were preparing to leave but instead stops so the hindquarters are momentarily presented.

36. Bird dog - exaggerated strut performed by the males with the tail up. Periodic freezes give the impression of a bird dog.

37. Peer - animal stands bipedally with hands on thighs peering about as if looking for something in the distance.

38. Hip touch - direct/receive - a gesture preliminary to a mount in which the actor pulls upward on the pelvis of the recipient, encouraging the latter to stand. Or, rather than pulling, the actor may simply tough the hip area on one or both sides of the recipient.

39. Present - direct/receive - actor orients hindquarters toward another while sitting with the posterior raised slightly off the ground. Occasionally an individual will stand while orienting hindquarters to another animal.

40. Manipulate object -animal looks at and touches or handles some object in the environment, for example a branch or a rock.

41. Threat to observer - an unprovoked animal begins to threaten the human observer. Occurs while the animal is in proximity to another monkey. This behaviour is thought to function as a courtship behaviour, since the threatening animal will try to enlist the aid of the other, and the other usually responds, if it does respond, by mounting the actor.

42. Slap ground - an animal repeatedly slaps the ground in a frustrated, agitated manner. This behaviour is also thought to encourage mounting.

43. Body jerk - A slight but noticeable jerk or spasm of the body. Often performed by estrous females who are in gross body contact with or in proximity to another animal. Appears to be associated with frustration or may be an attempt to prompt action (mounting) by the other animal.

44. Mount - direct/receive - one animal successfully climbs on other animal and thrusts for a couple of seconds. Double foot clasp position unless recorded differently in comments section. Typically a thrusting motion including intromission and thrusting.

45. Mount rub - direct/receive - mount with noticeable rubbing of gentalia against other animal. Usually females direct mount rubs to males or other females. Occasionally juvenile males will mount rub.

46. Mount ejaculation - direct/receive - pause in thrust sequence followed by noticeable ejaculate on genitalia.

47. Attempt mount - direct/receive - one animal attempts to mount another but is disrupted. No thrusting observed.

48. Backwards mount - a male mounts a female such that his hindlegs straddle her shoulders, and his head is near her hind region. May lip quiver or genital inspect. This behaviour is performed by only two animals.

49. Look back - direct/receive - animal being mounted turns to look at mounting animal.

50. Reach back - direct/receive - animal reaches back to touch or grab mounter during mount.

51. Food call - heard prior to and during feeding. Long elaborate coo type of call with rising intonations.

52. Alarm call - short, very uniform. Can often hear the ripples (pulses, not actual stops) through it. During the mating season this is often heard in a series of vocalizations by females who are trying to solicit a male.

53. Contact call - like a very short wimper or a coo; heard with or without screaming.

54. Defensive scream - less variability than estrus scream - shorter in length. Heard during agonistic encounters.

55. Estrous scream - a vocalization that sounds like screaming, lots of variability in intonations. Almost melodious sometimes. Often given by female who is obviously following a particular male.

56. Estrous hack - single coughing sound, repeated successively.

Analysis

The 140 hours of focal animal data were coded on IBM 80 column coding sheets. Each line on the coding sheet represented one line or entry of focal animal data (i.e. one behaviour). The variables included on each line were: ID of focal animal, various contextual information, sociological information about the focal animal, the behaviour from the ethogram list, the ID of interacting animal, sociological information about the interacting animal, the duration of the behaviour, and the stage of the mating sequence. The stage of the sequence variable indicated whether the behaviour took place during an actual mounting sequence, or whether it was non-copulatory behaviour. Only the non-mounting stages were considered in the analysis.

To minimize error in the keypunching, a printout of the data was obtained and verified with the original coding sheets. Also, SPSS descriptive statistics were used to detect any illogical entries.

The analysis of all 58 different ethogram units would be methodologically and conceptually impossible, therefore it was necessary to combine the ethogram units into higher level categories. This was done heuristically on the basis of the obvious function or purpose of the behaviour. For example, approach/follow/sit near/estrous hack and many other behavours were grouped into the higher level category of "proceptive behaviour". Thirteen general categories of non-mounting estrous behaviour resulted (see Table 2.1). Also, vocalizations were separated from proceptive behaviour for a second analysis to check the original results. This analysis revealed no new results, thereby confirming the correctness of including vocalizations in the proceptive behaviour category.

Since the role of the female in establishing mating pairs is of primary interest in this study, it was useful to analyse how females differed in the frequency with which they showed specific proceptive behaviours. For this, the

Table 2.1 - Heuristically grouped behaviour categories.

Proceptive/Solicitation Behaviour - follow/sit beside/sit near/ventral sit against/embrace/approach/increase proximity/lip quiver/walk by/walk past/walk around/chase/genital inspect/contact call/estrous scream/hip touch/present/manipulate object/ threat to observer/slap ground/mount rub/attempt mount/body jerk/crouch.

Advances/Solicitations Received - receive a follow/receive a sit beside/receive a sit near/receive a ventral sit against/receive an embrace/receive an approach/receive an increase proximity/receive a stare/ receive a lip quiver/receive a whirl pivot/receive a walk by/receive a walk around/receive a walk past/receive a chase/receive a genital inspect.

Rejection Behaviour - leave/decrease proximity.

Rejection Received - receive a leave/receive a decrease proximity.

Female Fear Indicators - flee/fear grimace/response move.

Fear Indicators Received - receive a fear grimace.

Dominance Behaviour - displace.

Submissive Behaviour - receive a displace.

Aggressive Behaviour - threat/lunge/aggressive chase/grab/bite/pin and bite/defensive scream.

Aggression Received - receive a threat/receive a lunge/receive an aggressive chase/receive a grab/receive a bite/receive a pin and bite/receive a back mount.

Affiliative Behaviour - groom/groom solicitation.

Affiliative Behaviour Received - receive a groom/receive a groom solicitation.

Solitary Estrous Behaviour - forage/walk/run/self groom/sit/manipulate nipples/peer/food call.

proceptive behaviours were analysed as individual ethogram units. Likewise, in considering the effects of the interacting male, both combined categories and specific behaviours were important. In this case, all specific non-copulatory sexual and aggressive behaviours that involved the males were separately analysed. It was thus possible to determine whether different males received different behaviours from the females and whether different males directed different behaviours to the females. Non-directed behaviours (eg. estrous scream or slap ground) were not considered.

The analysis was carried out in three steps. First, simple descriptive statistics and t-tests were used to meet the first research objective: the description of female courtship behaviour.

The second stage of the analysis was designed to meet the second research objective: to determine if different groups of females differ in the frequency, range or duration of various behaviours. The independent variables here were female age, rank, parity, presence of an infant and number of offspring. For rank, the population was divided into high, medium and low. The dominance hierarchy was provided by Arashiyama West Institute. Parity was divided into nulliparous, primiparous or multiparous. Presence of an infant was simply a 'yes or no' score depending on whether or not the female had a live infant from the 1982 birth season. The dependent variable list includes the frequency of heuristically lumped ethogram categories (eg. proceptive behaviour), the frequency of specific courtship behaviours (eg. 'present'), the range of courtship behaviours displayed, and the duration of various states (eg. 'groom'). For a complete list of variables see Table 2.2. The raw frequencies of each behaviour were adjusted to account for unequal sample hours on the females. A Pearson Correlation was used when testing the continuous variables of age and number of offspring. A Oneway Analysis of Variance was used to test for differences in behaviour based on rank, parity, and presence of an infant.

The third stage of the analysis was designed to meet the third research objective: to test for differences in behaviour based on characteristics of the interacting male. Here the independent variables were male age, rank, and spatial status. Again, rank was represented by a score of high, medium or low. Spatial status refers to whether the animal was central or peripheral in the troop. This is a relatively straightforward geographic distinction. The dependent variable list for this stage of the analysis includes the frequency of heuristically lumped ethogram categories, specific male courtship and aggressive behaviours, and specific female courtship behaviours which involve males. For a complete list of variables see Table 2.3. Since males were not equally sampled it was necessary

Table 2.2 - Variables for the analysis of female differences. Higher level behaviour categories are marked with an asterix.

INDEPENDENT

age
parity
rank
presence of an infant
number of offspring

DEPENDENT (Frequency of)

*proceptive behaviour
*advances received
*rejection behaviour
*rejection received
*fear indicators
*fear indicators received
*dominance behaviour
*submissive behaviour
*aggressive behaviour
*aggression received
*affiliative behaviour
*affiliation received
*solitary estrous behaviour
*non-vocal proceptive beh.
*vocal behaviour
follow
sit beside
sit near
ventral sit against
embrace
approach
increase proximity
lip quiver
walk by
walk past
walk around
genital inspect
chase
hip touch
present
threaten to observer
slap ground
alarm call
estrous scream
contact call
estrous hack
crouch
body jerk
duration of following
duration of grooming
range of proceptive beh. used

Table 2.3 - Variables for the analysis of interacting male differences. Higher level behaviour categories are marked with an asterix.

INDEPENDENT	DEPENDENT (Frequency of)
age	*proceptive behaviour
rank	*advances received
spatial status	*rejection behaviour
	*rejection received
	*female fear indicators
	*fear indicators received
	*aggressive behaviour
	*aggression received
	*affiliative behaviour
	*affiliation received
	follow
	sit beside
	sit near
	approach
	increase proximity
	lip quiver
	walk by
	genital inspect
	walk past
	hip touch
	present
	mount rub
	leave
	fear grimace
	response move
	groom
	male follow
	male sit beside
	male sit near
	male approach
	male increase proximity
	male stare
	male lip quiver
	male whirl-pivot
	male walk past
	male chase
	male genital inspect
	male grab
	male pin and bite
	male leave

to adjust the raw frequencies by dividing each frequency by the total number of entries on that particular male. Again the Pearson Correlation and the Oneway Analysis of Variance were used to test for significant results. In both the second and the third stage of analysis, all independent variables were tested against all dependent variables.

CHAPTER THREE

DESCRIPTION OF COURTSHIP

A very important consideration in the issue of female choice is the role that the females play in the establishment of mating pairs. Is it the males or the females that do most of the soliciting? A t-test comparing the number of female courtship behaviours (7173) to the number of male courtship behaviours (2085) observed was significant ($t = 4.55$, $df = 39$, $p = .000$). There is no reason to assume that female courtship behaviours were more heavily sampled since subjects were chosen only when displaying estrous behaviour and this almost always meant they were in association with a male. The use of the focal animal recording procedure ensured that all male behaviours were also recorded. This shows clearly that female Japanese monkeys do play a very active role in the establishment of mating pairs. In fact according to this these data, females are much more active than the males. This supports the assertion by Tokuda (1961/1962) that Japanese macaque males or females may solicit, but females solicit more frequently. Furthermore, in this study females did not even accept all of the advances that they received. A comparison of total number of male advances and total number of female rejections revealed that females reject 33.14% of the advances they received. Female rejection of a male involves little more than the female continually leaving the male when he sits near her and refusing to present for mount if she were to receive a hip touch. Basically the female will try to ignore the male, although sometimes she may go as far as to try to hide from him. Often an estrus female rejecting one male will be actively pursuing another. Obvious aggressive competition was never observed between males in such cases. Clearly then the females are not randomly promiscuous, but are instead selective, actively soliciting in some situations and actively rejecting in others.

Female Japanese monkeys use a variety of proceptive behaviours. Stephenson (1973) suggested that courtship involves four stages. (Stephenson is referring here to what I have termed proceptive or solicitation behaviour, and he is outlining the general pattern of female solicitation, which is the major portion of my female courtship data.) The first stage is advertising and monitoring, second is testing and closing inter-individual distance, third is attempting to establish a mount series and fourth is maintaining a mount series. (Only stages one to three are being considered in this report.) While there is no 'typical' or uniform behavioural pattern among the females, there is a repertoire of behaviours which may occur at each stage.

The first stage was observed much less frequently than stages two or three. Females displaying estrous behavour usually seemed to be directing the behaviour to a particular male. When observed, however, stage one seemed to be characterised by a general high level of excitement and was often associated with a great deal of vocalization. The ethogram category of solitary estrous behaviour (sitting, walking, running, self grooming, foraging, et cetera) perhaps best represents this stage. This behaviour was observed in females who also showed other behavioural signs of estrous. The female would run through this repertoire of behaviours repeatedly, performing each only briefly before hurriedly going on to another. Estrus screams, estrus hacks and a variety of contact calls enhance the general impression of hyperactivity and agitation. These females will cover great distances and it seems likely that they are either advertising or trying to select a potential partner. Certainly this noisy excited female draws a great deal of attention and she is often chased and occasionally bitten by a male. She may flee from the male and continue the behaviour pattern elsewhere or at this point she may begin to try to maintain proximity to the male. It is just as common for the female to try to gain proximity to a male who was not observed directing aggression (ex. chasing) to her.

The testing and closing of inter-individual distance involves a different repertoire of possible behaviours. Most commonly the female will simply follow and sit near the male. She may or may not vocalize. If vocalizations are present they can vary in kind, frequency, rate, and pitch. Basically the female will try to decrease the distance between herself and the male by subtly trying to inch her way closer, if they are already sitting in proximity, or by sitting a little closer to him each time she follows and sits near. Startled jumps and fear grimaces from the female are common in this stage, although occasionally the female will appear much more confident and simply walk right up and sit in body contact with the male. Either method may result in the female being chased and/or bitten by the male. Such aggression does not seem to discourage the females from further solicitation of that particular male.

Sometimes a female will employ a less direct, or more 'coy' strategy, walking in front of the male, presenting her hindquarters, lipquivering, and moving on. Any or all of the above behaviours may be displayed and often this results in the female being followed by the male.

Once the female has established body contact with a male and appears to be comfortable and not expecting aggression, a new repertoire of behaviours will begin. These behaviours are clearly designed to establish a mount sequence. Vocalizations are very common at this stage, with estrus hacks and contact calls being most frequent. Estrus hacks usually involve a jerking of the body, although body jerks also occur in silence. As time progresses and the male has not yet mounted, the female's level of agitation increases. Manipulation of small objects in the environment, slapping the ground and even threatening the observer will occur. The purpose of these behaviours appears to be to coax and urge the male to begin mounting. Presenting the hindquarters is probably the most obvious action the female can take. Some females will even go so far as to hip touch and mount the male. It should be clear that there is no one standard behaviour pattern here. The female may exhibit any or all of the above behaviours, and may even just sit patiently waiting for the male to initiate mounting. One tendency does prevail though: the onset of a regular mount sequence will result in the cessation of all such behaviours.

On many occasions more than one female was observed soliciting the same male at the same time. On at least three occasions outright aggression between the two females was witnessed, and it appeared that the higher ranked of the two would start the encounter by threatening and/or chasing off the lower ranked one.

The point to be emphasized here is variation. Each proceptive behaviour has a different overall frequency of expression. Some are much more commonly used than others.

Table 3.1 lists the proceptive behaviours and shows that percentage of overall proceptive behaviour that particular behaviour represents. This gives some indication of the relative importance of each specific behaviour in terms of the female's total solicitation repertoire. This is of course based only on a quantitative comparison. It is not possible at this point to assess the qualitative differences in the behaviours and undoubtably such differences are crucial in suggesting that some behaviours are more important than others.

As well as the wide range of possible behaviours available to the animals, there is a great deal of variation between individuals in the expression of proceptive behaviour. This includes both the total frequency of all proceptive behaviour and the frequency of specific solicitation behaviours. That some females show a much higher frequency of proceptive behaviour was demonstrated by a comparison of the values for the 10 highest and the 10 lowest 'proceptors' (see Tables 4.3 and 4.4 for a list of these females and their frequency of overall proceptive behaviour). The mean of the high group (X = 89.54) is considerably different than the mean for the low group (X = 10.62). Clearly there are large differences in the solicitation rates of different females.

Table 3.1 - List of all proceptive behaviours and their percentage of the total frequency of all proceptive behaviour.

Contact Call	22.20%
Estrous Hack	13.40%
Estrous Scream	10.13%
Sit Near	8.61%
Approach	8.71%
Follow	6.64%
Sit Beside	6.43%
Increase Proximity	5.56%
Hip Touch	3.81%
Mount Rub	3.27%
Body Jerk	2.83%
Ventral Sit Against	1.97%
Present	1.63%
Threat to Observer	1.53%
Walk Past	1.20%
Walk Around	0.65%
Slap Ground	0.54%
Alarm Call	0.33%
Crouch	0.33%
Attempt Mount	0.22%
Walk By	0.11%
Lip Quiver	0.11%
Embrace	0.11%

Having demonstrated that great variability in behaviour patterns exist, it is necessary to try and account for this variation. A consideration of the effect of some sociological differences between the females is the subject of the next chapter.

CHAPTER FOUR

DIFFERENCES BETWEEN FEMALES

The description of the behavioural repertoire of female courtship and the consideration of the role of the female compared to the male is an important element in attaining a true understanding of female choice. In this chapter I will proceed with the investigation of female courtship behaviour by trying to account for some of the behavioural differences in terms of differences between the females. As discussed in the introduction, a few studies have tried to determine the variables that might affect partner choice, however none have addressed the issue of how females exercise choice; of how they solicit partners. Both overall rate of solicitation and differences in specific courtship behaviours need to be considered. An investigation into the variables that might affect the female's courtship behaviour should logically begin with this consideration of the differences among the females themselves.

It was hypothesized that the variability in the frequency of proceptive behaviour might be due to sociological variables such as age, parity, rank, presence of an infant, and number of offspring. Each variable was tested for differences in total frequency of proceptive behaviour. Despite the great individual variability, this analysis revealed remarkable homogeneity in the frequency of proceptive behaviour among the sociological groupings (see Table 4.1 and 4.2) although there was a trend ($p = 0.08$) for primiparous females to exhibit more proceptive behaviour than nulliparous and multiparous females. To double check this finding, the 10 subjects with the highest and the 10 subjects with the lowest frequency of proceptive behaviour were compared for differences in the mean age, rank, parity, and number of offspring in each group. This analysis fully supported the conclusion of homogeneity for again no significant differences between the sociological groups were found. On the basis of this analysis, the hypothesis that sociological differences between the females will explain different solicitation rates must be rejected. The explanation for the extreme individual variability in frequency of proceptive behaviour must be elsewhere. However, even a subjective examination of the females comprising the high and low groups (see Table 4.3) revealed little that would explain the variation. Three previous Arashyiyama West researchers (Linda Fedigan, Larry Fedigan, Jeff Bullard) also examined the two lists of females for commonalities or differences and none could be discerned.

Table 4.1 - Results of the Analysis of Variance on the Frequency of Proceptive Behaviour by Parity, Rank, and Presence of an Infant.

	Mean Frequency of Proceptive Behaviour	Standard Deviation	F Ratio	Probability
Parity				
Nulliparous	54.84	24.89	2.613	0.08
Primiparous	67.13	47.41		
Multiparous	38.14	28.59		
Rank				
High	45.20	43.24	0.075	0.92
Medium	50.44	26.64		
Low	46.34	30.67		
Presence of Infant				
Yes	47.06	29.46	0.000	1.00
No	47.10	37.10		

Table 4.2 - Results of the Pearson Correlation of Frequency of Proceptive Behaviour with Age and Number of Offspring.

	Correlation Coefficient	Probability
Age	-0.1468	0.183
Number of Offspring	-0.1108	0.248

Table 4.3 - List of the 10 females with the highest frequency of proceptive behaviour. Total sample = 40, therefore the top 25%.

Frequency of Proceptive Behaviour	I.D. Number	Age	Parity	Rank	Number of Offspring	Presence of 1982 Infant
164.8	125	7	Primip.	High	1	No
104.5	257	5	Primip.	Med.	1	Yes
102.7	36	19	Multip.	Low	8	No
102.0	13	9	Multip.	High	3	Yes
92.3	292	4	Nullip.	Low	0	No
76.0	44	10	Multip.	Med.	3	No
67.0	91	6	Nullip.	Low	0	No
62.9	51	7	Primip.	Low	1	No
62.0	33	5	Primip.	High	1	Yes
61.2	34	16	Multip.	Med.	6	Yes

Table 4.4 - List of the 10 females with the lowest frequency of proceptive behaviour. Total sample = 40, therefore the bottom 25%.

13.6	60	14	Multip.	Med.	4	No
20.6	158	6	Primip.	High	1	No
13.6	62	11	Multip.	Med	4	Yes
10.5	161	10	Multip.	Low	2	No
8.5	64	5	Nullip.	High	0	No
8.0	66	13	Multip.	Med.	3	No
8.0	73	11	Multip.	Low	4	Yes
7.0	63	11	Multip.	Low	3	Yes
4.0	68	11	Multip.	High	2	No
4.0	133	17	Multip	High	8	No

One possible explanation could be that the high 'proceptors' were sampled at different stages of the menstrual cycle than were the low. Presumably female receptivity and proceptivity would correlate with the fertile phase. Unfortunately, complete estrous data on each female were not collected so it is impossible to investigate this at this time. But as Fedigan points out, in primates the correlation between motivation or willingness to mate and the ovarian cycle is not clear and "all primate sexual behaviour seems to be relatively emancipated from direct hormonal controls" (1982:144).

The only explanation then for the great variability observed in the expression of overall proceptive behaviour must be idiocycratic variation or, more likely, some as yet undefined variables. Possibilities for future research into this issue will be discussed in Chapter 6.

While the sociological variables of age, rank, parity, presence of an infant and number of offspring do not explain total frequency and rate of proceptivity they do shed some light on differences in the expression of specific proceptive behaviours. In other words, these factors do seem to influence <u>how</u> the females solicit mates. See Table 4.5 for the statistically significant behavioural differences for each variable.

Table 4.5 - Results of the Oneway Analysis of Variance for Female Rank, Parity and Presence of an Infant, and the Pearson Correlation Coefficients for the Number of Offspring and Age. Only those behaviours with at least one significant result are presented. Higher level behaviour groupings are marked with an asterix.

Sociosexual Behaviours	Sociological Variables				
$\bar{X}$ Frequency of:	Rank	Parity	Infant	No. Offspring	Age
*rejections received	high low p=0.0218 f=4.262	NSD	with without p=0.0052 f=8.820	r=0.2834 p=0.038	NSD
sexual presentations	NSD	null prim mult p=0.0002 f=11.143	NSD	r=-0.2433 p=0.054	NSD
estrous scream	NSD	p n m p=0.0257 f=4.049	NSD	NSD	NSD
solitary estrous behaviour	NSD	NSD	with without p=0.0011 f=12.568	NSD	NSD
ventral sit against	NSD	NSD	with without p=0.0367 f=4.687	NSD	r=0.24.1 p=0.056

Table 4.5 cont.	Rank	Parity	Infant	No. Offspring	Age
alarm call	NSD	NSD	with without p=0.0321 f=4.952	r=0.3841 p=0.005	r=0.3932 p=0.004
body jerk	NSD	NSD	with without p=0.0413 f=4.461	NSD	NSD
follow	NSD	NSD	with without p=0.0264 f=5.340	r=0.3051 p=0.021	r=0.2888 p=0.027
walk past	NSD	NSD	NSD	r=0.2426 p=0.054	r=0.2812 p=0.031
approach	NSD	NSD	NSD	NSD	r=0.2861 p=0.028
genital inspect	NSD	NSD	NSD	NSD	r=0.2462 p=0.052
duration of grooming bouts	high med. p=0.0463 f=3.103	NSD	NSD	NSD	r=-0.1119 p=0.022

Age and presence of an infant showed the most significant behavioural differences (seven and six respectively), and next is the number of offspring, which significantly correlates with five behaviours. Rank and parity each showed significant differences with only two behaviours. Rank of the female seemed to be one of the less useful of these variables in accounting for variation in the frequency of courtship behaviours. The results do indicate that low ranking females receive less rejection from males than do either high or medium ranked females, and that high ranked females groom for longer bouts than do medium or low ones.

Only two significant results were obtained in the analysis of parity. First, multiparous females present less than do primiparous , and primiparous less than nulliparous. In other words, nulliparous females present the most. The second finding was that primiparous females do the most estrus screaming, considerably more than either multiparous or nulliparous. It is interesting to note that primiparous females did show a trend toward highest mean frequency of overall proceptive behaviour (see Table 4.1).

The presence of an infant from the 1982 birth season did seem to influence a number of the females' behaviours. These females had a significantly higher frequency of following males and they were heard alarm calling significantly more often. "Ventral sit against" and "body jerk" were significantly less frequent for these recent mothers, as was the display of solitary estrous behaviours. In other words, the females with an infant performed the behaviours characteristic of the advertising and monitoring stage less than did those without an infant, and this is the most significant behavioural difference between females with and without an 1982 infant. Females with an infant were also significantly more likely to receive rejection from the males than were those without.

The number of offspring that a female had in her lifetime seemed to influence a number of behaviours. A significant positive correlation was found between number of offspring and the frequency of "follow", "walk past", and "alarm call". The significant negative correlation with the frequency of presenting suggests that the more offspring a female had, the less likely she was to present to the male. Females with a greater number of offspring were also rejected significantly more often by males.

The female's age appears to be the most influential variable of all those tested. Significant correlations were found with 7 behaviours. Age is positively correlated with the frequency of "follow", "ventral sit against", "approach", "walk past", "genital inspect", and "alarm call". Age is negatively correlated with the duration of grooming bouts, that is, older females groom for shorter durations.

At first glance these results seem somewhat scattered, and no overall pattern is apparent. In fact, for some of these results no intuitively satisfactory explanation is available. However upon closer examination it becomes apparent that the age of the animal influences the courtship behaviour in an understandable way. The similiarities in the results due to age and number of offspring are not surprising given that these two variables are themselves highly correlated (r = 0.9261, p = 0.000). In social animals such as Japanese monkeys, and primates in general, learning is an important, if not crucial factor in the development of behaviour. It is clear that many behaviour patterns change as an animal grows up and becomes more and more a part of the society, observing the behaviour of others as well as experiencing life itself. In terms of courtship behaviour, the predominant change seems to be an increased level of sophistication, a tendancy for the females to calm down and behave in a more self assured, less frantic manner than when they were young and inexperienced. For example, the 'coy' courtship pattern described in chapter three is best represented by the "walk past". Both age and number of offspring show a significant positive correlation with the frequency of "walk past". As mentioned above, this pattern usually results in the male following the female. Furthermore, this strategy seems less likely to result in the female being attacked in some way by the male.

Through a process of trial and error, and by observing the courtship behaviour of older female monkeys, the maturing animal may become more likely to copy and eventually to adopt this behaviour into its own repertoire.

Other behaviours which support this idea that the females are becoming more efficient and more experienced as they get older are "present" and "alarm call". In Japanese monkeys, sexual presentations are relatively rare; the more common practice is for the male to hip touch the female when he is ready to mount. Nulliparous females, which are generally young animals, show significantly more sexual presentations. This is in line with the overall appearance of agitation and impatience. Frequent sexual presenting would be expected of animals that have not yet learned that there are other, less obvious, ways of prompting a male to mount. This notion is further supported by the tendancy (p = .0659) for nulliparous and primiparous females to slap the ground more than multiparous females and by the tendency (p = .0732) for nulliparous females to threaten the observer more than primiparous or multiparous ones. Eventually they may learn that mounting will start without excessive presentations and it is therefore a waste of energy to do so. Furthermore, it appeared that the more agitated the female was, the more likely she would be to annoy her partner and subject herself to attack.

Unfortunately this notion cannot be supported statistically at this time, since no negative correlation was found between the age of the female and amount of aggression received. It is also possible that the females simply become so subtle that they can no longer be detected when they are presenting.

Alarm calling by an estrous female is often done within a string of vocalizations. It may occur almost as an accident, or it could possibly be a form of dishonesty ...the female is trying to trick the male into rushing over to her. If this were the case, certainly it is a behaviour that would have to be learned, and the fact that it correlates with age might support this explanation. It seems more likely though that some other explanation exists to explain the alarm call during the mating season, since the reaction to it tends to be minimal as might be expected, for it would indeed be similar to crying wolf. There are two other possible explanations for this observed result. Firstly, number of offspring and age would be positively correlated with having an infant since no nulliparous female could have an infant, and almost all primiparous females sampled had an infant in 1981, and not in 1982. Females with an infant showed a significantly higher frequency of alarm calling, which may simply be due to the fact that they had an infant to protect and were therefore more likely to overreact to perceived threats. If this is the case, the correlation of age and number of offspring with alarm calls may be an artifact of this relationship. The alternative explanation is that the observed results are simply due to the rarity of this behaviour, and the statistical significance may be a result of sampling error. In fact this may also be the explanation for the correlation between age and the frequency of genital inspects, for they too are very rare.

The physical presence of an infant has some rather predictable effects on behaviour. Females with infants, for example, show a greatly reduced frequency of ventrally sitting against a male. This is understandable since the infant, if with the mother, is usually at the nipple. The mean frequency of solitary estrous behaviours is also low for females with infants, and this is not surprising since this non-sexual behaviour category represents the stage where the female is doing the most running about. It seems reasonable to expect that a mother could not monitor her infant's activities while moving rapidly throughout the enclosure.

Enomoto (1974) reports that females without an infant showed more positive sexual behaviour. The results of my analysis did not confirm his finding, particularly in terms of overall proceptive behaviour, since females with infants had the same frequency of proceptive behaviour as those without, and no specific solicitation behaviours (except "body jerk") were more frequent in those without an infant. In fact, females with an infant showed significantly greater frequency of following and solitary estrous behaviours a find which is not readily explained. Enomoto found that females with infants neither showed nor received positive sexual behaviour. This study showed that females with infants received significantly more rejections. Takahata (1980) reports from his study that females with surviving infants had lower overall sexual activity than those without. These differences between studies may be due to different research design or to cultural, biological, or ecological differences in the troops studied. The "every other year" birth pattern of the females at Arashiyama West appears to have altered in recent years (Fedigan, personal communication) possibly due to food availability, and this might explain the difference in the results.

Other researchers have considered the variables of age and rank in the study of Japanese monkey sexual behaviour. Age and female sexual behaviour has been studied by Eaton (1978), Hanby & Brown (1974), Fedigan and Gouzoules (1979) and Wolfe (1978), although not necessarily in the same way. Fedigan and Gouzoules (1978) looked at consort pairs and found that monkeys tend to choose partners of their own age group, and similarly, Hanby and Brown (1974) report that young females consort with pre-pubertal males and older females with post-pubertal males. Eaton looked at the frequency of ejaculations received and found that "pubescent females received significantly fewer ejaculations than adult females without infants, but they did not differ significantly from those with infants" (1978:52). It is important to note here that each of these studies considers age and sexual behaviour in a very different manner than did the present study, and it is therefore not reasonable to compare the results. Wolfe (1978) however did support the notion of sexual immaturity in young females (though not specifically in proceptive behaviour) and states that "the attainment of sexual maturity by adulthood can be viewed as a learned process leading to efficiency and prowess" (1978:55).

Studies which deal with rank and sexual behaviour are numerous, and tend to approach the issue from the perspective of rank and reproductive or mating success. (This controversy was discussed briefly in chapter one.) The rank of the female and how it relates to differences in sexual behaviour, particularly courtship behaviour, has not been the focus of research. Both Takahata (1980) and Cochran (1979), however, report no significant correlation between sexual activity and the females' rank. Cochran specifically stating the "dominance rank of the females did not seem to influence the expression of female sexual initiations" (1979:350). The results of the present study support these findings. Wolfe (1979), looking at consort pairs, reports that adult monkeys prefer to mate with someone of their own rank.

Other than the effect of age on the actual solicitation pattern, the sociological variables of the female are not very predictive in terms of how or how much she solicits partners. The physiological basis of proceptive behaviour, as mentioned earlier, is not believed to be a direct or even important indirect predictor, however it is likely that this issue needs to be reconsidered. At least in rhesus monkeys, new evidence suggests that underlying endocrine factors strongly influence female solicitation behaviour, and social variables such as rank do not appear to override this effort (Cochran, 1979). Possibly a more complete understanding of the physiological basis of reproduction and sexual behaviour is a necessary path for future research despite the apparent emancipation from hormonal control. In Japanese monkeys this will be a particularly great challenge, since there is no apparent cyclicity to the occurrence of estrus (Wolfe, 1979) and since not only are the external indicators extremely variable, but also their relationship to internal events is not clear.

The observed changes in proceptive patterns based on sociological variables are best explained as a function of age, learning and experience. None of the sociological variables tested seem to explain differences in overall solicitation rates. Other factors must control or influence this behaviour. The sociological characteristics of the interacting male is a primary alternative, and this is the subject of Chapter 5. Other alternative research paths will be discussed in chapter 6.

CHAPTER FIVE

DIFFERENCES BASED ON THE INTERACTING MALE

In this chapter, I will move on to the third research objective: to try to account for variability in female courtship based on the characteristics of the interacting male. The suggestion here is that females might behave differently towards different males. As discussed in the introduction, a number of studies have tried to approach the issue of female choice by investigating the relationship between the male's mating success and factors such as rank, aggressiveness, and tendency to display (on structures in the environment). There has been no analysis of the behaviour of the female and how it might change depending on the interacting male. For this study, the different sociological groupings for the males were tested for differences in behaviour received from the females, and behaviour directed at the females. Exploring the basic behaviour differences that occur with different males is a crucial element in the study of female choice.

It was hypothesized that some of the variability in female behaviour might be due to the sociological variables of male age, rank, and spatial status. Each variable was tested with 40 behavioural units (see Table 2.3 for list of behavioural units), and the significant results of the three male variables are presented in Table 5.1.

Contrary to what we might expect given the emphasis on rank in the literature, male rank does not seem to be significantly affecting the frequency of very many female behaviours. One clear result is that high ranking males leave females significantly more often than do either medium or low ranked ones. The other clear result is that females show fear indicators to medium and high ranked males more than to low. Note that the list of behaviours tested contained some combined behaviour categories and some specific ethogram behaviours. The results concerning the frequency of "fear grimaces" and "response moves" are repetitious of the "fear indicators" result, since they comprise the "fear indicators" category.

Spatial status is also responsible for only one significant result. Central males are more likely to show rejection behaviour ("leave") than are peripheral ones. That is, females are more likely to be rejected or left by central males. Table 5.1 shows significant results with two behaviours for spatial status - male leaves and male rejections - but again, the former is a specific behaviour and it is the main component of the male rejection category.

As was the case with the female variables, age of the male appears to be the most influential factor in terms of variability in courtship behaviour. First of all,

TABLE 5.1 Results of the Oneway Analysis of Variance for the male rank and spatial status and the Pearson Correlation Coefficients for male age. Higher level behaviour groupings are marked with an asterix. Only those behaviours with at least one significant result are presented.

Sociosexual Behaviours	Male Sociological Variables		
$\bar{x}$ freq. of	RANK	SPATIAL STATUS	AGE
*rejection by male	NSD	central peripheral p=0.0249 , f= 5.932	NSD
*male advances	NSD	NSD	r=.5474 p=.002
male follow	NSD	NSD	r=.4736 p=.006
male sit near	NSD	NSD	r=.5763 p=.001
male approach	NSD	NSD	r=.5582 p=.001
male increases proximity	NSD	NSD	r=.4770 p=.006
male lip quiver	NSD	NSD	r=.4863 p=.005
male walk past	NSD	NSD	r=.4110 p=.017

TABLE 5.1 cont.	RANK	SPATIAL STATUS	AGE
male leave	high med p=.0136, f=4.213	central peripheral p=0.0388, f= 4.929	NSD
*female fear indicators	med low p=.0234, f=4.662	NSD	r=.3760 p=.027
female fear grimaces	med low p=.0391, f=3.901	NSD	r=.3999 p=.019
female response moves	med low p=.0539, f=3.450	NSD	r=.3154 p=.054
female lip quivers	NSD	NSD	r=.3234 p=.055
female walk by	NSD	NSD	r=.3144 p=.055
genital inspect by female	NSD	NSD	r=.3583 p=.002
female leaves	NSD	NSD	r=.5475 p=.033
female fear grimaces	NSD	NSD	NSD
groom by female	NSD	NSD	r=.3784 p=.026
*rejection by female	NSD	NSD	r=.5441 p=.002

age is positively correlated with a variety of male advances. Older males showed a significantly greater tendancy to "follow", "sit near", "approach", "increase proximity", "lip quiver" and "walk past" females. In other words, females are more likely to receive these behaviours from older males than they are from younger ones. Females also direct a variety of behaviours differentially to older males. To older males the females show significantly more rejection behaviour ("leaves") and more indications of fear ("fear grimaces" and "responses moves"). "Lip quiver", "walk by", and "genital inspect" also show a significant positive correlation with the age of the interacting male. The only significant negative correlation obtained was with the frequency of grooming. The females were significantly more likely to groom younger males than they were older ones.

The importance of learning and experience in behavioural development was mentioned in chapter 4. It seems reasonable that the differential behaviours received by differently aged males is a function of this same process. More importantly in terms of female choice is the effect that the age of the male has on the behaviour of the female. Notably absent is any tendency for females to show obvious and direct solicitation behaviours like "approach" and "follow" differentially to different aged males. There is no clear indication that females solicit more or less based on the age of the males. In fact, the data indicate that females tend to show more rejection to older males, which suggests that they "prefer" older males less. However, it should be kept in mind that older males also show more overall advances to the females, and specifically more direct solicitations such as "approach", "follow", "sit near" and "increase proximity". The apparent tendency for females to reject older males may be a result of the greater number of advances received rather than an indication of an age preference.

"Lip quiver", "walk by" and "genital inspect" by the female are positively correlated with the age of the interacting male. If we treat "lip quiver" as part of the more sophisticated or "coy" courtship pattern that has been described, we see that females are less likely to utilize this pattern when dealing with younger males. This is assuming of course that the correct meaning or function of the behaviour has been determined. With behaviours such as "walk by" and "genital inspect", there is even greater uncertainty. As noted in chapter 4, genital inspects are very rare, and the statistical result may be due only to this. Nonetheless, until we are reasonably certain of the function or meaning of these less obvious behaviours, sound explanations of the observed differences must be postponed.

The data indicate clearly that females are more likely to show indications of fear to older and higher ranking males. Whether it is age or rank that is the critical variable is not clear since they too are postively correlated. The courtship behaviour of the male Japanese monkeys does involve considerable "elements of intimidation" (Fedigan, 1982: 145), so it is not surprising that the females are indicating fear. However, the results of this study do not indicate any tendency for the females to receive more courtship chases or other forms of aggression from older males.

Enomoto suggests that "there is a relation between female fear and the dominance rank order of the male" (1974:270). He points out that during the non-mating season there is little sexually related interaction and that behaviour such as sitting together or grooming occurs infrequently and only between established pairs. Since breeding season brings with it a need for contact between the sexes that is not otherwise occurring, new behaviour patterns are necessary. My results show fear on the part of the females toward older and higher ranked males. The data presented by Enomoto (1974) show a higher frequency of appeasement behaviour from higher ranked males. Both of these results support the contention. Furthermore, Enomoto reports that higher ranked males show a higher frequency of several types of positive behaviour. This is similar to my finding that older males show higher frequency of a number of solicitation behaviours. While the true appeasement value of these behaviours is not known, it is very possible that something like "lip quiver", which is believed to function as a distance decreaser, may have an appeasement function in the courtship context.

A few of the results obtained in this analysis are not readily explicable. Both central and high ranking males (these two measures are also correlated) show a tendency to reject or leave females. There is no corresponding tendency for females to solicit these males differentially. Also the results indicate that females are more likely to groom younger partners than they are older ones. The explanation for either of these results is not clear.

This analysis of the behaviour of the females in terms of the sociological characteristics of the male does shed some light on the nature of the courtship process and indirectly on female choice, however it also brings to the surface some problems with this approach to female choice. Certainly we would expect the sociological characteristics of the male to have a considerable influence on the courtship behaviour which they receive from the females, yet according to these data, the most clear cut results involve "female rejection" and "female fear indicators". Neither age, rank, nor spatial status of the male are responsible for any difference in the overall solicitation rate of the female. There was no indication, for example, that higher ranked males were more "popular" or received any more advances. It has been demonstrated that females are actively soliciting males and that they actively reject some of the advances which they receive (Chapter 3). Since the sociological differences between the females are not responsible for this we expect the basis for the choice to lie elsewhere, probably in some characteristic of the male. I think all Arashiyama West researchers would agree that certain individual males receive much more solicitation from many more females than do others. For example, Male #129 has been nicknamed "Rocky II" because of his remarkable popularity with the female monkeys. "Rocky II" is high ranking (second highest in the troop), 11 years old and definitely a central male. Another example is Suma, who is the highest ranked male in the troop, 18 years old and of course central. Subjectively I would say that Suma was one of the least popular animals as far as receiving sexual advances from the females. In fact he appeared to receive a great deal of rejection when he made sexual advances. Rocky II was rarely, if ever, rejected by a female. Subjectively we must admit that age, rank and spatial status are not clear predictors of male sexual popularity. This is supported by the statistical analysis which indicates that we must rule out these sociological variables as being the basis for the difference in female solicitation rates and courtship patterns. What immediately presents itself as an alternative research pathway is the analysis of the behaviour of the male and how this affects the courtship behaviour of the female. This would involve a complex sequential analysis since each behaviour of each animal may be affecting the course of the courtship process, and any number of responses and reactions to any number of behaviours is possible. Of course if the study of primate behaviour has yielded any insights, it has forced us to accept the complexity of primate social life. Undoubtedly, the underlying rules of the courtship process will reveal themselves only once all behavioural, sociological, physiological, biological, cultural and even ecological variables are considered, and this will necessarily involve a deeper understanding of the relationships among these variables themselves.

CHAPTER SIX

CONCLUSION AND SUMMARY

In the theory of sexual selection, there is controversy over the relative importance of the processes of epigamic selection (female choice) and intrasexual selection (male competition). The problem lies in determining the relationship between these two forces, and in deciding which is the creative force in sexual selection. There has been a bias in the literature favoring male competition as the main process affecting the formation of mating pairs. The notion that females are sexually passive, simply accepting male solicitations has been prevalent. Those that consider female choice do so from the perspective that variables such as rank provide some males greater access to estrous females, rather than from the perspective that females prefer males of higher rank. Studies which focus on the behaviour of the female during the formation of mating pairs are necessary if we are to gain a more complete understanding of the role of the female in the choice of partners and in the formation of the mating pairs. Courtship behaviour is particularly important because courtship helps construct the male-female bond that is necessary for a successful mating.

The purpose of this study was to investigate the courtship behaviour of female Japanese monkeys. The repertoire of female solicitation behaviour was described and it was demonstrated that female Japanese monkeys have a wide range of courtship behaviours and also that there is great variability in expression between females. Furthermore, females play a more active role in the solicitation of mates than do the males and they reject over 30 percent of the advances they receive.

The comparison of the females on the basis of age, parity, rank, number of offspring, and presence of a recent infant reveals no significant differences in overall rate of solicitation or proceptive behaviour. In fact there was remarkable homogeneity. On the basis of this analysis it is concluded that none of these variables, when tested alone, accounts for the fact that some of the females solicit much more than do others (see Table 4.3). In terms of specific proceptive behaviours, the data suggest that female age has an effect on behaviour. As females get older, they tend to get more relaxed and 'sophisticated' in their solicitation patterns, and are less likely to show nervous or impatient types of behaviour. Other than this age related finding, it must be concluded that the sociological variables analyzed are not predictive of the overall amount of proceptivity shown or of the specific solicitation pattern utilized. The factors which cause or at least influence the observed variation must lie elsewhere.

An attempt was made to account for the variability in female courtship based on the characteristics of the interacting male. It was hypothesized that the sociological variables of male age, rank and spatial status might be responsible for the behavioural differences of the female. Age of the male proved to be the most important of the three studied. Most interesting in terms of female choice is that females show more rejection behaviour to older males than to younger ones. It is possible though that this result is due to the greater number of advances received from older males, rather than an indication of female preference. There is no indication that females are directing more of any solicitation behaviours to different aged males. They are more likely to show indications of fear to both older and higher ranked males, yet they are not receiving any more aggression from them. This is thought to be a result of the need for contact during the mating season that is not normal during the rest of the year. Older males show more lip quivers and this may be interpreted as appeasement behaviour.

The females do play an active and variable role in the formation of consort pairs, however the sociological variables tested are not directly predicting the expression of female courtship behaviour. Now that these variables have been examined, there are a number of alternative paths of inquiry that may be taken in order to determine what factors underlie the way in which the females are expressing their choice of mates.

Probably the most fruitful line of research is one that will determine the response of the females to specific male behaviours and to overall behaviour patterns. If we assume that all courtship behaviour is intended (by at least one participant) to lead to a successful mating, then it should be possible to identify which courtship patterns are successful and which are not. This will give a more direct indication of partner choice by focusing the courtship patterns which lead to successful pair formation.

Given the complexity of primate social life, a multifactoral approach will probably yield the most informative results. Refining the sociological variables to account for the correlation between the variables themselves is a first step. Investigating much more specific male - female combinations (eg. high multiparous with low peripheral) is another option. A variety of other variables (examples: canine length, body weight) should also be considered.

A comparison of pre- and post- conception courtship behaviour and a comparison of the courtship patterns of those females that conceive and those that do not will be particularly enlightening. Courtship behaviour around the time of conception is the most, or perhaps the only courtship behaviour that is relevant in terms of sexual selection. Pre- and post- conception sexual behaviour has been investigated by Fedigan and Gouzoules (1978), Stephenson (1974), Hanby et al (1971) and Eaton (1974), but all from the perspective of the rank of male consort partners. Data are currently being collected at Arashiyama West Institute on the 1983 births. These data will be the basis for a follow up study of pre-and post- conception behaviours.

Summary

The issue of female choice has been insufficiently dealt with in the primate literature and this has lead to a view of the female as being essentially passive in the formation of mating pairs. This is a study of the courtship behaviour of female Japanese Monkeys. Courtship behaviour is important in the construction of the male-female bond. The objectives of the study were to 1) describe the repertoire of female courtship behaviour and the role of the female in establishing mating pairs; 2) to compare females on the basis of age, parity, rank, number of offspring and presence of a recent infant to test for differences in courtship patterns; 3) to relate female courtship behaviour to the characteristics of the interacting males.

The study was performed on a naturally occurring troop of Japanese macaques that was transported intact to Texas in 1972 where they now range semi-free in a 50 acre enclosure. Focal animal data were taken on 40 female subjects who displayed behavioural indications of estrus. Analysis of Variance and Pearson product - Moment Correlation were used to analyze the effects of the sociological variables on a variety of specific behaviours and combined ethogran categories.

A comparison of the total number of female solicitations to the number of female advances received revealed that females play a more active role in soliciting partners than do the males. They also reject more than 30 percent of the advances they do receive. There is great variety in the courtship repertoire, however three stages leading to actual mounting can be outlined. They are advertizing and monitoring; testing and closing inter-individual distance; and, attempting to establish a mount series. Among the 40 subjects, there was a great deal of variation in the total amount of courtship or solicitation behaviour shown.

An attempt was made to determine some of the female variables that affect the expression of courtship behaviours. The variables tested were age, rank, parity, number of offspring, and presence of an infant. According to the data, none of these variables were responsible for the variability in overall frequency of proceptive behaviour, however the age of the female did affect the frequency of specific proceptive behaviours. As the females get older they tend to become more efficient and sophisticated in their solicitation patterns. It is suggested that other variables, for example the physiological stage of estrus, might be more important than sociological variables in influencing proceptive behaviour.

The age, rank, and spatial status of the interacting male were then tested in order to check for differences in the behaviour of the females. The results show that females show more fear indicators to higher ranked and older males. They also rejected older males more, but this could be due to the increased number of advances received by older males. It is suggested that in future research the analysis of the effects of the behaviour of the interacting male will be more informative since these data indicate that their sociological characteristics do not greatly affect the behaviour of the females.

Having determined that the sociological variables of female age, rank, parity, presence of an infant, number of offspring or male age, rank and spatial do not have a direct or controlling influence on female courtship behaviour, it is possible to go on to alternative lines of research. Multifactoral and behaviour variable approaches are suggested. A follow up study is underway which will compare pre- and post- conception behaviour.

References

Altmann, S.A.
1962 A Field Study of the Sociobiology of Rhesus Monkeys, Macaca Mulatta. Ann. N.Y. Acad. Sci. 102: 338-435.

Baxter, M.J. and L.M. Fedigan
1979 Grooming and Consort Partner Selection in a Troop of Japanese Monkeys (Macaca fuscata). Arch. Sex. Behav. 8: 445-468.

Beach, F.A.
1976 Sexual Attractivity, Proceptivity and Receptivity in Female Mammals. Horm. and Behav. 7: 105-138.

Blurton-Jones, N.G. and J. Trollope
1968 Social Behaviour of Stumptailed Macaques in Captivity. Primates 9: 365-394.

Carpenter, C.R.
1942 Sexual Behaviour of Free Ranging Rhesus Monkeys (Macaca mulatta). J. Comp. Psych. 33: 113-162.

Chevalier-Skolnikoff, S.
1975 Heterosexual Copulatory Patterns in Stumptail Macaques (Macaca arctoides) and in Other Macaque Species. Arc. Sex. Behav. 4(2): 199-220.

Cochran, C.G.
1979 Proceptive Patterns of Behaviour throughout the Menstrual Cycle in Female Rhesus Monkeys. Behavioural and Neural Biology 27: 342-353.

Conway, C.H. and C.B. Koford
1964 Estrous Cycles and Mating Behaviour in a Free-Ranging Band of Rhesus Monkeys. J. Mammal. 45: 577-588.

Czaja, J.A. and C. Brelert
1975 Female Rhesus Sexual Behaviour and Distance to a Male Partner: Relation to Stage of the Menstrual Cycle. Arch. Sex. Beh. 4: 583-597.

Drickamer, L.C.
1974 Social Rank, Observability and Sexual Behaviour of Rhesus Monkeys (Macaca mulatta). J. Reprod. Fert. 37: 117-120.

Eaton, G.G.
1974 Male Dominance and Aggression in Japanese Macaque Reproduction. IN Reproductive Behaviour, W. Montagna, ed., New York: Plenum Press.

Eaton, G.G.
1978 Longitudinal Studies of Sexual Behaviour in the Oregon Troop of Japanese Macaques. IN Sex and Behaviour, Status and Prospectus, T.E. McGill, D.A. Dewsbury and B.D. Sachs, eds., New York: Plenum Press,

Enomoto, T.
1974 The Sexual Behaviour of Japanese Monkeys. J. Human Evolution. 3: 351-372.

Enomoto, T.
1978 On Social Preference in Sexual Behaviour of Japanese Monkeys (Macaca fuscata). J. Hum. Evol. 7: 283-293.

Enomoto, T.
1981 Male Aggression and the Sexual Behaviour of Japanese Monkeys. Primates 22(1): 15-23.

Fedigan, L.M.
1982 Primate Paradigms. Montreal: Eden Press.

Fedigan, L.M. and H. Gouzdules
1978 The Consort Relationship in a Troop of Japanese Monkeys. IN Advances in Primatology Volume 1: Behaviour, D. Chivers, ed., London: Academic Press.

Hanby, J.P., Robertson L.R. and C.H. Pheonix
1971 The Sexual Behaviour of a Confined Troop of Japanese Macaques. Folia. Primat. 16: 123-143.

Hanby, J.P. and C.E. Brown
1974 The Development of Sociosexual Behaviours in Japanese Macaques, Macaca Fuscata. Behaviour 49(1-2): 152-196.

Herbert, J.
1968 Sexual Preference in the Rhesus Monkey (Macaca mulatta) in the Laboratory. Anim. Beh. 16: 120-128.

Kaufman, I.C.
1965 A Three Year Study of Mating Behaviour in a Free-Ranging Band of Rhesus Monkeys. Ecology 46: 500-512.

Lemmon, W.B. and E. Oakes
1967 'Ticing' Between Stumptail Macaques During Mating. Lab. Primate Newsletter 6: 14-15.

Michael, R.P. and D. Zumpe
1970 Sexual Initiating Behaviour by Female Rhesus Monkeys (*Macaca mulatta*) under Laboratory Conditions. Behaviour 36: 168-186.

Michael, R.P. and D. Zumpe
1971 Patterns of Reproductive Behaviour. *In* Comparative Reproduction of Nonhuman Primates, E.S.E. Hafez, ed., Springfield: C.C. Thomas.

Michael, R.P., Bonsall, R.W. and D. Zumpe
1978 Consort Bonding and Operant Behaviour by Female Rhesus Monkeys. J. Comp. Physiol. Psych. 92: 837-845.

Michael, R.P., Wilson, M.I. and D. Zumpe
1974 The Bisexual Behaviour of Female Rhesus Monkeys. *In* Sex Differences in Behaviour, R.L. Friedman, R.M. Richart and R.L. Vande Wiele, eds., New York: John Wiley and Sons.

Modhal, K.B. and G.G. Eaton
1977 Display Behaviour in a Confined Troop of Japanese Macaques (*Macaca fuscata*). Anim. Beh. 25: 525-535.

Morris, D.M.F.
1956 The Function and Causation of Courtship Ceremonies. *In* Patterns of Reproductive Behaviour. New York: McGraw-Hill Book Company, 1970.

Nigi, H.
1975 Mestrual Cycle and Some Other Related Aspects of Japanese Monkeys (*Macaca fuscata*). Primates 16(2): 207-216.

Nigi, H.
1976 Some Aspects Related to Conception of the Japanese Monkey (*Macaca fuscata*). Primates 17(1): 81-87.

Phoenix, C.H.
1978 Sexual Behaviour of Laboratory - and Wild-Born Rhesus Monkeys. Horm. and Behav. 10: 178-192.

Ralls, K.
1977 Sexual Dimorphism in Mammals: Avian Models and Unanswered Questions. Amer. Nat. 111: 917-938.

Southwick, C.H., Beq, M.A. and M.R. Siddigi
1965 Rhesus Monkeys in North India. IN Primate Behaviour, L. Devore, ed., New York: Holt, Rinehart and Winston.

Stephenson, G.R.
1973 Testing for Group Specific Communication Patterns in Japanese Macaques. IN Symp. IV Congr. Primatol. Volume 1: Precultural Primate Behaviour. Basel: S. Karger.

Stephenson, G.R.
1974 Social Structure of Mating Activity in Japanese Macaques. IN Symp. 5th Congr. Int'l Prim. Soc., S. Kondo, M. Kawai, A. Ehara and S. Kawamura, eds., Tokyo: Japan Science Press.

Takahata, Y.
1980 The Reproductive Biology of a Free-Ranging Troop of Japanese Monkeys. Primates 21(3): 303-329.

Taub, D.M.
1980 Female Choice and Mating Strategies Among Wild Barbary Macaques (Macaca sylvanus L.). IN The Macaques: Studies in Ecology, Behaviour and Evolution. D.G. Lindburg, ed., New York: Van Nostrand Reinhold Co.

Tokuda, K.
1961-2 A Study of the Sexual Behaviour in a Japanese Monkey Troop. Primates 3: 1-40.

Tokuda, K., Simons, R.C. and G.D. Jensen
1968 Sexual Behaviour in a Captive Group of Pigtailed Monkeys (Macaca nemestrina). Primates 9: 283-294.

Trollope, J. and N.G. Blurton-Jones
1970 Breeding the Stumptail Macaque. Lab. Anim. 4: 161-169.

Wilson, M.E.
1981 Social Dominance and Female Reproductive Behaviour in Rhesus Monkeys (Macaca mulatta). Anim. Behav. 29: 472-482.

Wilson, M.E., Gordon, T. and D. Chikazawa
1982 Female Mating Relationships in Rhesus Monkeys. Amer. J. of Primat. 2: 21-27.

Wolfe, L.D.
1981 Display Behaviour of Three Troops of Japanese Monkeys (Macaca fuscata). Primates 22(1): 24-32.

Wolfe, L.D.
1978 Age and Sexual Behaviour of Japanese Macaques (Macaca fuscata). Arch. Sex. Beh. 7(1): 55-68.

Wolfe, L.D.
1979 Behavioural Patterns of Estrous Females of the Arashiyama West Troop of Japanese Macaques. Primates 20: 525-534.

APPENDIX 1

Major Faunal and Floral species in the Enclosure.

FAUNA

Common Name	Latin Name
Vervet Monkeys	Cercopithecus aethiops
Desert Cottontails	Sylvilagus sp
Skunks	Mephistis mephistis
Jack Rabbits	Lepus sp
Ground Squirrels	Spermophilus sp
Domestic Geese	
Rattlesnakes	
Chicken snakes	
Indigo snakes	

*Plus a variety of birds and small lizards.

FLORA

Common Name	Latin Name
Mesquite	Prosopsis julifora
Acacia	Acacia sp
Hackberry	Celtis sp
Whitebrush	Aloysia sp
Awn grass	Tridens sp
Buffle grass	Cenchrus sp
Burr grass	Cyperus sp
Windmill grass	Chloris sp
Winterwheat (planted)	

APPENDIX 2: Example of Focal Animal Data Sheets used (with sample entries)

SUBJECT: 49

DATE: Oct. 31, 1982

TIME: 08:00 hrs.

CONTEXT: sitting with 284 and 68. Infant playing nearby

TIME	BEHAVIOUR	DIRECTION	OTHER	
08:00:00	sit			
:05:26	walk			
:05:45	approach	→	129	
:05:48	sit beside	→	129	
:06:10	leave	←	129	he appears to be following #117
:06:15	follow	→	129	
:06:40	sit near	→	129	
:06:52	threat	→	117	
:07:00	leave	←	129	