THE UNIVERSITY OF CALGARY

The Effect of Subsequent Birth and Birth Season on Mother-Two Year Old Offspring Interactions in *Macaca fuscata*

by

Christine E. Giancarlo

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF
MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "The Effect of Subsequent Birth and Birth Season on Mother-Two Year Old Offspring Interactions in *Macaca fuscata* " submitted by Christine E. Giancarlo in partial fulfillment of the requirements for the degree of Master of Arts.

Supervisor, Dr. P. J. Asquith, Anthropology

Dr. M. S. M. Pavelka, Anthropology

Dr. V. Haines, Sociology

June 3, 1993

Abstract

The subject of this study is whether the presence of a neonatal sibling alters a Japanese macaque mother-offspring relationship. A second question is whether birth season itself has an intradyadic effect. Forty-two females, each of which had a two year old offspring, were observed over a four month period before and during the birth season of 1991 (i.e., February through May, 1991). The eighteen pregnant subjects who produced a neonate during the study experienced significant decreases in dyadic interaction with their two year olds following parturition. Birth season was not found to significantly alter the nonpregnant mother dyads. The presence of a neonate correlates with a decrease in mother-offspring interactions. The effect of subsequent birth on mother-offspring relationships has not been studied previously in this species. The effect of birth season on nonparturant mother-offspring dyads has not been exclusively tested in any primate species.

Acknowledgments

This field research study has been, for me, a life experience as rich as its primatological worthiness. Those who were involved provided me with the tools necessary to successfully complete the project. My heartfelt appreciation goes to each of these persons.

I thank Dr. J.D. Paterson for his faith in me as a field researcher and for facilitating my return to the field site in 1992. I am grateful to Dr. Mary McDonald Pavelka for her interest in my project and assistance with travel arrangements and accommodation on site.

During the crucial five months of data collection in 1991, one person is ultimately responsible for my success. To that person who, with her unbelievable knowledge bank, was there to assist me in the field , who ensured that my children received the best of care, who made Valentine's Day and Easter unforgettable for them, and who believed in the importance of my work, I can only say a very inadequate thank you. That person is Ms. Lou Griffin, my friend.

I owe much to Lou's family as well, for putting up with our long hours and unexpected emergencies. Frank, your "rescue" of my children and me on a scorching day will be remembered. I thank Megan and Griffin O'Neill, with whom my children shared their love of life.

Back in Calgary, during the painstaking months of data editing and analysis, I wish to thank Ms. Gisela Engels who gave analytical advice regarding the presentation of my data. To Gisela, I extend my deepest gratitude for your commitment and the meticulous methodology given to my statistical analysis. The long hours of frustrating number crunching went far beyond the call of duty. Dr. Pascale Sicotte also ki ndly shared her expert knowledge with me in the utilization of statistical tests and Dr. J. DiSanto gave of his time to clarify some analysis-based concerns. Your efforts are much appreciated.

During the final months of thesis preparation, I appeciated the guidance of Dr. Pamela Asquith as supervisor whose genuine regard for the science of primatology was reflected in a rigorous approach to the analysis.

To Ms. Myrna Haglund, Ms. Jill Ogle and Ms. May Ives, the administrative staff, backbone of the Anthropology Department, a warm thank you for ongoing moral support as well as your assistance getting through various "red tape" situations.

I now shift my focus to another vital and very real aspect of my success in this project. The hours required of a graduate student on campus and in front of a computer are seemingly endless at times. In order for me to accomplish my goal, I needed frequent assistance with child care. My preschool age son and daughter were welcomed at any time by their grandparents, Caterina and John Giancarlo. Without their help, this thesis would never have materialized. Thank you for your love and support.

My own parents, Eve and Bill Barker, I thank for instilling in me a respect for all species and the curiosity to pursue behavioural studies. They also have spent many hours in the grandparent role, enabling me to further my writing. For the many ways in which you have influenced my life, I thank you from the bottom of my heart.

To Grandma Mann, I wish to acknowledge your contribution as the role model you have been for dedication and commitment to a project. Your remarkable literary talent has been inspiring, to say the least!

In conclusion, there are three persons whom I have purposely left until the end of these acknowledgments. This is because they are my life; my family. My husband, Luigi, provides the foundation on which a successful life is built. His steadfast and unconditional support allows me the ability to advance my career. I could not be both mother and student without such a partner and for these things, I am truly grateful to you. Devon and Carmen, you are the great inspirations for my fascination with children of all primates. You kept me busy in the field but I would not trade those precious months for the world.

This book is dedicated to my

children,

DEVON WILLIAM and CARMEN OLIVIA

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CHAPTER ONE

Overview of the Research Project

Introduction

Mother-infant bonding is deeply entrenched within the repertory of primate behaviour. The complexity of this relationship has been the subject of much scientific research, conducted both in laboratory settings and in behavioural observation within free-ranging environments. An established bond between a mother and her infant is often permanent though never static.

This study specifically investigates the intradyadic relationship between mothers and their two year old offspring during the months preceding and during birth season. Two year olds are a unique age group within the *Macaca fuscata* species. They are often still obtaining some nourishment from mother's milk although these youngsters are fully capable of dietary independence (Hiraiwa, 1981). Two year olds are undergoing a transitional phase of ontogeny in which they move from a mother-dependent state at age one year to an independent state by age three years (Fedigan, 1992). A number of variables may alter the dynamic of the dyad over time, including ontogeny, sex of the offspring and whether or not the offspring's mother produces any future progeny. I have focussed my field research on the change within this dyad as a result of subsequent birth. The study also considers whether birth season itself has a significant effect on mother-two year old offspring dyads who do not experience the addition of a neonate, and whether the presence of a one year old sibling affects the dyad. Offspring within the forty-two subject dyads range in age from twenty-one to twenty-four months at the beginning of the data collection period. The study population of *Macaca fuscata* is situated in South Texas, and was a semi free-ranging group of five hundred monkeys at the time of this study.

The field research was conducted over a five month period in 1991 beginning in January and terminating at the end of May. Data were collected from February through May. This time period facilitated my observation of the subjects prior to the birth season and through most of the 1991 neonatal additions. In order to evaluate mother-offspring relationships following a birth, it was necessary to collect data on the relationship dynamic prior to delivery of the new infant. I have included January in my research period since January 4 was my arrival date at the site. During the remainder of the month, I was occupied with familiarizing myself with the area and the monkeys.

The effects of subsequent birth on mother-offspring (see below for ages of offspring studied) dyads have been documented in a number of studies involving various monkey species (e.g., Chism, 1986, for lactating mothers and their infants in *Erythrocebus patas* ; DiGregorio et al., 1987, for mothers and 13 to 33 month old offspring, mean age at sibling birth was 22 months in *Macaca mulatta* ; Holman et al., 1982, and Golopol, 1979, for mothers and yearling infants in

Macaca mulatta ; Lyon et al., 1985, for a nuclear family including a 26 month old female, 13 month old male and 7 month old female in *Callimico goeldii* ; Lee, 1983, for mothers and either one, two or three year old offspring in *Cercopithecus aethiops* ; Singh and Sachdeva, 1977, for lactating mothers and their infants in *Macaca radiata*), but there is a lack of information on the subject for Japanese macaques, regardless of age of offspring (Negayama et al., 1986).

Japanese macaque mothers of two year olds allocate much of their time budget to activities such as grooming and maintaining close proximity to their offspring. From the data obtained through this project, percentage values indicate that these mother-offspring dyads spend approximately 20.7% of their time within five metres of proximity. The remaining 79.3% of the monkeys' time budget is comprised of individual non-dyadic activity, independent of this study's focus. Within this 20.7% figure are the smaller percentage activities of grooming, contact and proximity. These behaviours together with intradyadic conflict events represent the total dyadic interaction witnessed over the course of 156 hours.

The Study Species

Japanese macaques are indigenous to the islands of Japan, occurring at higher altitudes along mountain slopes between latitudes of 31.0 and 41.2 degrees North. They are medium sized, quadrupedal monkeys, males on average approximately 14.6 kilograms while females average 12.3 kilograms (i.e., in Japan; Nakamichi, 1989). Adult males tend toward a taller, broader morphology with more muscle and fur on the shoulders and hips than adult females. They also have much larger canine teeth. Sexual dimorphism is moderate but appears accentuated during the annual breeding season. At this time, some males develop a shoulder "cape" of fur, which gives the impression of larger body size.

Both sexes have pink faces and pink genitalia, though there is significant individual variation in dermal tone. In the breeding season, bare skin is noticeably enhanced to a near-scarlet colour. Fur colour is also variant and ranges from golden to brown or gray. Eye colour also varies from brown or hazel to green or blue. These differences are most often related to individual, matrilineal, seasonal and age variability (Fedigan, 1992).

Japanese macaques are adept both in the trees and on the ground. Their natural habitat is mountainous broad-leafed or montane forest and dietary items include nuts, buds, berries, shoots, leaves and even bark. They may be classified as omnivorous due to some observations of insect, egg and crustacean consumption. Japanese macaques are, unlike most other primate species, able to withstand cold winters and deep snow. Often in the native habitat, temperatures drop below -5 degrees Celsius and there may be snowfalls of up to three metres.

Macaca fuscata has proven to be a very adaptable primate species. One troop (Arashiyama A) was successfully translocated to the Arashiyama West Primate Center, now

renamed the South Texas Primate Observatory, in 1972. Daily temperatures in the Japanese macaques' new habitat often reach 37 degrees Celsius (Collinge, 1987; Fedigan, 1982) during the dry, hot summers.

Social Organization

Matrilineal kin groups are the mainstay of Japanese macaque society. These family groups are closely associated with a small number of central, adult males and are loosely connected with many peripheral males. These peripherals may be natal males who are in the process of emigrating or they may be unrelated individuals who seek membership in the troop. The mean adult sex ratio is approximately one male to four or five females. There are usually many related, breeding-age females and several unrelated, breeding-age males within the whole group which also contains elderly, juvenile and infant monkeys. Some all-male groups have been observed which may consist of siblings or peers who peripheralized together, and solitary males are not uncommon. Matrilineages, or parts of them, may emigrate from the main troop and become all-female groups (Fedigan, 1992).

Breeding in Japanese macaques is highly seasonal, females and males often forming several consortships for mating purposes within a few months. There is no clear evidence to indicate that there is recognition of paternity or that biological fathers form close bonds with their offspring (Fedigan, 1982). Group membership, though stable for females, is unstable for males who often leave the natal troop (Sugiyama, 1976).

Movement of the troop during foraging is amoeboid, with a central male somewhere near the middle of any new pseudopods and a number of adult females and infants close by. The whole troop will then catch up and surround this protrusion and continue to slowly "flow" along. Adults of both sexes are seen to climb trees sporadically during foraging to scan the environment, perhaps acting as lookouts for the whole troop. It appears that the central males are the focus during foraging, adult females monitoring their locations for defensive protection but some females do not focus upon or follow such males. In addition, not all adult males perform these vigilance activities (Fedigan, 1992), but this structure appears to be the norm (Sugiyama, 1976).

The Study Population

In 1972, a population of one hundred forty-nine Japanese macaques were translocated to Texas from the original, larger Arashiyama troop living on the mountain slopes near Kyoto in Japan. The translocation was a response to growing irritation on the part of agriculturalists who complained about the monkeys destroying their crops.

The Texas group was re-named "Arashiyama A" and was located in the southernmost sector of the state, close to the Mexican border. They have since been relocated to a fifty-acre

site near Dilley, one hundred twenty-eight kilometres south of San Antonio. The climatic variation is substantial in this semi-arid region, winter nights occasionally dropping below zero degrees while summer diurnal temperatures often exceed thirty-seven degrees Celsius.

The "Arashiyama A" group has adapted remarkably well. Its population size now is approximately five hundred monkeys and annual birth numbers have exceeded eighty in recent years. Mortality rates are very low for this group.

The group is composed of three smaller troops, two of which have emigrated from the original troop. The main troop is the largest of the three, having approximately four hundred members. The splinter group began with emigration from the main troop of one fragment of a lineage and has since grown to approximately fifty monkeys. Peripheral males make up the third group and membership appears to be open. Some of these males join either the main or the splinter troops when the opportunity arises (e.g.,death of an influential male).

Subsistence of the troop is heavily reliant upon natural forage and the monkeys have discovered new edible items which are far removed from the diets of their Japan-living counterparts. These items include prickly pear cactus, mesquite and acacia. The monkeys are also supplemented daily with grain and "monkey chow" in order to ensure a nutritional balance.

The monkeys are maintained in their natural social groupings where interference by humans is minimized. The group has been studied since the early 1950s in Japan and now in Texas, thus providing complete genealogies and life histories of all animals. The individual ranks within the social hierarchy, established by observation of agonistic signals, are monitored and recorded regularly (Lou Griffin, personal communication; Collinge, 1987). The monkeys are habituated to the presence of at least one behavioural researcher.

Identification of the Subjects

After my arrival at the South Texas Primate Observatory, I underwent a process of informal orientation during which time I became familiar with both the site and the subject species. Due to the large size of the enclosed area, I spent some time mapping the terrain and ground cover in order to find subjects more easily when beginning a focal animal sample. I also assisted in the maintenance activities of the site, an important role for the researcher utilizing the site for her/his own research purposes. Along the same lines, I was familiarized by the director with the procedures associated with capture and treatment of the monkeys such as tattooing for identification.

During this same period, I pored over the census in search of monkeys who fulfilled the criterion of being mothers of two year olds (i.e., offspring born in 1989). Forty-two focal animals were thus selected. These represented every type of mother in terms of age, parity and rank. as described on pages 28 and 29 of Chapter three.

Perhaps most challenging was the process of becoming familiar with the subjects themselves, forty-two monkeys from a population of five hundred, residing in two troops. This was achieved through a visual process of elimination. For instance, first I became accustomed to the physical appearance of adult females as opposed to juveniles of both sexes and adult males. Then I began to note the locations of certain animals throughout the day. Some monkeys could almost certainly be found on the periphery of the troop while others were mostly central. Now I focussed on the actual physical appearance of my subjects; such factors as hair, eye and face colour, abnormalities like missing digits, scars, nipple length, and unique gait (e.g., a limp). Only when I could accurately identify each subject at a glance did I commence data collection.

The Census

The subject animals were selected according to their status in relation to each criterion for this study. In order to do this, I used the information in the written census. The site director of the Observatory confirmed the appropriateness of my choices. Although I wanted to have as balanced a representation as possible between nonpregnant and pregnant animals, I had no knowledge of the pregnancy status of each subject.

This is a semi free-ranging population of Japanese macaques in which environmental and social factors are not manipulated to the extent they would be in a captive situation. A captive situation allows for best accuracy of the census information since paternity can be proven and infants and mothers can be physically isolated from other dyads. However, the observed behaviour is frequently uncharacteristic for the species in the wild.

At the South Texas Primate Observatory, the census has been maintained painstakingly over generations of macaques from the population's origin in Japan to the present. In my study, one subject is listed in the census as having given birth to twins in 1990. I had no way to ascertain positively that this in fact was the case but the subject mother was observed in contact and alternately nursing two infants. This individual also had a 1989 offspring and fulfilled the remaining subject criteria. The question of census accuracy is a valid one and must be taken into consideration when observing free-ranging populations.

Terminology

Throughout the research project, the mother-two year old offspring dyad is sometimes referred to as "the dyad" and the use of the word "offspring" refers to the youngster(s) born in 1989. Offspring are nearing or have recently had their second birthdays and are experiencing the second birth season since their own births. For the purposes of this study, an infant refers to an individual of one year old or less. The study is a direct comparison of mother-offspring dyads prior

to and at birth season or for those pregnant subjects, pre- versus post-parturition. The dyad in this research project always consists of a female subject and her two year old offspring.

Overview

In the following five chapters, the research project will be presented, the methodology laid out, and the data analysed for its implications with regard to mother-offspring relationships surrounding the birth season in Japanese macaques.

Chapter two reviews parental investment theory from the perspective of Robert Trivers (1972) in order to understand the motivation of mothers to care for and raise their young to an age of independent survivability. Though this study does not test parental investment theory, it is concerned with maternal care of two year old offspring, a segment of the bigger picture that is parental investment. Maternal care patterns are also species-specific and in Japanese macaques the matrilineal kin group is the backbone of the society . Affiliative intradyadic behaviours comprise the statistical analysis since the study species maintains close mother-offspring bonds in the long term, oftentimes for life (Fedigan, 1992).

Current information on maternal care patterns in the primate literature are examined across species. Agonism is rare between mothers and their progeny in Japanese macaques due to this tendency toward a semi-permanent relationship (Collinge, 1985). Intradyadic conflict is usually related to weaning behaviour in the study species (Collinge, 1987). Reasons for this conflict are examined with attention given to Trivers' parent-offspring conflict paper (1974). Over time, an infant is subject to ontogenetic processes that undoubtedly affect its behaviour. As an offspring matures, its dependence on the mother declines as its own self-sufficiency increases. In this study, mothers, rather than offspring are the focal animals so effects of ontogeny cannot be analysed. However, effects of birth season are tested for and ontogeny would be considered a potential factor in any significant intradyadic changes. However, ontogeny is probably not a major factor in dyadic alteration during this study since the research period spans only four months. The supposed decay of the close mother-offspring bond may be accelerated by the addition of a neonate to an established dyad.

Parturition is examined across primate species in order to recognize the signs of imminent delivery of a neonate amongst the chosen subjects. Since this study concerns Japanese macaques in a semi free-ranging situation, it is necessary to anticipate and identify changes in a subject's behaviour at the commencement of labour in order to prevent misinterpretation of her social dynamics (i.e., seclusion). Initial changes in a dyad following the new sibling's birth may be temporary so data was collected as long as possible, up to two months, post-partum in order to balance a short-term change.

There is a lack of literature concerning the effects of subsequent birth on established mother-offspring dyads for Japanese macaques. This topic has been studied to some extent in other primate species as discussed in the chapter. The results of these studies are presented as a prediction of repercussions within a Japanese macaque dyad upon the arrival of a neonate. This chapter concludes with a reference to the following research project, the focus of my study, as an inquiry into Japanese macaque maternal behaviour.

Chapter three details the project methodology. The method of data collection utilized in this study was Focal Animal Sampling (Altmann, 1974). I used a field computer rather than the traditional pencil and paper system and this format is described. The amount of data collected is broken down by subject and then by hour of day. Most of the samples were collected during the diurnal periods of highest activity and the subjects were recorded as equitably as possible (see Limitations of the research, Chapter six). The representation in the data of non-pregnant versus pregnant subjects turned out to be almost equivalent, as revealed at birth season. There were nineteen births in 1991 from a possible forty-two subjects. One of these subjects, Be596671, was considered separately (see below). The subject animals are then identified by census name and mother-type according to six other categories. These include age, parity, troop membership, and rank as well as sex of each mother's offspring and infant (i.e., where applicable). The number of data hours collected for each subject is then tabled.

Chapter three then specifies the four research questions to be addressed and the hypotheses associated with them. The behaviours that were statistically analysed included all affiliative activities, grooming, contact and proximity. Due to the overall infrequency of intradyadic agonism, qualitative data were recorded on mother-offspring conflict behaviour. The section entitled "Analysis" explains the group categorization of forty-one of the subjects, and the study periods that form the comparative basis for dyadic interactions before and at birth season. In table 3.5, the number of data hours collected in the two study periods are listed by group. Finally, the method for statistical analysis and graphics is outlined.

In Chapter four, the results of the statistical tests are illustrated. Each research question is explored by means of the data collected in each study period, pre-birth season (or pre-parturition) and birth season (or post-parturition).within each of the three affiliative behaviour categories.

Chapter five contains a discussion of apparent trends in affiliative behaviour observed in mother-offspring dynamics over the two study periods. The results from each research question are explained according to situational factors and available literature. Conflict, the indicator of intradyadic tension, is descriptively compared between study periods for each group. Although data in this format cannot provide conclusions, it is useful as tentative support for significant behavioural changes determined by the results in Chapter four. Lastly, the chapter discusses the single subject, Be596671, who had both offspring and infant and then delivered a neonate

during the study. Her data is tabled by behavioural category and descriptively compared to that for the other groups in order to speculate on similarities between certain mother-types.

Chapter six gives some overall conclusions based on the study regarding effects of subsequent birth on mother-offspring dyads as well as the potential effect of birth season on those nonpregnant mother dyads. The chapter also considers some limitations of the research project, within the framework of inherent problems encountered in the field situation and then those associated with the process of data analysis upon my return home. Finally, avenues for further research related to the project topic are suggested.

CHAPTER TWO

Theoretical Perspectives on Maternal Care

Survivability in infant mammals is dependent upon the care-giving of a parent or parents, for at least the period commencing at birth until the infant is nutritionally independent (i.e., weaned). This parental care begins at conception and for some species, may not terminate until either the parent or the offspring dies. Humans, as well as some nonhuman primate species (e.g., Japanese macaques), exhibit this tendency toward life-long parental investment patterns (Sluckin, 1986).

Parental Investment

According to Robert Trivers (1972), parental investment is defined as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (p. 139). It includes metabolic investment in primary sex cells but refers to any investment, such as feeding or guarding the young, that benefits the offspring. It excludes any expended effort in finding a member of the opposite sex or in subduing members of one's own sex in order to mate with a member of the opposite sex, since such effort usually does not affect the survivability of the resultant offspring (Trivers, 1972).

One of the underlying tenets of sociobiological theory, and the implication of Trivers' parental investment theory, is that females and males experience continual conflicts of interest and only cooperate insofar as their previous investment in one jointly conceived offspring or set of offspring forces them to do so (Fedigan, 1992). The production and rearing of one offspring has energetic, and more importantly "fitness", costs, in terms of other potential offspring. Since each offspring is an independent investment in a finite world, increasing investment in one individual tends to decrease the possibility of investment in others. The goal of every individual, according to Trivers (ibid.), is to successfully raise to reproductive age as many offspring as possible. One's inclusive fitness is thereby maximized by having the best possible representation of one's genes in the next generation. The premise is that in order to further her/his own reproductive success, each parent will act so as to bear the minimum cost of each offspring. The optimal strategy for each parent following copulation and conception is therefore to abandon the offspring to the other parent to rear and to move on to further offspring production (Trivers, 1972).

Female mammals, with an initial larger investment due to their larger sized gamete (i.e., ovum), are saddled with a handicap at the moment of conception (cf. Daly, 1978). They also have a biological limitation in the number of possible offspring so they choose mates with care, either

selecting males with visible evidence of vigour and fitness in a genetic sense, those that maintain an area of adequate resources for the future infant, or males that demonstrate a likelihood of contributing to rearing the infant by employing various forms of parental care, such as food-sharing and protection from predators (Fedigan, 1992).

The male's most efficient strategy is to leave the female immediately after mating and to impregnate as many females as possible. Males act to conceive as many offspring as they can, whereas females act in order to successfully rear as many young as they produce. These strategies result in antagonism between the sexes (Trivers, 1972).

Trivers' point of view is challenged by Daly (1978) who explains that males do invest significantly in terms of energy and risk to future fitness in order to reach the point of copulation with females. Competition between males for proximity to and courtship of females is enormously costly to males. However, these costs do not directly affect the survival chances of resultant offspring. It is argued that infant loss is of greater consequence to females than to males, due to the male's higher reproductive potential. There are, as yet, insufficient data regarding the number of infants that the most successful male can produce compared to that of the female in a lifetime (Fedigan, 1992). Males may reproduce heavily during a few peak breeding years and not at all in others, thereby reducing their over all success to the same level, or even less than that of females (Daly, 1978).

Consistent with Trivers' (1972) parental investment theory, mothers are undoubtedly the first, and usually the primary, care-givers to their biological offspring (Dunbar, 1988). Nonhuman primate infants, though more precocious than humans, are entirely dependent as neonates upon their mothers for survival (e.g., food, protection, warmth). The mother-offspring dyad is the basis of perhaps the most intense social relationship, the maternal bond (Altmann, 1980), which often endures past the age of offspring survivability (Fedigan, 1992).

This chapter reviews the current literature surrounding one aspect of parental investment, maternal care (i.e., having energy and "fitness" costs, Trivers, 1972) of offspring, with a special emphasis on the change elicited by the subsequent birth of a sibling. When a neonate is born into an existing dyad, this significantly alters that mother-offspring relationship (DiGregorio et al., 1987). The parturitional event, including pre- and post-partum behaviours, is crucial to the observer in order to evaluate changes in the dyadic relationship. As well, birth season itself is considered as a potential disruptive force affecting mother-offspring dyads since other researchers have found changes in maternal behaviour associated with birth season activity within the troop (Ehardt, 1987). Several primate species will be discussed, including the Japanese macaque (*Macaca fuscata fuscata*) which is the focus of my field research.

Maternal Care-giving Patterns:

Primate infants depend exclusively on their mothers for at least the period until they are weaned, between the ages of one and two years for Japanese macaques (Fedigan, 1992). It is also in the mother's best interest to successfully rear the infant, thereby increasing her own inclusive fitness (Trivers, 1972). Trivers suggests that the nature and course of parental behaviour can be predicted by viewing it as a function of the costs affecting the parent's reproductive success and the benefits to the survivability of the current offspring. When the costs to the mother's fitness are greater than the benefits, she will be selected to avoid investment in the offspring. Conversely, the offspring will continue to seek maternal care as long as the benefits are greater than the costs to its own fitness (Trivers, 1974).

Conflict during socialization of the offspring, as during weaning and adolescence, is not only a consequence of the mother's culture (i.e., sensu Trivers, 1974) versus the biology of the offspring but is also due to the biology of both, each member of the dyad representing different "fitness" interests. Conflict will ensue when the offspring attempts to improve its fitness at the expense of the mother's. Whereas the mother seeks to maximize her reproductive success by returning to estrous as soon as possible, the offspring who is already self-sufficient may continue to seek maternal care by suckling or maintaining close proximity to its mother for protection from other troop members or predators. The offspring's long-term association with the mother diminishes her ability to produce more infants so it is expected that intradyadic conflict episodes will increase with time, once the infant has reached independent survivability (Trivers, 1974).

However, this state of conflicting agendas is temporary and is resolved when fitness costs to the offspring are greater than benefits. By delaying the mother's subsequent production of infants, the offspring is limiting its own fitness since any siblings would be related to it by one half. Since most mother-offspring conflict is related to weaning in nonhuman primates (Gouzoules, 1980) and most intradyadic conflict observations in my study were of this nature (38 of a total 42 eventsor 89%), the length and intensity of the weaning conflict period is correlated with the offspring's relatedness to mother's future infants. The lower the offspring's relatedness, the longer and more intense the expected weaning conflict. Those species in which unrelated males commonly father a given female's successive offspring are expected to show stronger and more persistent intradyadic weaning conflict (Trivers, 1974). This is the case in the study species, *Macaca fuscata* (Fedigan, 1992). Conflict patterns do not appear to be affected by the sex of the infant (Fairbanks and McGuire, 1985, for vervets; Nakamichi, 1989, for Japanese macaques).

McKenna (1979) has criticized the Trivers model of parental investment by examining the offspring's potential to gain as well as the mother's, should she produce subsequent offspring, especially if the additional progeny are full siblings of the first offspring. These siblings increase both the offspring's and the mother's fitness equally since they all share the same degree of

genetic relatedness (i.e., 1/2). It may be selectively advantageous for first-born offspring to willingly leave their mothers as soon as they reach the point of independent survivability. Alternatively, the older offspring may leave initially following a sibling's birth but return soon after to act as a helper in raising its new sister or brother. Instances of older offspring allomothering their siblings are common in Japanese macaques, especially when the older sibling is at least three years of age (Hiraiwa, 1981; Eaton et al., 1986). Perhaps the offspring benefits more than the mother does since its own reproductive behaviour is years away and through the mother's reproductive efforts, the offspring gains much while investing nothing (McKenna, 1979).

In terms of parental investment, in this study limited to maternal care of two year old offspring, the subsequent birth of a neonate into an established dyad will have an effect which falls within a range of adaptive behaviour patterns. These vary from complete separation of dyad members (i.e., mother and offspring) to intradyadic conflict as a result of conflicting agendas (Trivers, 1974) to a continued intradyadic association which benefits both members (i.e., increased "fitness" by genetic relatedness to the neonate (McKenna, 1979).

Limited evidence indicates that in several monkey species mother-offspring dyads show a decrease in positive interactions such as grooming and close proximity, in conjunction with and following the birth of a sibling (DiGregorio et al, 1987; Lyon et al, 1985). In these species (Chism, 1986, for *Erythrocebus patas* ; DiGregorio et al., 1987, for *Macaca mulatta* ; Holman et al., 1982, and Golopol, 1979, for *Macaca mulatta* ; Lyon et al., 1985, for *Callimico goeldii* ; Lee, 1983, for *Cercopithecus aethiops* ; Singh and Sachdeva, 1977, for *Macaca radiata*), offspring of both sexes show a sharp decrease in positive mother-offspring interactions upon the addition of a sibling. Parent-offspring conflict is subject to both environmental and social factors. In the present study, environmental factors are relatively constant since all members of the population are exposed to similar stimuli (e.g., weather, predation) and are provisioned with adequate food and water for subsistence. The social factor (addition of a neonate) is investigated in order to examine the behavioural adaptation pattern which is adopted by mother-offspring dyads in Japanese macaques.The pattern for this study species has not been previously studied but it is known that Japanese macaques practise long term relationships amongst matrilineal kin groups. Female offspring are bonded for life with their matrilineal kin whereas males have an unstable relationship, due in part to a tendency to roam (Fedigan, 1992). Though male offspring usually emigrate in free-range populations (Gouzoules, 1984), this tendency is not always the case in the semi free-range situation. On numerous occasions, I observed adult males in contact with or in proximity to their mothers and other kin (personal observations, 1991 and 1992; as per communication with LouGriffin, 1991).

The effect of birth season is a potential factor in altering mother-offspring relationships, even when the mother is not pregnant. Worlein et al. (1988) observed a "clear period of disruption" in the mother-infant relationship during mating season in Japanese macaques (November through January). Infant-directed conflict behaviour increased and affiliative behaviours such as grooming decreased markedly. After mating activity ceased, the prior close relationship between mother and infant resumed until the birth of a sibling occurred a few months later. The disruption caused by the mating season was not replicated at birth season, except in those dyads that experienced a subsequent birth (Worlein et al.,1988).

In a study of non-pregnant Japanese macaques, female subjects without dependent infants were found to alter their behaviour toward other females during birth season, preferentially approaching and remaining in proximity to mothers with neonates (Ehardt, 1987). Movements toward these mothers were subtle and usually consisted of reaching out a hand toward the mother and neonate and spending a substantial amount of time staring at the pair. In addition, non-pregnant females groomed and approached non-kin infants (i.e., approximately one year old), usually those of high-ranking mothers, more often than they approached those belonging to their own matriline. This behaviour contrasts with the characteristic preferential association in this species with members of one's own kin group (Ehardt, 1987). This study will examine whether there is a birth season change in intradyadic interaction within those dyads which did not experience a 1991 birth.

Ontogenetic Effects on the Mother-Offspring Dyad

A cross-species survey of general care-giving patterns amongst nonhuman primates demonstrates a remarkable similarity. This consistency is most striking between the great apes and Old World monkeys. Although there are qualitative differences in specific behaviours (e.g., infant carrying, types of contact interactions), the majority of differences are largely quantitative rather than in kind. They are usually related to the greatly protracted period of infancy in the great apes (Higley and Suomi, 1986). An exception to this trend is the infant's choice of play partner. Limited evidence suggests that Old World monkey mothers do not play with their infants so there is a peer orientation to such activities. In the apes, the mother is often the infant's major play partner, especially during the first two years (Nadler, 1980).

Dunbar (1988) acknowledges two major stages in the ontogeny of a nonhuman primate infant. The first stage encompasses the period during which the infant is totally dependent upon its mother for nourishment, care and transport; in effect for survival. In Old World monkeys, this period lasts for the first six to twelve months of the infant's life. The second stage begins at the point at which the offspring is somewhat independent, being mobile and able to find food, yet not

completely weaned. The infant is well acquainted with the troop's diet and can actively avoid ingesting secondary compounds which are potentially harmful. This second ontogenetic stage ends when the offspring can effectively fend for itself within the adult social group. In Old World monkeys, this stage occupies the interval between one and four years of age. It is characterized by the assimilation of essential survival skills. These include recognition of appropriate food sources and their locations, water sources and safe sleeping sites, and the ability to move through the environment while minimizing one's exposure to predation (Dunbar, 1988). This study involves mothers with offspring who are within Dunbar's second stage of development. These two year olds are in the process of assimilating the life skills necessary for independent survival (Fedigan, 1992). Dunbar's two stages are characterized as follows:

Stage one For the neonate, mother represents an introduction into the complex social world in which it must survive. The first few days after birth are crucial for the dyad. Bonding is the key mechanism at work while the mother is relatively inactive and her infant is weak. It spends the vast majority of its time sleeping (Sluckin, 1986). The wakened infant spends long periods staring into the mother's face and responding to her eye contact. Lip-smacking by the mother may be employed to regain the infant's attention and restore eye contact (Mendelson, 1982). The mother frequently grooms, licks and adjusts to the infant's positions during the first few days (Mitchell and Brandt, 1975).

Except for a few prosimians (Berman, 1984), all other nonhuman primates carry their newborns with them, usually by way of the infant's clinging to the mother's ventral fur. The infant is initially carried and nursed by the mother at all times (Chalmers,1980). In the first thirty days, as rhesus macaque neonates increase in social responsiveness, maternal grooming shows a concomitant increase (Harlow, 1963). Although difficult to test this supposition, it appears that these activities play an important role in inducing and maintaining maternal behaviour (Hoff et al, 1981). The pattern begins to change by the time the infant is a few weeks old (Ingram, 1977). At this age the infant begins to explore its proximal environment, moving a few metres away from its parent whenever she settles to feed or rest. As the infant matures, time spent away from the mother increases while contacts with other troop members, especially kin, multiply (Dunbar, 1988).

Even at two weeks of age, infants demonstrate a keen interest in food items that the mother chooses, often nuzzling her mouth to taste a given item. Although the infant suckles, the Japanese macaque mother does not otherwise provide food items to the infant but is very tolerant of its retrieval of scraps while sitting with her. The dyad will also frequently eat from the same food source. Mothers will brush away inedible or toxic items from their infants' hands (Fedigan, 1992).

In a study carried out by Murray and Murdoch (1977) on Japanese macaques, contact between dyad members occurred in 87% of all scored intervals and was accompanied by nipple

contact in 69% of these. Mutual separation for this age group occupied only 5% of all scored intervals and always lasted less than thirty seconds. Dorsal riding increased in frequency over time and was dependent upon dyadic preference (Murray and Murdoch, 1977).

Solitary Play: By five weeks of age, Japanese macaque infants begin to engage in "solitary play" (Murray and Murdoch, 1977). This consists mostly of exploration of the proximal environment and the manipulation of objects which she/he finds within it. Until seven weeks of age, infant leaves are more common than mother initiated ones but even earlier, mothers begin to engage in regular social activities. Such re-integration promotes the commencement of dyadic mutual independence (Bramblett, 1976).

Parallel Play: Although ventral contact is still the primary state of the dyad members by twelve weeks of age, 47.3% of observed intervals, the infant by now spends almost 10% of its time devoid of mother contact and the distance during these independent episodes increases to a mean of five metres (Bramblett, 1976). The predominant play category at twelve weeks of age is "parallel play" in which the infant is active near but not touching another infant (Bramblett, 1976). There are documented cases of infants, whose mothers die at this stage, surviving if another group member adopts the orphaned individual. An adoptive adult is usually a member of the same matriline as the adopted infant (Tartabini, 1979). Although Japanese macaques are not fully weaned until age one, or more commonly two, years, infants have sufficient knowledge and digestive tract maturation to locate and ingest enough forage for sustenance (Fedigan, 1982).

Associate Play: At twenty-one weeks of age, infants begin the period characterized by "associate play" which involves rough and tumble interaction. Usually two individuals engage in physical contact, chasing, biting, grappling with and sitting astride one another. This behaviour mirrors the dominance rank positions held by infants' mothers. Those infants with higher ranking mothers frequently mount, sit on and bite other infants, whereas those of subordinant parentage frequently assume submissive postures during associate play episodes (Bramblett,1976). As infants gain in size and age, play group sizes also increase. Dominance interactions during play begin to take on a serious tone and infants select play partners on the basis of kinship, particularly between mothers. The effect of this selectivity is to reduce dominance disparity between the players (Bramblett, 1976; Higley and Suomi, 1986).

Jean Piaget (1971) identified four periods in human primate cognitive development (i.e., sensorimotor, pre-operational, concrete operational, and formal operations). His research subjects were children but the first three of his categories position nonhuman primate development within a cognitive framework as well (Piaget, 1967 and 1971). The fourth and final category (i.e., formal operations) has not yet been conclusively tested for (Fedigan, 1992). The first "sensorimotor" period extends from birth to twenty-four months of age in humans and involves the conceptual development of time, space, causality and object permanence (Piaget

and Inhelder, 1969). Nonhuman primates are thought to accomplish the sensorimotor criteria by the age of six months (Fedigan, 1992).

Stage Two Dunbar's second ontogenetic stage corresponds well with Piaget's second and third periods. The third period probably continues into adulthood in nonhuman primates. The second "preoperational" period occurs between ages two and seven years in humans and six months to at least two years in the Japanese macaque (Piaget, 1969; Fedigan, 1992). The subjects in the present study have offspring that fall within the parameters of Piaget's second period. These two year olds are transitional in that they are still partially dependent upon their mothers (e.g., nursing) but are nearing the third "concrete operations" period at which time they will be considered independent troop members. Two years of age usually marks the attainment of independence in Japanese macaques and the termination of Dunbar's Stage Two (1988) The mother-offspring dyad remains important in the preoperational period. Infants model their behaviour closely upon that of their mothers in such activities as eating, socializing (e.g., submitting to or dominating other troop members) and in the selection of friends (deWaal, 1990). They are also dependent upon their mothers for protection. If the infant is threatened, although she might be some distance away, a mother will grimace in fear or counter attack as if she is the direct receiver of the aggression (Fedigan, 1992).

The essential difference between a subject in the sensorimotor as opposed to the preoperational period is that the former is relatively restricted to direct interactions with the environment, whereas the latter is capable of manipulating symbols that represent the environment (Phillips, 1975). Except for transivity, wherein a subject can infer that A>C because A>B and B>C (Gillan, 1981), little research has been done explicitly on this period using nonhuman primates. There is however, a large and growing body of knowledge indicating that some animals use concepts that represent environmental entities or events (Thomas, 1980).

The third "concrete operational" period is characterized by the individual's advancement from overt reactions to perceptions. The child, or nonhuman primate, conserves quantity and number, constructs the time and space that she/he will live within as an adult, and establishes foundations for the fourth stage in the case of humans, perhaps in other primates too (Piaget, 1969). This period can be assessed in primates by the individual's recognition that quantity remains equal when a liquid is poured from one tall and narrow vessel into another short and wide vessel. Although researchers have reported substantial success by testing both *Macaca mulatta* and *Pan troglodytes*, it is uncertain whether these animals correctly judge the stimuli as equal because they are adept estimators of equivalence, or because they utilize the concept of conservation (Thomas and Walden, 1985). They concluded that without a verbal explanation, neither process can be accepted as the mechanism at work(ibid.).

The fourth "formal operations" period has never been tested for in nonhuman primates (Thomas and Walden, 1985). Cornell (1978) raised theoretical and methodological questions about testing procedures typically used with and designed for humans. Piagetian data are confounded by this species-specific variable but they serve as a hypothetical basis for cognitive development which proceeds through the ontogeny of nonhuman primates.

Dunbar's (1988) second stage reflects two kinds of problems for a primate mother: Firstly, she must deal with all the attention received from other troop members and secondly, she must control her infant's behaviour to prevent its loss or separation should she move or be forced to move. Attention from other individuals declines during this stage as the novelty of the new infant fades but the need for control by the mother increases as the infant becomes more independent. The problem of infant control involves the coordination of infant's with mother's behaviour. If a female frequently retrieves her infant from several metres away, she will be expending unnecessary energy (Dunbar, 1988). When ecological conditions are marginal, the survival of the dyad may be dependent upon whether mother-infant behaviour meshes or not (Trivers, 1972).

An active infant utilizes mother's milk for adequate caloric ingestion. While the offspring is still relatively dependent upon the mother for nutrition through suckling, it is often more economical for her to carry it even short distances. If the infant walks instead, its mother is still expending energy. Due to the low conversion coefficient of lactation and high energy consumption of an active infant, mothers sometimes burn fewer calories in the long term by carrying their infants (Dunbar, 1988).

Dietary independence from the mother signifies its locomotory independence simultaneously (Higley and Suomi, 1986). Independent survivability occurs at one to two years of age in apes and some monkeys (Goodall, 1967 for chimpanzees.; Fedigan, 1992 for Japanese macaques). In the callitrichids, it occurs by age three to four months (Ingram, 1977; Wright, 1986).

Parturition

Labour varies enormously among primate species. Even within one species there is often significant individual variation. Rhesus macaques were observed to labour for a range of twenty-three seconds to over thirty-four hours in six births (Negayama et al, 1986). Chimpanzees born in captivity vary from thirty minutes to eight hours (Tinklepaugh and Hartman, 1930; Sluckin, 1986). Some of this variability is due to the fact that there are often few indications that the fetus is about to be delivered. Mothers who give few, if any, external signs of contractions during labour are likely to be credited with shorter labour periods than those who are demonstrative (Chalmers, 1980). A study of three captive births in Patas monkeys showed no regular and obvious changes in the intensity of labour as parturition neared. All three females averaged fifteen to twenty contraction seconds per minute. They changed position frequently, either standing

quadrupedally, sitting, squatting or lying down, and occasionally each locomoted during contractions. The females sometimes emitted barely audible, squeaking gasps during the strain of hard contractions, otherwise they were silent throughout the process (Hemmalin and Loy, 1989). Remaining quiet during parturition is clearly adaptive for all non human primate species since this substantially reduces the risk of predation while vulnerable to attack.

For captive gorillas, pre-partum behaviours are often undetected but a few isolated reports contain a fairly consistent description. This includes the assuming of a prone position immediately prior to delivery with the mother crouching on knees and elbows (Rumbaugh, cited in Nadler, 1974). When labour could be observed, it was characterized by a general restlessness, facial grimacing, straining and bearing down, slight twitching of the leg muscles and grasping or pulling at the cage bars (Nadler, 1974).

Parturition in Japanese macaques most often occurs in the early morning hours. Signs of labour include frequent squatting and the passing of mucous. Immediate post-partum behaviours suggest that the new mother is temporarily isolated from social contact (Fedigan, 1992). Primarily she rests, mostly sleeping and sitting for the first few hours after birth. Once delivered, a neonate is licked clean by its mother who may also then consume the placenta a few minutes after its expulsion. Placentophagy has been correlated with the level of orality represented by maternal licking behaviours. There is some evidence indicating that placentophagy may induce maternal bonding and appropriate care behaviours but it is unclear what mechanism triggers this relationship (Brandt and Mitchell, 1973). Grooming of the infant by the mother occurs during 6% of the day following a birth and consists mainly of inspection of the infant's body and genitalia. Other troop members will keep their distance from the dyad, often by as much as four metres, in clear avoidance behaviour. Juveniles and other infants show interest in the new addition but are restrained from close approach by their mothers. A nursery group will usually disperse if a new mother attempts to join it (Fedigan, 1992).

In a study of rhesus macaques housed in three nuclear family groups, contacts by mothers with other progeny were also minimal in sharp contrast to the pre-partum situation in which females were often observed grooming and/or sitting close to their other offspring (DiGregorio et al., 1987). By the second day following birth, the rhesus macaque mothers, carrying their new infants ventrally, tried to resocialize, first with their siblings and progeny, then cautiously approaching other mothers. These mothers were met with explicit avoidance responses by the approached individuals including threats, stares and quick exits. They were successfully reintegrated after a few persistent attempts (DiGregorio et al, 1987).

Reproductive Success

Parturition marks the commencement of an enduring mother-infant relationship. A mother must abruptly adjust to the presence of a stranger, the neonate, who suddenly appears close to her. Though strangers are often the target of aggression and repulsion, these reactions do not often occur in primate mothers upon arrival of their new infants (Kemps and Timmermans, 1982). However, new mothers do exhibit some restlessness, excitement or fear at parturition. There also seems to be a cumulative effect of previous birth experiences, multiparous mothers indicating a lower arousal level (Brandt and Mitchell, 1973).

In baboons, general time budget data show that towards the end of pregnancy, mothers spend 43% of their time feeding, 23% in locomotion, 17% resting and 17% engaged in social activity (Altmann, 1980). During this period, as during lactation, mothers must balance between investment in their own survival and that of the infant. In marginal ecological conditions, a mother can easily over-tax herself, thereby reducing her own survival prospect, but at the same time she must expend energy to nourish her offspring in utero or post-partum through lactation. Altmann (1980) estimated that mortality rates for adult lactating females are approximately double those values given during other stages of the reproductive cycle.

According to Chalmers (1980), a macaque or baboon female usually delivers her first infant at three or four years of age. Chimpanzees achieve sexual maturity much later, usually at about age nine (Chalmers, 1980). Japanese macaques produce their first infants at age five or six whereas rhesus macaques can be fertile as young as three and a half years old (Wolfe, 1984).

From the Arashiyama A troop there is no evidence to suggest that infants of low-ranking mothers experience greater mortality rates than those of higher ranking parentage. There is no association between mother rank and reproductive success, at least in this macaque population (Wolfe, 1984). This may be a function of a stable environment in which there are adequate resources for the whole population, therefore there is no nutritional deficit amongst low-ranking mothers.

The number of offspring that a female will produce, if she consistently finds an appropriate breeding partner, will depend upon the length of her interbirth intervals. Species-specific data for the Japanese macaque suggest that one to two years is the common interval. In the semi free-range situation, an interbirth interval of one year is not uncommon since females enjoy a stable food supply and are less vulnerable to predation than their wild counterparts(Fedigan, 1992; Hiraiwa, 1981). A reduction in interval is largely the result of a shorter period of lactation and significant stores of body fat in well nourished females. Some monkeys in the Texas semi free-range population (S.T.P.O. census) of Japanese macaques frequently experience one year intervals between births. A mother's age and parity status also affect her reproductive success. Although a stillbirth or loss of an infant can have dire consequences for a female's fitness level,

she will usually compensate by the rapid resumption of fertility and estrus, if the infant died before age six months (Wolfe, 1984).

A female's age at the time of pregnancy is important. Once past her reproductive prime, a mother's increased mortality risk results in a lower potentiality for rearing a future offspring in addition to her current infant. If an older mother terminates maternal care early on in order to reproduce again before her life ends, she may consequently lose both infants. There is insufficient time to rear this final infant to independence and the mother's under-investment in the previous offspring will place its life in jeopardy (Dunbar, 1988). In this case, a female is better off to concentrate on the successful rearing of the current infant, investing in it until adulthood is attained. It is beneficial then, for the period of parental care to increase as a female approaches the end of her reproductive life. Evidence supports this contention by indicating that interbirth intervals invariably widen as females of all species age (Collinge, 1987). Similarly, lactation in older females may also last longer as a function of extended maternal investment. A longer nursing period would increase the survivability of the infant, thereby increasing the mother's inclusive fitness as well.

Consistent differences in the temperaments of infant rhesus macaque infants born to primiparous and multiparous mothers have been detected that may be attributable to maternal care variation (Hooley and Simpson, 1981). In Japanese macaques, primiparae tend toward more idiosyncratic behaviour than do multiparae as observed by Brandt and Mitchell (1973) in twelve captive, but wild caught female subjects. Among multiparae, those having at least two offspring were uniformly adequate whereas those with a single birth experience varied in maternal ability (Brandt and Mitchell, 1973). It should be noted that this study was executed on subjects who were captured from the wild for laboratory research. Due to the presence of external stressors in the new environment, such as cage confinement and human contact, these monkeys may not be a valid indicator of normal parous female behaviour.

Tanaka (1989) in a study of free-ranging Japanese macaques, found that in the first six months of their infants' lives, multiparous mothers rejected suckling attempts and prompted independence more often than primiparous mothers did. By month eight following birth, parity differences in maternal behaviour are substantially reduced. Infant gender does not appear to affect parity differences in care-giving. Instead, mother-infant behaviour is largely determined by the mother (Tanaka, 1989).

Effects of Subsequent Birth on a Mother-Offspring Dyad

The birth of a younger sibling in nonhuman primates appears to influence mother-offspring relationships much more than any other factor does, at least in Japanese and Patas macaques, respectively (Nakamichi, 1989; Chism, 1986). Soon after the initial change in dyad

interaction due to parturition, mothers and older offspring commonly resume their close relationship. For daughters, this bond may be life-long but it most often weakens between sons and mothers in Japanese macaques once a son reaches adolescence (Nakamichi, 1989).

In the *Callitrichidae* including *Callimico goeldii* , offspring remain with the natal group consisting of mother, father and two or more offspring. They often exhibit delayed sexual maturation and expend energy by alloparenting younger siblings. Observations of parents threatening offspring in some instances indicate that other variables also affect the mother's reaction following parturition. Such threats would probably lead to dispersion of the natal group in the wild (Lyon et al, 1985). One documented case that occurred in captivity involved a family of five *Callimico* that experienced a subsequent birth. Following the arrival of the neonate, the mother forced peripheralization of the two year old. This may have occurred as a function of that family's excessive group size for this species so it is unclear whether the neonate was in fact the motivation or instead that any extra individual would be subject to this mother's response (Lyon et al., 1985).

Garber et al. (1984) have shown that tamarin parents who enlist the assistance of their older offspring are more successful in rearing their infants than those who do not. This study supports the strategy discussed earlier (page 11) of continued association of mother-offspring dyad members following a subsequent birth. Mothers may be more inclined to tolerate the presence of older daughters rather than sons, thus enabling young females to learn appropriate maternal behaviours. In Japanese macaques, juvenile daughters (i.e., at least three years of age) may be permitted to hold the infant but the mothers remain close enough to easily retrieve their neonates if necessary (Collinge, 1987). Juvenile males also occasionally exhibit allomothering behaviour toward their infant siblings though this has not been as frequently observed as with daughters (Collinge, 1987).

Proximity scores decreased measurably, 33-56% respectively, when two female Patas infants were observed in relation to their mothers during the month following their siblings' births. After this initial repulsion however, one year olds of both sexes were tolerated by mothers in proximity (Chism, 1986). In Patas groups, associations between mothers and sons persist through the offspring's first three years while those of daughters and mothers are usually permanent (Chism, 1986).

Even as she approaches estrus, a baboon mother begins to reject the infant who is still partially dependent upon her (Altmann,1980). This finding supports Trivers' theory in that a mother-infant dyad will develop conflicting agendas since the mother is predisposed to mate and produce another offspring (Trivers, 1974). Furthermore, evidence demonstrating that "only" offspring of cycling females display more stress reactions as they grow older, indicates that the estrus state of a mother contributes to the offspring's behavioural strategies (Collinge, 1987).

Distress reactions and attempts at the nipple were the only offspring behaviours significantly correlated with the weaning behaviour of mothers. This suggests that variability in behavioural repertories of offspring can be predicted by proximate causes such as the level of maternal rejection (Altmann, 1980). The positive relationship of offspring distress reactions during weaning does not conclusively indicate that the mother's rejections are the root cause of the distress. A review of field studies on mother-offspring interactions suggests that this is, however, generally the case (Gouzoules, 1980; Nicholson, 1982; Collinge, 1987).

In Patas monkeys, infant nursing ceases only when the next sibling is born, usually at the end of the first year of the offspring's life (Berman, 1984). A mother will prevent or discourage nursing of the older infant by pushing it off the nipple, swiping the infant off her ventrum by moving an arm across the chest, pulling the nipple out of the infant's mouth by raising an arm or leaning on elbows to effectively deny nipple access. A persistent infant may be swatted or bitten by the mother but usually the mother will concede after a brief struggle. Mothers also try to distract infants from suckling by initiating play or by grooming them. After a second infant is born, the first, whether fully weaned at parturition or not, is totally refused mother's milk (Chism, 1986).

Upon the birth of a sibling, rhesus infants increase in several measures of interaction with mothers, males and neonates. Simultaneously, interactions with peers drop off dramatically over the post-partum year (Berman, 1984). A subject group whose mothers were pregnant but failed to deliver viable offspring showed no significant alteration in total levels of peer interaction. They did increase some interactive behaviours with unrelated infants and adults. Female siblings interacted much more often than males did with new siblings; those less than six months old. Between six and twelve months of age, infants' interaction efforts were directed towards juvenile siblings of both sexes. Older siblings play a significant role in the socialization of infants and promote their independence from mothers (Berman, 1984).

Juvenile siblings who are closer in age to the neonate, encourage independence more than those several years senior. Males siblings appear to promote infant independence more than female siblings do (Hooley and Simpson, 1983). Older sisters and brothers may adopt a younger sibling who has been orphaned at an early age. Such adoptions have been cited for Japanese macaques by Gouzoules (1984).

The biggest disadvantage of a neonate to an older sibling is the sudden decrease in maternal care allocated to the older offspring (Trivers, 1972). The accompanying sibling rivalry, so well documented in humans (Dunn et al., 1981), has certain similarities in the nonhuman primate world, as when individuals actively prevent or interrupt suckling attempts by their new siblings (DiGregorio et al., 1987; Holman and Goy, 1988). This phenomenon is less documented for nonhuman primates than humans and reports of sibling reactions to a subsequent birth are conflicting. In juvenile subjects, some reseachers have observed decreases in measures of

proximity and amount of time spent with mothers when new siblings are born (e.g., Singh and Sachdeva, 1977, for free-ranging bonnet macaques; Hanby, 1980, for laboratory housed rhesus macaques; Holman et al, 1982, for male rhesus macaques in a zoo group). Other studies indicate increases in proximity and contact with mothers following sibling birth (eg. Ransom and Rowell, 1972, for olive baboons; Bolwig, 1980, for captive pigtail macaques and olive baboons). The present study tests where Japanese macaques lie in the range of these effects of subsequent birth on mother-offspring dyadic relations.

Yearling rhesus macaque infants appear to be more disturbed by new siblings than were two and three year olds. Golopol (1979), reported major changes in one year olds of this species as early as the second trimester of their mothers' pregnancies, still three months prior to the new sibling's birth. These changes included a decrease in total interactions with parents in the home cage and were more pronounced in female than male infants. Possibly, this decline was a trend occurring independently of the mother's pregnancy as it coincided with natural weaning behaviour and growing confidence of the infant. No changes in grooming, huddling, playing or agonism were observed during the study. It is necessary to point out that the absolute frequency of interactive initiation with mothers decreased during pregnancy but the relative strength and quality of mother-infant relationships did not (Golopol, 1979).

Following birth, neonates take over the ventral carrying positions on their mothers' bellies so maternal contact with previous offspring necessarily decreases. Initiations toward the mother for grooming and playing by the older offspring decrease but offspring-directed initiations by mothers increase, especially towards older female offspring (DiGregorio, 1987). First offspring attempt interaction with new siblings frequently, females initiating more often than males. These interaction attempts are not always approved of by rhesus macaque mothers, judging by an increase in threats by mothers towards older offspring (DiGregorio, 1987).

At two years of age, play with peers is the most prevalent behaviour pattern exhibited by both females and males. With the birth of new siblings, peer interactions decrease dramatically and continue this decline over the year following the birth. There appears to be a different emphasis on nuclear family-based activities at the expense of peer interactions (Ehardt, 1987). In DiGregorio's (1987) study on rhesus macaques, subjects were between thirteen and thirty-three months of age at the time of sibling birth. Decrease in peer interactions always commenced at the point of sibling birth, regardless of the age of a particular infant. Although the younger individuals initiated play with peers more frequently than older ones did, there were no significant differences shown in the pattern of changes between the two age groups when a new sibling arrived. Therefore the decrease in peer interactions is probably due to the presence of new siblings rather than normal ontogenetic processes (Ehardt, 1987). Also, the frequency of play interaction remained stable over the study period amongst those individuals without additional siblings with

whom to interact. Juveniles without new siblings also indicated higher levels of play with unrelated infants. Frequency of play with unrelated infants and adults increased in the post birth year only for subjects without new siblings (DiGregorio, 1987).

In rhesus macaques, yearling males often withdraw from mothers upon parturition but yearling females do not (Lee, 1983). Data found that three out of five vervets in a study were classified as "depressed", spending less time with mothers after a sibling's birth. These three animals were yearling males. Rhesus females from two to three years old tend to be more disruptive and aggressive toward new mother-infant dyads than are juvenile males of the same age and yearlings of both sexes. It follows that two and three year old rhesus macaque females are most likely to increase the amount of time spent with mothers and kin after new siblings are born (Lee, 1983).

Rhesus macaques are relatively aggressive so close kin may prove to be "safe" interactive partners as opposed to non-kin. The tendency to gravitate towards one's mother and new sibling provides a safe opportunity to develop a relationship with that sister or brother. This benefits the older offspring by way of recruiting a future ally for support during conflict with other individuals. The inclusive benefit gained by both members of a closely knit sibling pair may thus outweigh any costs incurred by the older sibling's loss of parental care-giving (DiGregorio, 1987).

Summary

In nonhuman primates, maternal care is intensive and influenced by a multitude of individual, social and environmental factors. Mothers lactate for most, if not all, of the interbirth interval (Collinge, 1987). This nutritional predisposition necessitates close proximity of the infant to its mother at most times, thus strengthening the dyadic bond. The addition of a new sibling alters this pattern in some temporary ways, decreasing proximity and increasing dyadic confrontations. Some facilitated changes appear to be permanent, such as the completion of weaning and increased independence of the first offspring. Although there is a lack of available literature regarding the repercussions of sibling birth in Japanese macaques, a number of intradyadic consequences including a decrease in affiliative interactions and an increase in agonism can be predicted on the basis of information from other primate species.

Japanese macaques have an interbirth interval mean of 1.96 years (Fedigan, 1992). Therefore, mothers who are pregnant for the second time will often have a current two year old offspring. This age corresponds to Dunbar's (1988) second stage of development and to Piaget's (1969) preoperational period. Offspring at this stage are precocious, becoming more independent and increasingly adept at survival skills. Mothers are occupied with controlling the activities of these offspring, teaching them to mesh their behaviour with that of the mother so as not to be lost or harmed by such threats as predation or intragroup fighting.

Offspring prefer the company of females during this two year old period but this bias is inversely correlated with the individual's age. Mothers are encouraging their male offspring to become more independent while female offspring are remaining close to their mothers for a large portion of the day. With the birth of a sibling, offspring of both sexes are abruptly distanced from their mothers, usually only temporarily. Weaning is complete; mothers will not permit an older offspring to nurse once her neonate has arrived (Chism, 1986; Collinge, 1987). The heavy emphasis on peer-oriented play which predominated in the pre-parturitional phase gives way to more family, matrilineal kin-centred activity. Mother's rank within the troop may be a factor in maternal care but no evidence has been documented to support this hypothesis in the Arashiyama A group.

Which patterns of behaviour among separation, conflict or continued affiliation are functioning in the Japanese macaque following a subsequent birth is the topic of this research project. My field research on the effects of subsequent birth and if any, of birth season itself, on mother-offspring dyad interactions will shed some light on this behavioural aspect of *Macaca fuscata*.

CHAPTER THREE

Methods and Materials

Method of Data Collection

Observational data were collected by running the "Datac 6" program, developed by Paterson, Kubicek and Tillekeratne in1991, on a Tandy/Radio Shack Model 100 notebook computer, carried by the researcher (see "Appendix 1" for ethogram used). Samples of thirty minutes were recorded, using the Focal Animal protocol (Altmann,1974). Subjects were recorded on a rotational basis, once each before a subsequent round of sampling commenced. Exceptions to this rotational protocol occurred when, for instance, a subject disappeared. Sickness, social conflict, labour and delivery were recorded as reasons for temporary disappearances during this study. Both states and events were recorded by the researcher who monitored not only activities of the focal animal but also the proximity of offspring within five metres of her.

The data represent 156 hours of observation, composed of 312 thirty-minute samples. I estimate a total of at least one thousand hours spent on the field site. Besides the actual recording of data, the learning process of recognizing forty-two subjects quickly and accurately at a glance occupied my first six weeks in the field. Additionally, significant numbers of hours were spent searching for subjects over the fifty-acre home range in order to sample the animals using the rotational method.

Observations were recorded between 0600 and 2210 each day. These were the daylight hours between dawn and dusk. Fifty minutes of this data were collected after dusk, in the last ten minutes of five samples, in order to observe the monkeys congregating into kin groups for the night. Troop movement and foraging typified the early morning (0600-0930 hours) while socializing and resting were characteristic of late morning activities (0931-1200). Early afternoon (1201-1600) was less structured and varied amongst individuals. The early evening (1601-1900) was characterized by a period of troop movement and foraging, followed by the monkeys' re-assembling into family groups to settle for the night (1901-2210). The vast majority of data samples were intentionally collected during the monkeys' period of highest activity, between the hours of 0900 and 1600 hours. Table 3.1 shows the distribution of observations by hour. Figure 3.1 graphically illustrates this distribution.

Figure 3.1 Observational Hours

(Distribution of Observations by Time of Day)

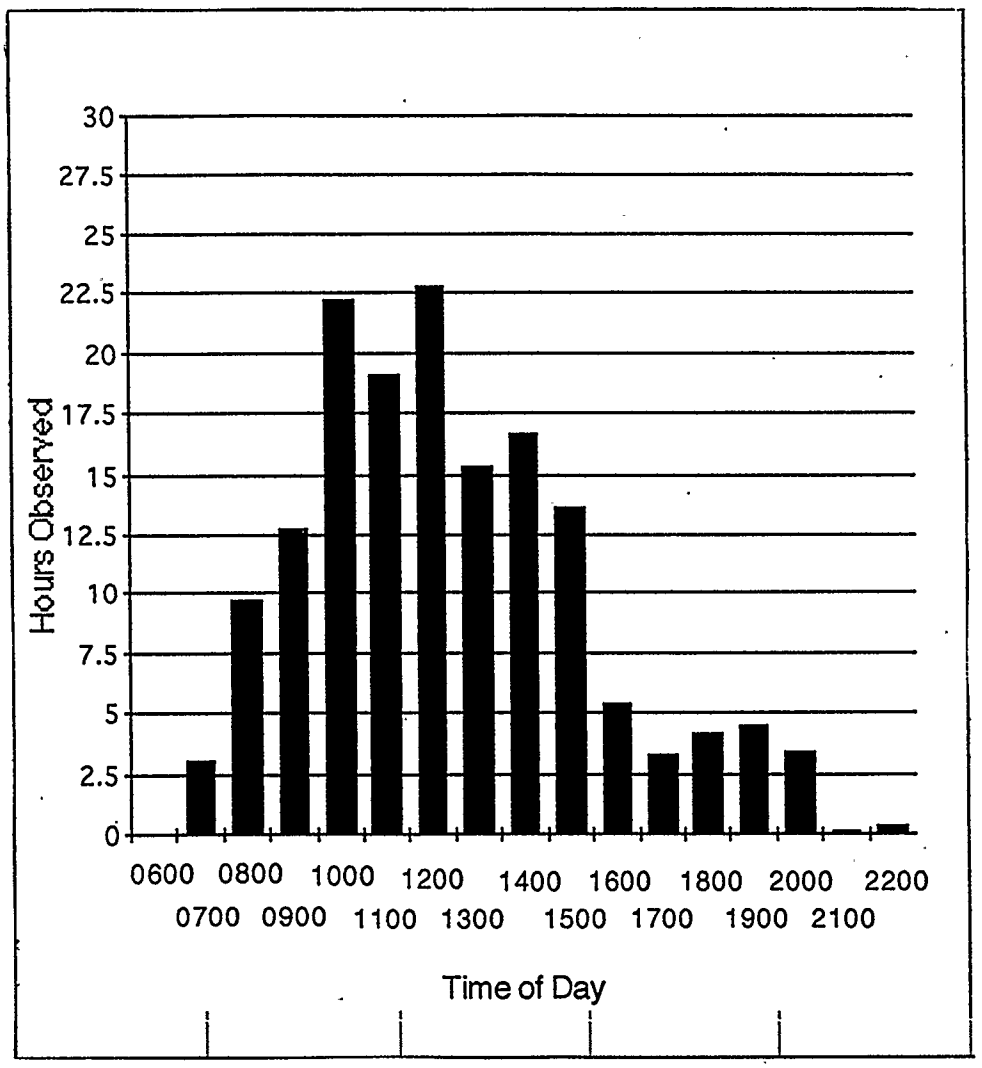

Table 3.1 Distribution of Observations by Time of Day

Time	Observational Hours	Standard Deviation	All Mother-Offspring Behaviours
Entire Population	156.00	.046	8318
06:00	.04	.006	3
07:00	3.04	.022	220
08:00	9.68	.021	719
09:00	12.76	.029	760
10:00	22.24	.059	1063
11:00	19.12	.040	1002
12:00	22.71	.062	1074
13:00	15.25	.035	791
14:00	16.58	.039	871
15:00	13.57	.058	639
16:00	5.39	.031	264
17:00	3.21	.035	158
18:00	4.08	.068	236
19:00	4.46	.015	312
20:00	3.38	.087	184
21:00	.16	.017	7
22:00	.34	.027	15

The Subject Animals

Forty-two female subjects which had delivered a viable offspring in 1989 were selected from the entire "Arashiyama A" population. Their pregnancy status at the point of selection was unknown to me. One of these subjects, Be596671, was the only female who had an offspring, an infant and a neonate. No other subject had three infants in three years. This mother is dealt with separately in the discussion. These animals represented all ranks, parity states, sexes of progeny, troop memberships and age categories as described below:

I selected the focal animals through examination of the South Texas Primate Observatory genealogical record and census, and by consultation with the site Director, Ms. Lou Griffin. Since the list of subjects includes virtually all mothers of two year olds at the Observatory, this is considered a representative sample of the larger population of all Japanese macaques in semi free-range conditions. Table 3.2 lists subjects by census name and then according to the following six demographic and social characteristics:

1) Subject Name: Each subject's name is her census identity. The first two letters are the abbreviated matriline name to which she belongs. These are followed by the birth year of the first recorded female in that given family, her daughter, her daughter's daughter and so on, respectively. The final two digits then represent the birth year of my subject.

2) Sex of 1989 infant: All subjects in my research study had an offspring born in 1989, 19 of these two year olds were female, 22 were male and one of undetermined sex died shortly after the 1991 birth season commenced (early April).

3) Sex of 1990 infant: Fourteen of the total 42 subjects also had an infant born in 1990. Those who did not are given the designated symbol "n/a". Of the 15 one year old infants born, 6 are female and 9 are male, one subject (Be596678) having had male twins.

4) Age: This column indicates the subject's age as either old, average or young. Old animals were those born between the years of 1967 and 1972 inclusively; average were in their breeding prime, born between 1974 and 1981 inclusively, and young were categorized as those born in or between 1982 and 1984. There were 10 old, 19 average and 13 young research subjects.

5) Parity: This category indicates a subject's maternal status, such that she is either multiparous, having had offspring prior to the 1989 birth or primiparous with the 1989 birth being her first. Multiparity accounts for 36 of my subjects and primiparity for 6 of them. The two states are abbreviated in table 3.2.

6) Troop membership: Since there are two separate troops at the Observatory, subjects from both were sampled. In the main troop, 34 subjects fit my criteria for selection (i.e., having a two year old offspring, accessibility for observation) while 8 in the splinter troop were observed.

7) Rank: Within each of the two troops, a social hierarchy is maintained though the status of any individual within it is not usually permanent (Fedigan, 1992). Certain matrilineages tend toward the higher ranking end with regard to other families. Within a matriline, individuals also have a rank order. Occasionally, an individual from a low ranking matriline is accepted as high by the whole troop if that monkey uses political manipulation to ascend the hierarchy (i.e., main troop's alpha male; personal communication with Lou Griffin, 1991). For this study, subjects were ranked according to observed interaction with other troop members. By offering a preferred food item, I could monitor the response of individuals who assumed dominant positions close to the food source. Other monkeys would allow a high ranking individual first access. My observations were then compared for accuracy to the records kept by the site director. Rank is certainly neither absolute nor static but is an indicator of a monkey's social position at the time of study. I have accorded each of my subjects the designation of either high, medium or low rank as social actors within each of the two entire troop structures. There are 11 subjects of high, 14 of medium and 17 of low rank within the social hierarchy.

Table 3.2 Demographic and Social Characteristics of Subjects

Subject Name	Sex of: 1989 Infant	1990 Infant	Age	Parity	Troop Membership	Rank	* Group
Be586469	female	n/a	old	multi	main	high	3
Be596671	female	female	old	multi	main	high	-
Be596677	male	male	avg	multi	main	high	2
Be596678	female	male twins	avg	multi	main	high	2
Be596679	male	male	avg	multi	main	high	2
Be586481	female	n/a	avg	multi	main	high	3
Be5966-7984	female	n/a	young	multi	main	high	3
De6575	died	male	avg	multi	main	medium	2
De6581	male	n/a	avg	multi	main	medium	3
De6583	female	male	young	multi	main	medium	2
Ki67	male	n/a	old	multi	main	medium	1
Ki6782	male	n/a	young	multi	main	low	3
Ki6783	male	n/a	young	primi	main	low	1
Ku6570	male	n/a	old	multi	main	low	3
Ku6779	male	n/a	avg	multi	main	low	1
Ku657081	female	n/a	avg	multi	main	low	1
Ku6981	male	female	avg	multi	main	low	2
Ma6068	male	n/a	old	multi	main	low	1
Ma606975	male	male	avg	multi	main	low	2
Ma606978	male	n/a	avg	multi	splinter	low	3
Ma646984	female	n/a	young	primi	splinter	low	3
Me7182	male	n/a	young	multi	main	low	1
Mi6471	female	n/a	old	multi	main	high	3
Mi667284	male	n/a	young	primi	main	high	3
No6270	male	female	old	multi	main	low	2
No6279	female	n/a	avg	multi	main	medium	3
No627083	female	n/a	young	primi	main	medium	3
No6169-7583	male	female	young	multi	main	medium	2
Pe647281	male	n/a	avg	multi	main	low	3
Pk6576	female	female	avg	multi	splinter	high	2
Rh586369	male	n/a	old	multi	main	low	1
Rh5869	female	female	old	multi	main	low	2
Rh626775	female	n/a	avg	multi	main	medium	1
Rh6977	male	male	avg	multi	splinter	medium	2
Rh586981	male	n/a	avg	multi	splinter	medium	1
Rh697782	female	male	young	multi	splinter	medium	2
Rh5863-6983	male	n/a	young	primi	splinter	low	3
Ro69	female	n/a	old	multi	main	high	3
Ro637380	female	n/a	avg	multi	main	medium	3
Ro637382	female	n/a	young	multi	main	medium	3
Ro6684	female	n/a	young	primi	main	medium	3
Sh6479	male	n/a	avg	multi	main	low	1

*See explanation of groups following on page 30.

The number of data hours collected for each of the forty-two subject animals is compiled in Appendix 3, table 1.

Development of the Research Questions

Since affiliative behaviours such as grooming are utilized to strengthen and maintain the bond between nonhuman primate mothers and their offspring (Worlein et al., 1988; Harlow, 1963), this study investigates maternal care patterns in Japanese macaques by way of measuring the amount of time that subject mothers spent engaged in affiliative behaviours with their two year old offspring. In the study species, the spectrum of affiliative activities between mothers and their offspring includes grooming, contact and proximity (Fedigan, 1992; Murray and Murdoch, 1977). Time spent in mother-offspring contact is considered to be an indicator of a close intradyadic bond (Koyama, 1991; Wolfe, 1984). Dyads who maintain a proximity of five metres or less each remain within the visual field of the other. Mothers can respond to the defensive needs of their offspring and can communicate information either vocally or through facial expression and gesturing, whereas with a greater intradyadic distance dyad members become independent of the other's influence (Worlein et al., 1988). Proximity (i.e., intradyadic distancing of 5 metres or less) is considered in this study to be an indicator of maternal care of offspring. These three behavioural variables are indicators of maternal care of the two year old offspring under the different social conditions that are tested in this study.

The behaviour categories of mother-offspring interactions are as follows:

1) Grooming: This category includes only mother to offspring grooming.

2) Contact: Recorded when mother and offspring were physically touching.

3) Proximity: All data collected when mother and offspring were within five metres of each other are included in this category.

4) Conflict: These data include all observed intradyadic agonistic events which include pinching, restraining, threatening and weaning. For detailed definitions of these behaviours, refer to Appendix 1.

The first three categories, the quantitative and affiliative behaviours form the basis for the statistical analysis. The fourth, conflict, is the qualitative, agonistic category and is discussed descriptively and independently of the other three in the discussion.

The subjects were divided into four groups according to the number of progeny each had within two years of age and whether each produced a neonate in 1991during the study period. Groups one, two, and three comprise the data for statistical analysis. In addition, there is a single subject, Be 596671,who had three infants within three years (i.e., in 1989, 1990, and1991). I

have included the data from Be596671 in the discussion as a qualitative description and separately from the three groups that were tested statistically.

Group one is comprised of those ten subjects who had no further offspring than the one produced in 1989. Group two includes the thirteen subjects with both 1989 and 1990 born offspring. The remaining group involves the subjects who experienced a birth in 1991. Group three includes eighteen monkeys who have both 1989 and 1991 born offspring.

Table 3.3 Group Membership

Nonpregnant Group One	Nonpregnant Group Two	Pregnant Group Three
Ki67	Be596677	Be586469
Ki6783	Be596678	Be586481
Ku6779	Be596679	Be59667984
Ku657081	De6575	De6581
Ma6068	De6583	Ki6782
Me7182	Ku6981	Ku6570
Rh586369	Ma606975	Ma606978
Rh626775	No6270	Ma646984
Rh586981	No61697583	Mi6471
Sh6479	Pk6576	Mi667284
	Rh5869	No6279
	Rh6977	No627083
	Rh697782	Pe647281
		Ro69
		Ro637380
		Ro637382
		Ro6684
		Rh58636983

The third year of life (i.e., commencing at second birthday) is a transitional state for Japanese macaques who are neither infant nor juvenile (Fedigan, 1992). This study focusses on mothers with youngsters of this age who are within Dunbar's second stage of development (refer to Chapter two, page 16). Whereas infants are still receiving much of their daily nutrition by suckling, two year olds are able to consume the diet characteristic for the species and spend much time actively foraging, usually in proximity to their mothers. During this third year, "offspring" rapidly become increasingly independent, spending more time in peer groups and away from mothers. By the beginning of the third year and sometimes earlier, they are completely weaned and come into contact with mothers less frequently during the daylight hours than previously (personal observations, 1991 and 1992). In order to identify possible changes in the behaviour of the mother-offspring dyad during the course of this transitional period, I divided the data into two study periods. The birth season was considered as a possible factor for intradyadic change (Ehardt, 1987), while those dyads who experienced a birth were expected to show altered interaction patterns (DiGregorio, G. et al., 1987; Lyon, M. et al., 1985).

The highest concentration of 1991 births within the troop occurred near mid-April (S.T.P.O census). In accordance with this birth activity, nonpregnant subject samples were assigned to the arbitrary "a" pre-birth season (February 20 to April 15th inclusive), or to the remaining "b" birth season period (April 16 through May 26). The samples of the 18 subjects who delivered 1991 infants were designated individually as "a" or "b", pre- or post-parturition. In the tables, the group number is followed by either an "a" or "b" to designate this pre-parturition or post-parturition study period.

Table 3.4 illustrates the distribution of the total data file (156.00 -3.54 = 152.46 hours) over the three groups. The two time periods, designated as pre-birth season (or pre-parturition) and birth season (or post-parturition) are compared by hours of observation. The precise number of observational hours per group and study period are listed.

Table 3.4 Total Data Hours by Group and Study Period

Group	Hours	Mean(hrs/ behaviour)	Standard Deviation	Variance	All Mother-Offspring Behaviours
Entire Population	152.46	.019	.046	.002	8156
1a	17.06	.021	.043	.002	801
1b	19.47	.019	.043	.002	1031
2a	22.55	.021	.053	.003	1094
2b	25.42	.017	.042	.002	1497
3a	46.19	.020	.056	.003	2345
3b	21.79	.016	.028	.001	1388

Data were collected in order to answer four research questions which evaluate the effects of birth season and subsequent birth on intradyadic interactions by measuring amounts of time mothers spent with offspring in each of the three affiliative behaviours, grooming, contact and proximity .

The first question investigates the effect of birth season on affiliative intradyadic interactions (i.e., grooming, contact and proximity) within those dyads consisting of only a nonpregnant mother and her two year old (i.e., group one). This hypothesis necessitates an effect of birth season activity (i.e., a decrease in affiliative behaviours) on all mothers of two year olds , not just those who produced neonates during the study. This explanation is supported by Ehardt's (1987) study in which nonpregnant mothers without dependent infants were found to associate at birth-season with non-kin new mothers and their neonates more often than members of their own matriline. The study did not address the effect, if any, of birth season on maternal care amongst mothers with specifically two year old offspring. Since these dyads have no additional infants or neonates, it is expected that birth seasonal effects will be most evident in this group of macaques. Any changes observed within these group one dyads at birth season will not

be influenced to a substantial degree by ontogeny since the study encompasses only four months. Birth season was assigned to the study period following April 15th as the population's highest concentration of births occurred within this period (S.T.P.O. census). The effect of birth season on mother-offspring dyads is considered in this study since both Worlein et al. (1988) and Ehardt (1987) found differences in maternal behaviour that occurred in conjunction with this period (see Chapter two). In the Worlein et al. study (1988), disruption of the dyad at birth season occurred only if a given mother produced a neonate. Notwithstanding, this study re-examines whether nonpregnant mother dyads undergo similar changes in the intradyadic relationship.

The second research question also deals with the potential change in intradyadic dynamics in conjunction with birth season with the exception being that nonpregnant mothers in these dyads have an additional one year old infant (i.e., group two). Birth season effects were tested by comparing the affiliative behaviours of these group two dyads before and at birth season.

The third research question deals with the effect of subsequent birth on mother-offspring interaction. The alternative hypotheses were generated from the nonhuman primate literature on this topic (e.g. DiGregorio et al., 1987; Golopol, 1979; Lee, 1983; Lyon et al., 1985). The overall prediction is a decrease in intradyadic affiliative behaviours following parturition (DiGregorio et al., 1987). The eighteen pregnant subject dyads (i.e., group three) were observed prior to and following delivery of their neonates. Each subject could have a different parturition date so data was assigned to either study period (pre-parturition ,"a", or post-parturition ,"b") according to the date of each individual's delivery.

These questions deal with intradyadic dynamics between the two study periods, pre-parturition or pre-birth season and post-parturition or birth season. The individuals in each of the three groups are consistent between the two study periods, sample size is small and distribution of the data is unequal in all cases so these related samples (i.e., same animals in both period "a" and "b") for each question are treated using the Wilcoxon matched-pairs statistical test (Siegal and Castellan, 1988).

Question four is concerned with the continuity of maternal care patterns between those nonpregnant mothers with an additional infant (group two) and those with only the two year old offspring (group one). It is possible that the presence of the one year old infant is disruptive to the intradyadic relationship since a given mother's time budget is divided between two progeny rather than just one (i.e., the two year old). Furthermore, the literature indicates some marked decreases in intradyadic affiliative behaviour associated with the birth of a neonate in other monkey species (e.g., DiGregorio et al., 1987) but it is unclear whether disruption to the dyad persists over the long term. Perhaps the mother-one year old infant relationships that were disrupted by the subsequent births in 1990 had regained their former strength a year later , in 1991, when the

yearlings reached two years of age. The data are compared over the entire study rather than separately by each study period (pre-birth season "a" and birth season "b") since both groups are members of the same population and are therefore exposed to similar environmental and social elements. In order to test for significant differences in maternal care between group one and group two, these independent samples (i.e., different subjects in group one and group two) are subjected to the Mann-Whitney U statistical test. As in the previous three questions, sample sizes are small and data are unequally distributed which warrants the utilization of non-parametric statistics (Siegal and Castellan, 1988).

Group three, the pregnant-mother dyads, are not compared with either of groups one or two as the data are not consistent between pregnant subjects and those that were non-pregnant. Pregnant subject dyads were observed before and after parturition whereas data from the non-pregnant dyads were divided into the two study periods by the arbitrarily set date of April 15. It would be of interest to investigate the difference in maternal care between pregnant mothers and those who are non-pregnant but this study limits the analysis to comparison of nonpregnant groups and the comparison of maternal care before and following birth season or parturition (see Limitations of the Research, Chapter six).

The data are converted to percentages for analysis, due to the unequal amounts of data between the two study periods and between individual subjects (see Limitations of the Research, Chapter six). The affiliative behavioural data (i.e., grooming, contact and proximity to two year old offspring) for each subject in a given study period was divided by her total observational time in all behaviours within the same given study period and then multiplied by one hundred in order to achieve the percentage of a subject's time budget spent in a particular (i.e., grooming, contact or proximity) affiliative intradyadic behaviour. These percentages were calculated for each subject using the following formula:

$$\frac{\text{Sum (mins)of a Behaviour (pre-birth*, birth season*, or all) data for given subj.} \times 100}{\text{Total mins. data for that subject (pre-birth*, birth season*, or all)}} = \%$$

*pre-parturition and post-parturition in the case of group three

Data converted into percentage format by subject are presented in similar table form for the purpose of statistical analysis.

Finally, the results of the significance tests are given which reject or fail to reject each hypothesis. Research questions one, two and three involve related samples; that is, the same subjects are compared between the pre-birth season (pre-parturition), "a", (to April 15, inclusive) and the later birth season (post-parturition), "b", (April 16 to May 26) in order to examine the possibility of change in dyadic relationships. The null hypothesis of no significant change in dyadic relationships for these three questions was assessed using the Wilcoxon matched-pairs

signed-ranks test. A negative rank occurs when a given percentage value is greater in the early ("a") as compared to the later ("b") study period. A positive rank occurs when a given percentage value is less in the pre-birth as compared to the birth season period. Ties indicate instances in which pre-birth (pre-parturition) and birth season (post-parturition) percentages are equal.

Question four involves unrelated samples; two different groups of subjects are compared over the entire study. This question determines whether or not the additional infant in group two changes the relationship within the mother-offspring dyad. The Mann-Whitney U test was employed in order to evaluate the directional differences exhibited. In all statistical tests used for this analysis, the level of significance was set at 0.05 which is the accepted level for behavioural studies within the social sciences (Siegel and Castellan, 1988). Data analysis was achieved through the SPSS 5.O statistical software program. Tables were incorporated into the text using Microsoft Word 4.0 and the graph was produced by the SPSS graphics sub-program.

Research Questions

For the purposes of this study:

Offspring= two year old (1989 born)

Infant= one year old (1990 born)

Group 1a= pre-birth season; mother and offspring (10 dyads)

1b= birth season; same 10 mother and offspring dyads

Group 2a= pre-birth season; mother, offspring and infant (13 dyads)

2b= birth season; same 13 mother-offspring dyads with infants

Group 3a= pre-parturition; pregnant mother and offspring (18 dyads)

3b= post-parturition; same 18 mother-offspring dyads with neonates

1. Is there a change in pattern of maternal care of offspring between the pre-birth season (Feb. 21-April 15 , "a") and the birth season (April 16-May 26, "b") within those dyads with only a two year old (group 1)?

Hypotheses:

(1)Ho: There is no difference in the amount of time spent grooming.

(2)Ho: There is no difference in intradyadic contact time.

(3)Ho: There is no difference in time spent in intradyadic proximity.

(USE WILCOXON MATCHED-PAIRS TEST)

2. Is there a change in pattern of maternal care of offspring between the pre-birth season (Feb. 21-April 15, "a") and the birth season (April 15-May 26, "b") within those dyads with an additional one year old infant (group 2)?

Hypotheses:

(1)Ho: There is no difference in the amount of time spent grooming.

(2)Ho: There is no difference in intradyadic contact time.

(3)Ho: There is no difference in time spent in intradyadic proximity.

(USE WILCOXON MATCHED-PAIRS TEST)

3. Within group 3, is there a change in pattern of maternal care of offspring in the pregnant mothers between pre-parturition ("a") and post-parturition ("b")?

Hypotheses:

(1)Ho: Intradyadic grooming time does not change following birth.

H1: Mothers groom offspring less following birth.

(2)Ho: Intradyadic contact does not change following birth.

H1: Mothers and offspring spend less time in contact following birth.

(3)Ho: Intradyadic proximity does not change following birth.

H1: Mothers and offspring spend less time in proximity following birth.

(USE WILCOXON MATCHED-PAIRS TEST)

4. Is there a difference in pattern of maternal care of offspring between mothers with only a two year old (group 1) and those who also have a one year old infant (group 2)?

Hypotheses:

(1)Ho: There is no difference in time spent grooming offspring between group 1 and group 2.

H1: Group 1 spends more time grooming offspring than group 2.

(2)Ho: There is no difference in intradyadic contact time between group 1 and group 2.

H1: Group 1 spends more time in intradyadic contact than group 2.

(3)Ho: There is no difference in time spent in intradyadic proximity between group 1 and group 2.

H1: Group 1 spends more time in intradyadic proximity than group 2.

(USE MANN-WHITNEY U TEST)

CHAPTER FOUR

Results

Mothers of two-year-olds spend a large part of their time involved in activities such as grooming and maintaining close proximity to their offspring. From the data obtained in this project, percentage values indicate that these mother-offspring dyads spend approximately 20.7% of their time within five metres of proximity. The remaining 79.3% of the monkeys' time budget is comprised of individual non-dyadic activity, independent of my study's focus. Within this 20.7% figure are the smaller percentage activities of grooming, contact and conflict. These behaviours together with proximity represent the total dyadic interaction witnessed over the course of 152.46 hours.

For each of the four research questions, raw data are presented in table format. The letter "a" beside group numbers 1 and 2 designates the pre birth-season period of the data collection, February 21 to April 15, 1991 inclusive. A "b" following group numbers 1 and 2 indicates the birth season period which was April 16 to May 26, 1991 inclusive. For group 3, "a" and "b" designate pre- and post-parturition, respectively, for individual subjects. The first column lists the subjects within a given group, second is the grooming results, third is contact, and then proximity, each behaviour's data divided into the two study periods, "a" and "b". The last column lists the total number of data minutes for each subject within the given study period and group. Many subjects have a different number of total data minutes, largely due to the time constraints of the study. Within the four possible months of data collection, subjects gave birth and /or temporarily disappeared, rendering total minutes of data unequal between subjects. The results of the four research questions follow:

Research Question 1: Is there a change in pattern of maternal care of offspring between the pre-birth season (Feb. 21-April 15 , "a") and the birth season (April 16-May 26, "b") within those dyads with only a two year old (group 1)?

Group one is comprised of those ten subjects who had only a two year old offspring born in 1989. The second year of life is known to be a transitional one for youngsters in which they change from a state of semi-dependence on the mother into self-sufficient, independent individuals (Fedigan, 1992). Question 1 concerns the possibility of intradyadic change over the course of the four month study. Without the presence of an additional, younger sibling, two year olds are presumed to maintain stable relationships with their mothers. The hypotheses reflect this expectation.

The sum of data minutes per subject in each of the three behaviour categories are listed for group one in table 2 of Appendix 3. Raw data (i.e., Appendix 3, table 2) were converted into percentage format using the earlier stated formula (see Chapter three, page 35). The number of minutes of a subject's given behaviour, either grooming, contact or proximity in the "a" or "b" study period was divided by her total minutes of observational data in either "a" or "b" for that subject and then multiplied by one hundred. The resultant percentages in table 4.1 yield the subject's relative amount of time spent in a given intradyadic behaviour.

Table 4.1 Group One: Behavioural Data in Percentages by Subject and Study Period

	Grooming		Contact		Proximity	
Subject	a	b	a	b	a	b
Ki67	0.00	1.80	1.65	17.11	13.40	25.13
Ki6783	0.00	0.00	4.49	2.09	4.49	2.70
Ku6779	1.57	15.65	4.21	28.50	11.64	36.93
Ku65-7081	2.32	5.97	46.29	17.44	46.29	17.44
Ma6068	0.00	0.00	25.75	5.97	30.08	16.36
Me7182	0.00	0.00	2.31	0.53	11.94	2.58
Rh58-6369	0.00	16.23	14.19	25.35	30.36	34.19
Rh62-6775	1.77	0.00	31.29	7.60	56.44	9.32
Rh58-6981	0.00	0.00	0.00	0.17	0.00	4.71
Sh6479	15.54	3.43	23.32	8.22	24.21	18.94

When the pre-birth season was compared to the birth season period, inferential statistics determined whether there was a statistically significant change in relative amount of time spent in intradyadic interaction. The Wilcoxon matched-pairs test was employed for each behaviour category.

(1)Ho: There is no difference in the amount of time spent grooming.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	2	4	4	10
Mean Rank =	2.50	4.00		

Z = -1.1531

2-tailed P = .2489

1-tailed P = .1245

Hypothesis One failed to be rejected, based upon the failure to achieve statistical significance.

(2)Ho: There is no difference in intradyadic contact time.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	6	4	0	10
Mean Rank =	5.83	5.00		

Z = -0.7645

2-tailed P = .4446

1-tailed P = .2223

Hypothesis Two failed to be rejected, based upon the failure to achieve statistical significance.

(3)Ho: There is no difference in time spent in intradyadic proximity.

	Neg.Ranks	Pos.Ranks	Ties	Total Subject
	6	4	0	10
Mean Rank =	6.00	4.75		

Z = -0.8664

2-tailed P = .3863

1-tailed P = .1932

Hypothesis Three failed to be rejected, based upon the failure to achieve statistical significance. There was no significant change in maternal care of offspring during the entire study.

Research Question 2: Is there a change in pattern of maternal care of offspring between the pre-birth season (Feb. 21-April 15, "a") and the birth season (April 15-May 26, "b") within those dyads with an additional one year old infant (group 2)?

Group two is comprised of thirteen individuals, all of whom have a two year old offspring and an additional one year old infant in their care. The one year interbirth interval is approximately a year shorter than the free-ranging norm for Japanese macaques (Wolfe, 1984; Fedigan, 1992). In a semi free-ranging population such as the South Texas Primate Observatory, the resident animals are provisioned as a supplement to foraging and females usually have a higher daily caloric intake than comparable females living in the wild. The result is a higher fertility rate. Question 2 is concerned with the possibility of disruption of a mother-offspring dyad in conjunction with the birth season in those dyads having an additional one year old infant. The hypotheses reflect the prediction of a stable mother-offspring relationship between the pre-birth and the birth season.

The sum of data minutes per subject in each of the three behaviour categories are listed for group two in table 3 of Appendix 3. Raw data were converted into percentage format using the earlier stated formula (see Chapter three, page 35). The number of minutes of a subject's given behaviour, either grooming, contact or proximity in the "a" or "b" study period was divided by her total minutes of behavioural data in either "a" or "b" for that subject and then multiplied by one

hundred. The resultant percentages in table 4.2 yield the subject's relative amount of time spent in a given intradyadic behaviour.

Table 4.2 Group Two: Behavioural Data in Percentages by Subject and Study Period

	Grooming		Contact		Proximity	
Subject	a	b	a	b	a	b
Be59-6677	4.72	0.00	30.24	12.36	30.24	24.73
Be59-6678	0.00	0.00	0.72	10.60	5.36	44.69
Be59-6679	0.68	0.00	2.74	19.13	3.21	26.44
De6575	0.00	0.00	5.36	1.02	9.87	4.56
De6583	7.88	6.30	27.28	17.11	31.31	54.72
Ku6981	1.49	2.97	30.81	9.94	30.81	17.23
Ma60-6975	4.94	0.00	5.78	3.36	6.22	17.01
No6270	0.00	0.00	2.99	2.80	5.36	7.02
No6169-7583	0.00	0.00	0.00	1.33	0.00	1.79
Pk6576	6.74	3.90	18.99	11.72	18.99	16.76
Rh5869	5.79	26.64	11.93	28.64	14.29	28.76
Rh6977	6.09	13.44	9.67	17.61	22.06	25.93
Rh69-7782	0.00	3.57	0.70	20.86	0.70	35.28

When the group two subjects are compared between the pre-birth season and the birth season, inferential statistics determine whether there is a statistically significant change in relative amount of time spent in intradyadic interaction. The Wilcoxon matched-pairs test was employed for each behavioural category.

(1)Ho: There is no difference in the amount of time spent grooming.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	5	4	4	13
Mean Rank =	4.20	6.00		

Z = -0.1777

2-tailed P = .8590

1-tailed P = .4295

Hypothesis One failed to be rejected, based upon the failure to achieve statistical significance.

(2)Ho: There is no difference in intradyadic contact time.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	7	6	0	13
Mean Rank =	6.43	7.67		

Z = -0.0349

2-tailed P = .9721

1-tailed P = .4861

Hypothesis Two failed to be rejected, based upon the failure to achieve statistical significance.

(3)Ho: There is no difference in time spent in intradyadic proximity.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	4	9	0	13
Mean Rank =	5.50	7.67		

Z = -1.6423

2-tailed P = .1005

1-tailed P = .0510

Hypothesis Three failed to be rejected, based upon the failure to achieve statistical significance.

There were no significant changes in the three measures of affiliative maternal care of offspring (i.e., grooming, contact and proximity) during the study in those dyads with an additional one year old infant.

Research Question 3: Within group 3, is there a change in pattern of maternal care of offspring in the pregnant mothers between pre-parturition ("a") and post-parturition ("b")?

Group three is comprised of eighteen subjects who had only a two year old offspring in the early study period but were also pregnant during this time. At birth season, these mothers produced neonates. Question 3 concerns the effect of birth of a neonate on the mother-offspring dyad. Due to the mother's increased caloric expenditure through lactation and time constraints following birth, she will be unable to maintain the level of offspring-focussed care. The mother-offspring pair will be expected to change in dynamic, with an overall decrease in intradyadic interactions. The hypotheses reflect this expectation.

The sums of data minutes per subject in each of the three behaviour categories are listed for group three in table 4 of Appendix 3. These raw data were converted into percentage format using the earlier stated formula (i.e., Chapter three, page 35). The number of minutes of a subject's given behaviour, either grooming, contact or proximity in the "a" or "b" study period was divided by her total minutes of behavioural data in either "a" or "b" for that subject and then

multiplied by one hundred. The resultant percentages in table 4.3 yield the subject's relative amount of time spent in a given intradyadic behaviour.

Table 4.3 Group Three: Behavioural Data in Percentages by Subject and Study Period

	Grooming		Contact		Proximity	
Subject	a	b	a	b	a	b
Be58-6469	1.49	0.00	24.27	0.90	38.84	7.20
Be58-6481	6.82	8.67	33.92	19.13	36.75	28.97
Be5966-7984	5.14	0.00	18.14	0.00	24.41	0.77
De6581	11.05	4.85	29.11	4.85	33.98	9.93
Ki6782	0.19	0.00	3.77	0.00	34.56	5.32
Ku6570	1.06	0.00	3.10	0.00	11.11	0.00
Ma60-6978	0.46	0.00	4.34	3.74	18.96	7.42
Ma64-6984	0.00	0.00	0.00	0.00	0.00	0.00
Mi6471	5.21	0.00	9.16	1.20	9.16	34.62
Mi66-7284	0.00	0.00	0.29	0.00	0.29	7.95
No6279	3.99	0.00	8.85	0.00	11.82	0.84
No62-7083	1.19	23.07	22.52	23.07	59.74	35.96
Pe64-7281	0.68	0.00	8.72	0.13	17.25	5.92
Ro69	0.00	0.00	0.81	8.41	3.46	31.40
Ro63-7380	2.87	0.00	34.69	2.22	35.79	44.48
Ro63-7382	16.72	9.91	51.59	16.88	59.78	35.21
Ro6684	0.69	0.00	10.90	0.00	19.42	20.16
Rh5863-6983	0.00	0.00	0.00	0.00	0.00	0.00

When the pre-parturitional data from group three are compared to the post-parturition period, inferential statistics determine whether there is a statistically significant change in relative amount of time spent in intradyadic interaction. The Wilcoxon matched-pairs test was employed for each behavioural category.

(1)Ho: Intradyadic grooming time does not change following birth.

H1: Mothers groom offspring less following birth.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	12	2	4	18
Mean Rank =	7.00	10.50		

Z = -1.9775

1-tailed P = .0240

The alternative hypothesis is supported by the high level of significance. A decrease in intradyadic grooming is indicated by the higher number of negative ranks (i.e., 12 to 2).

(2)Ho: Intradyadic contact does not change following birth.

H1: Mothers and offspring spend less time in contact following birth.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	14	2	2	18
Mean Rank =	9.14	4.00		

Z = -3.1025

1-tailed P = .00095

The alternative hypothesis is supported by the high level of significance. A decrease in intradyadic contact is indicated by the higher number of negative ranks (i.e., 14 to 2).

(3)Ho: Intradyadic proximity does not change following birth.

H1: Mothers and offspring spend less time in proximity following birth.

	Neg.Ranks	Pos.Ranks	Ties	Total Subjects
	11	5	2	18
Mean Rank =	9.27	6.80		

Z = -1.7581

2-tailed P = .0787

1-tailed P = .0394

The alternative hypothesis was supported, therefore matching theoretical expectations, by the achievement of statistical significance. This result indicates a decrease in proximity based on the larger number of negative ranks (i.e., 11 to 5).

The hypotheses in Question three indicate a significant change in the pattern of maternal care of offspring in those dyads which experienced a birth during the study.

Research Question 4: Is there a difference in pattern of maternal care of offspring between mothers with only a two year old (group 1) and those who also have a one year old infant (group 2)?

Group one mothers have only one offspring, whereas those in group two have a one year old infant in addition to the two year old. Whether or not these mothers interact similarly with their respective offspring is the focus of question 4. The mother-offspring dyads of group two may spend less time in intradyadic interaction. The infant would be a major factor in such a discrepancy due to it's mother's necessary division of maternal care between that infant and its two year old sibling. Group one mothers are expected to devote more of their time to caring for the offspring, as the alternative hypotheses suggest. However, the accessibility to a stable food source in this semi free-range population may in fact allow females to care for more than one offspring without suffering substantial "fitness" consequences. Mothers who can produce and successfully rear more offspring are thereby increasing their own reproductive fitness.

Refer to tables 2 (group one) and 3 (group two) in Appendix 3 for the sums of behavioural data minutes per subject in each of the three behaviour categories for the entire study (i.e., "a" plus "b"). Table 4.4 lists the percentage data for group one within each behaviour category. Then table 4.5 lists group two percentage data in similar format.

Table 4.4 Group One: Total Behavioural Data in Percentages by Subject

Subject	Grooming	Contact	Proximity
Ki67	0.86	9.04	19.01
Ki6783	0.00	3.46	3.72
Ku6779	11.09	20.64	28.75
Ku657081	4.14	31.91	31.91
Ma6068	0.00	14.44	22.25
Me7182	0.00	1.55	7.93
Rh586369	9.28	20.57	32.55
Rh626775	1.01	21.14	36.26
Rh586981	0.00	0.10	2.76
Sh6479	8.27	14.25	21.05

Table 4.5 Group Two: Total Behavioural Data in Percentages by Subject

Subject	Grooming	Contact	Proximity
Be596677	2.65	22.40	27.82
Be596678	0.00	7.27	31.43
Be596679	0.46	8.21	10.97
De6575	0.00	3.19	7.21
De6583	7.20	22.92	41.34
Ku6981	2.68	13.98	19.86
Ma606975	2.12	4.39	12.39
No6270	0.00	2.91	6.07
No6169-7583	0.00	0.67	9.01
Pk6576	5.01	14.55	17.63
Rh5869	14.92	19.25	20.63
Rh6977	10.37	14.28	24.31
Rh697782	2.04	12.22	20.46

Using the Mann-Whitney U test, group one was compared with group two in order to test the three hypotheses.

(1)Ho: There is no difference in time spent grooming offspring between group 1 and group 2.

H1: Group 1 spends more time grooming offspring than group 2.

Mean Rank	**Cases**	**Group**
11.60	10	1
12.31	13	2

Exact 2-tailed P = 0.8315

Corrected for ties

Z= -0.2534

1-tailed P= .4000

The null hypothesis one failed to be rejected.

(2)Ho: There is no difference in intradyadic contact time between group 1 and group 2.

H1: Group 1 spends more time in intradyadic contact than group 2.

Mean Rank	**Cases**	**Group**
12.80	10	1
11.38	13	2

Exact 2-tailed P.= 0.6482

Corrected for Ties

Z= -0.4961

1-tailed P= .3099

The null hypothesis two failed to be rejected.

(3)Ho: There is no difference in time spent in intradyadic proximity between group 1 and group 2.

H1: Group 1 spends more time in intradyadic proximity than group 2.

Mean Rank	Cases	Group
12.80	10	1
11.38	13	2

Exact 2-tailed P.= 0.6482

Corrected for Ties

Z= -0.4961

1-tailed P= 0.3099

The null hypothesis three failed to be rejected. Therefore, there was no statistically significant difference in maternal care between groups one and two as demonstrated by the results of the three tests above.

CHAPTER FIVE

Discussion

The discussion is comprised of three sections. First, the results of the four research questions are discussed with special attention given to the observational data of individual subjects that do not fit within the pattern for that given group as a whole. Possible explanations are examined which may account for such idiosyncracies, based on a given subject's status (i.e., refer to table 3.2) within her troop. Findings are related to the questions raised in Chapter two of the thesis regarding where Japanese macaque mothers fall within the range of parental investment strategies adopted for their two year old offspring following the subsequent birth of a neonate.

Next, conflict data which were collected during the study are described for group three. They only suggest possible trends in mother-offspring agonistic behaviour since all instances are events, measured in frequency. The other three behaviour categories are states, measured in minutes of duration. Frequencies are also extremely low, disallowing the application of inferential statistics. Conflict directed at the two year old offspring, as a behaviour category is considered in this study as a qualitative description of non-affiliative intradyadic interactions and another possible parental investment strategy.

Finally, the single female, Be596671, is discussed within the parameters of all four behaviour categories (i.e., including conflict). Since this macaque delivered three neonates in three years, she does not fulfill membership in any of the three groups but her ongoing care of all three youngsters is of interest. Her data is presented descriptively in percentages and compared with that from the three groups in order to speculate on which mother-type Be596671 most closely resembles, if any.

Implications of the Analysis

The results for research question 1 determined that two year olds without younger siblings and their mothers (i.e., group 1) had a stable relationship which was not affected to any statistically significant degree by the birth season activity (i.e., period "b"). Since the age of two years is a transitional year, one in which offspring achieve independent survivability, it is probable that the major increase in offspring independence from mother occurs later in the year. Two year old Japanese macaques fall within Dunbar's second ontogenetic stage (1988, refer to page 16), and operate within the Piagetian "preoperational " period of cognition. By the end of the third year (i.e., by the third birthday), Japanese macaques achieve independence as fully integrated troop members (Fedigan, 1992) which coincides with the termination of Dunbar's second

ontogenetic stage. Independent three year olds correspond to Piaget's third "concrete operations" period. Therefore within the third year of life, youngsters of the study species move from a period of partial reliance, including nutritional supplementation through nursing, upon their mothers (i.e., "preoperational" period) to complete independent troop living (i.e., "concrete operations period). Offspring during this study were barely two years of age (i.e., 21 to 27 months old, fromFebruary to May, 1991) so the expected offspring behaviour is more characteristic of a two rather than a three year old. Youngsters closer to the age of three are much larger and more gregarious than they are at their second birthday (personal observations, 1991 and 1992), an observation which conforms to theoretical expectations based on Piaget's cognitive periods (1971) and Dunbar's ontogenetic stages (1988).

The overall time spent in intradyadic interaction did not change to a statistically significantly degree at birth season but the proportion of affiliative behaviours changed. Whereas group one members spent an average of 2.12% of their time grooming offspring in the pre-birth season, this changed to 4.31% at birth season, a percentage increase of 197.6%. It is noteworthy that although grooming behaviour almost doubled from the pre-birth season to the birth seaon, it still only occupied 4.31% of group one mothers' daily time budget. Furthermore, only four of the ten group one members increased the amount of time spent in intradyadic grooming and there is no evidence in the literature to suggest that increased intradyadic grooming is a predicted consequence of overall increased troop activity (personal observations 1991 and 1992) during birth season.

Intradyadic proximity and contact were more conclusive indicators of the maternal care pattern as mothers spent a greater percentage of their time in these behavioural categories (i.e., approximately 23% in proximity and 15% in contact). The data for contact and proximity indicate a decrease at birth season in six of the ten group members. Time spent in contact showed a decrease of 26.4% at birth season, from 15.35% to 11.3%. Proximity time decreased to 16.83% from 22.89% or a percentage decrease of 26.5%. There was no statistically significant change in intradyadic interaction associated with birth season however. The decreases observed in the affiliative behaviours of contact and proximity may be an artifact of the limited observation time and sample size but appear to correspond to the effects of subsequent birth on mother-offspring dyads in other monkey species (Chism, 1986; Lyon et al., 1985; Berman, 1984; DiGregorio et al., 1987). Further research could determine whether birth season does in fact affect nonpregnant mother-offspring dyads since Ehardt's study (1987) found nonpregnant females to associate with non-kin mothers and their neonates more frequently than members of their own kin during the period of birth season.

Only two subjects in group one had female two year old offspring. The data for these individuals, Ku657081 and Rh626775, correlate well with that of the other eight mothers with

male offspring (refer to table 4.1, page 39). This dyad similarly experienced marked decreases in both contactand proximity (i.e., 46.29% to 17.44%, a decrease of 165.1% in each of the two behaviours) behaviours and an increase in grooming activity (i.e., 2.32% to 5.97%, an increase of 157.3%). Therefore, in this group of nonpregnant mothers with only two year old offspring, sex of the offspring does not appear to be a factor in maternal care. This finding correlates with Tanaka's (1989) study of free-ranging Japanese macaques in which mothers did not vary the maternal care patterns of infants (i.e., up to one year of age) according to sex of their infant.

Results of research question 2 indicate that group two dyads also maintained stable relationships between the pre-birth season and the birth season. The statistical analysis indicated no significant alteration in intradyadic interaction at birth season (i.e., period "b"). Since age two is a transitional year, it is probable that the major increase in offspring independence occurs later in the year (refer to research question one, above). These dyads have already experienced the addition of a neonate a year earlier and yet their mother-offspring relationships remain intact. This finding conforms to a tendency toward life-long matrilineal bonding within the study species (Fedigan, 1992; refer to Chapter two, page 13).

Group two averages increased in all three affiliative behaviour categories but there is tremendous individual variation as indicated by five subject mothers who reduced their time spent in grooming offspring while four others increased this behaviour and another four mothers were never observed in intradyadic grooming (refer to table 4.2, page 41). Proximity time declined in four dyads but increased in the other nine. Average grooming time for group two increased by 48.1%, from 2.95% to 4.37%, at birth season but it was an equitably distributed spectrum of intradyadic grooming patterns amongst the group member dyads. There was no conclusive change of this behaviour in either direction (i.e., increase or decrease) at birth season.

Contact time increased slightly from 11.32% to 12.04%, a percentage increase of 6.4%. Time spent in proximity increased by 71.0%, from 13.72% to 23.46%. These behaviours indicate a theoretical trend toward increased affiliative intradyadic interaction at birth season within group two although statistical significance was not achieved. The increase at birth season in time spent in intradyadic proximity within group two dyads may be a strategy adopted by two year old offspring to encourage maternal care while their mothers are instead devoting time to non-kin mothers with neonates (Ehardt, 1987). This explanation is supported by contextual notes that recorded the relatively frequent (i.e., as compared to the pre-birth season) phenomenon of offspring loudly vocalizing from a distance of five metres or less while staring at their mothers who were within social groups of all adult females or mothers with neonates (personal observations, 1991).

The five mothers who had female offspring (i.e., Be596678, De6583, Pk6576, Rh5869 and Rh697782) were not observed to differ from those mothers with male offspring in type or amount of maternal care bestowed upon their offspring (refer to table 4.2, page 41). Therefore, within group two, there does not appear to be a sex difference in intradyadic dynamics which conforms to the theoretical predictions of Tanaka (1989) and Nakamichi (1989) based on their independent studies of free-ranging Japanese macaques.

Results from question 3 which investigated the effect of subsequent birth on eighteen mother-offspring dyads indicate that these group three dyadic relationships were altered in the post-parturitional period (i.e., "b"). The birth of the neonate resulted in some immediate changes within the mother-offspring dyad. Offspring spent less time with mothers in the post-parturition period and were observed in peer association more often (i.e., personal observations, 1991).

Inferential statistics determined that mothers in group three significantly decreased the time spent grooming their two year old offspring following parturition (refer to page 43). While pregnant mothers groomed their offspring for an average of 3.20% of their time, these grooming episodes occupied only 2.58% of their daily time budget following parturition. This is a decrease of 19.4%. Similarly, these dyads experienced a statistically highly significant decrease in contact time following their delivery of a neonate. Each dyad was observed in contact for a group average of 14.68% of the mothers' time budget in the pre-parturition study period (i.e., "a") but following the birth of a neonate, contact amounted to only 4.47% of the mother's time. This is a percentage decrease of 69.6%! Finally, the intradyadic proximity observed in the pre-parturition study period was also significantly reduced as indicated by the statistics in the post-parturition period, from 23.07% to 15.34%, a percentage decrease of 33.5%.

As hypothesized in the literature for other monkey species (Chism, 1986, for *Erythrocebus patas* ; DiGregorio et al., 1987, for *Macaca mulatta* ; Holman et al., 1982, and Golopol, 1979, for *Macaca mulatta* ; Lyon et al., 1985, for *Callimico goeldii* ; Lee, 1983, for *Cercopithecus aethiops* ; Singh and Sachdeva, 1977, for *Macaca radiata*), the effect of a subsequent birth is disruptive to an established mother-two year old offspring dyad, resulting in decreases in all affiliative behaviour categories (i.e., grooming, contact and proximity).

Two subject mothers, Ma646984 and Rh58636983, were never observed in proximity to their offspring (refer to table 4.3, page 43). Both of them were nervous around other monkeys, avoiding all but close kin members. They were also young (i.e., 7 and 8 years of age, respectively) and primiparous prior to the pregnancy in 1991, the two year old offspring having been their first babies. Parity is a known factor in the competence shown in mothering skills for all primates and mortality rates are higher in infants of primiparous mothers (Berman, 1984; Collinge, 1987). The two year olds of these two subjects were vigorous nevertheless which may be a consequence of

the stable semi free-range environment in which there is accessible food and defensive protection provided by other members of that offspring's matrilineal kin group (Fedigan, 1992).

Ma646984 resided in a peripheral group of males, one of whom was her brother (S.T.P.O census information). Her offspring was never seen during focal animal sampling and it was assumed to have died before commencement of data collection. However, during my last two days at the field site, Ma646984 was consistently seen accompanied by a two year old. This subject had previously moved away from her brother's group in the last few weeks of pregnancy to rejoin the main troop. It appears that her reunion with her offspring was associated with the return to her home troop. This offspring exhibited an unusual degree of maternal independence.

In the other situation, Rh58636983 was a member of the splinter troop and had two sisters with whom she regularly associated. She was the most difficult of the sisters to observe, moving quickly away when approached by a human or higher ranking monkey. It seems plausible that either the offspring spent most of his time near his aunts instead of his mother, or else he was as nervous as she was and reacted to human proximity by independently fleeing the immediate area. The offspring of Rh58636983 was known to be alive since he was observed in contact with his mother several times at nightfall (personal observations, 1991) but never during data collection.

Eleven mothers of group three had female offspring, seven had male. There were no apparent differences in affiliative maternal care patterns care between mothers of either-sexed two year olds as predicted in the literature by two studies of free-ranging Japanese macaques (Tanaka, 1989; Nakamichi, 1989). In the two anomalous cases of absent offspring discussed earlier, one was female and the other was male so the abandonment of the two year olds was not related to a sex-linked difference in maternal care.

The results from question four which investigated potential differences in maternal care of two year old offspring between those mothers with only a two year old (group one) and those with an additional one year old infant (group two) failed to achieve statistical significance. Group one mothers were found to be similar to those in group two, even though group two mothers had an additional infant in their care. This similarity in maternal care between these two groups is especially relevant since the results of research question three for group three established a highly significant correlation between parturition and the reduction in affiliative intradyadic behaviours. Since group three mothers decreased their overall time spent with offspring following delivery, it seems plausible that this effect (i.e., decreased affiliative intradyadic interaction following parturition) would also occur with those mothers who had one year old infants (group two) when their neonates were born. The negative effect (i.e., decreased affiliative behaviours) of neonatal interference in the dyadic relationship must be only temporary since

these group two mothers had resumed a close relationship with their two year old offspring by the time their subsequent infant was one year old. The data support this assumption. By the age of two years, the mother-offspring relationship had returned to one which is characteristic of all mother-offspring dyads. The infant, although receiving substantial maternal care, does not have a statistically significant effect on the relationship of its two year old sibling with the mother. The former intradyadic alteration that occurred at parturition is negated by the time the new baby reaches one year of age and the offspring is two (refer to page 46). This may be a unique phenomenon of semi free-range populations since mothers in this stable environment ingest sufficient calories to afford maternal care of two offspring. Mothers who produce a second neonate within a year are also maximizing their reproductive fitness as are their offspring who in some cases act as allomothers (Hiraiwa, 1981; Eaton et al., 1986). Older siblings enjoy fitness benefits through their genetic relatedness to their infant siblings (i.e., 1/2), especially since they (i.e., two year old offspring) are still several years away from sexual maturity (McKenna, 1979).

The amount of time spent in intradyadic interaction between group one and group two was not statistically significant in any of the three affiliative behaviour categories (refer to tables 4.4 and 4.5 on page 45). For grooming, group one spent an average of 3.47% of their time in the activity while group two spent 3.65%. This is a percentage difference of only 5.1%. Contact periods occupied 13.71% of group one dyads and 11.26% of those in group two, a percentage difference of 21.8%. Time spent in proximity amounted to 20.62% for group one and 19.16% for group two, a percentage difference of 7.6%. The difference in contact time between the two groups, though not statistically significant, is nonetheless worth noting as it is the most variant of the three affiliative behaviour categories. If there is in fact less contact time between group two mothers and their offspring, this is most likely due to the mother's time constraints caused by having two youngsters in her care rather than one (i.e., group one). Further study could determine whether this apparent trend in contact is significant.

Results of the present study suggest that the loosening of the mother-offspring bond following parturition may be only a temporary phenomenon. There were no significant differences found in affiliative intradyadic behaviours of those subjects with only two year olds compared to those with an additional one year old infant. The dyads that experienced birth of a neonate in 1991 were subject to the effects of subsequent birth a year prior to the present study. Over the next year, however, the mother-offspring bond regained its strength. By the time of this study, mothers with two year olds showed a characteristic relationship, regardless of whether or not they also had a one year old infant in their care. This consistency in mother-offspring behaviour may also be indicative of mothers and three year olds, so that those relationships disrupted by a neonate in 1991 may in fact show no significant difference a year later from similar dyads in which mothers did not give birth. This prediction is based on the fact that Japanese macaque families

(i.e., mother and her progeny) are often bonded for life, especially females with matrilineal kin (Fedigan, 1992; Ehardt, 1987).

In order to determine whether two year olds with new siblings (i.e., group three) experience permanent reductions in allocated maternal care, the intradyadic relationship needs to be continuously observed over the year following mother's parturition. It is possible that although the mother-offspring relationship has stabilized a year after a sibling birth, this is only the case when the offspring is two years old. The patterns of maternal care for three year old juveniles and their mothers may vary in correlation to the addition of a neonate the year before. Intradyadic relationships undergo changes in their dynamics as ontogeny progresses toward adulthood (Dunbar, 1988) but the mother-offspring bond probably remains strong based upon the species-specific tendency toward long-term bonds within matrilineal kin groups in Japanese macaques (Fedigan, 1992; Nakamichi, 1989)).

It would be difficult to measure differences in mother-juvenile dyadic relationships since a three year old Japanese macaque is independent and self-sufficient (refer to Piaget's "concrete operations" period, page 17). A characteristic mother-three year old dyad would probably be unaltered by the presence of younger siblings as the juvenile is not reliant upon the mother for survivability even though this species retains close ties with mothers in the long term, often permanently (Fedigan, 1992). A three year old juvenile would be useful as an allomother which is in both mother and juvenile's best interest from a "reproductive fitness" point of view (McKenna, 1979). I frequently observed three year olds in the presence of older and younger siblings and mothers, huddling together during bad weather and at nightfall (i.e., personal observations).

The age of attained independence is dependent upon other factors too, including the sex of an infant. Although no differences were found in intradyadic conflict according to sex of the infant, some affiliative behaviours including grooming and contact appear to be more frequent between mothers and daughters (Nakamichi, 1989; Fairbanks and McGuire, 1985; Wheeler, 1982). However, no major sex differences in mother-offspring care have been found in studies of wild groups where sample sizes are large enough to permit a quantitative comparison (Nicolson, 1982; Altmann, 1980). This possibility of differential maternal care according to the sex of the infant would prove a worthy topic for further research investigation.

Intradyadic Conflict

Mothers and offspring engaged in four categories of behaviour during the study period. The three affiliative behaviours, grooming, contact and proximity, were statistically analysed. The fourth behaviour category represents all intradyadic agonistic (i.e., conflict) events that were observed. In general, conflict events occurred infrequently and instantaneously. Although the affiliative categories provide the best indication of mother-offspring dynamics surrounding the

birth season due to their prevalence in mothers' daily time budgets (i.e., in this study, 20.7% of subject mothers' time was spent in intradyadic interactions) , conflict episodes are noteworthy in group three which experienced subsequent birth given Trivers' (1974) predictions. He speculated that intradyadic conflict would increase in frequency following a subsequent birth since the two year old offspring would continue to seek maternal care while the mother would terminate care of the self-sufficient offspring in order to invest in her neonate.

The following table 5.1 summarizes the frequencies of intradyadic conflict during total minutes of observation pre-parturition ("a") and then in the post-parturitional period ("b").

Table 5.1 Frequency of Conflict for Group Three in the Pre-parturitional ("a") and Post-parturitional ("b") Study Periods

Study Group/ Period	Frequency of Conflict Episodes	# Dyads Involved	Total Mins. Observed
3a	12	11	2771.47
3b	9	3	1307.22

Group Three was observed for 52.8% less time in the post-parturitional than in the pre-parturitional study period. Twelve episodes of conflict involving eleven dyads, out of a possible eighteen, occurred in the pre-parturitional period. Following parturition, nine episodes occurred involving three dyads. There was an apparent reduction in the incidence of conflict but this number must be examined within the constraints of the observational periods. Since period "b" is approximately one half the size of period "a", a conflict frequency value of one half that of period "a" would suggest a consistency in mother-offspring agonism during the study. The numbers instead indicate that nine, not six, episodes were observed post-parturition. Two out of three subjects involved in period "b" conflict were also in the data for period "a". The perceived trend is an increase in conflict episodes, not a decrease as the raw numbers suggest, for the group in the post-parturitional period.

The effect of a neonate on group three intradyadic conflict may increase the frequency of agonistic events though this was not tested for in the present study. There was an apparent increase in the number of conflict events in conjunction with the birth of the new baby. At the same time, the increase was not substantial so any neonatal effect is only speculative. Trivers' (1974) suggested that weaning represents conflicting agendas between a mother who seeks to produce and invest in a subsequent infant and her offspring who seeks to maximize its own fitness by maintaining maternal care (i.e., nutritional and protective) while still relatively small.

In this study, neonates who necessitate constant maternal care prevented offspring from being held, carried and nursed by the mother. Following parturition, offspring, who had until the birth supplemented their diets by suckling, were immediately cut off from that nutritional source. Their mothers actively prevented access to the nipple and were observed to conflict with offspring by pushing, hitting or biting them (personal observations, 1991). This offspring-directed agonism allowed the mother to invest in the dependent infant without compromising the survival of the self-sufficient, if reluctant,offspring. This qualitative account supports Trivers' (1974) hypotheses regarding parent-offspring conflict.

These findings regarding conflict behaviour necessitate further research in order to provide a statistically valid conclusion. Overall, the occurrence of conflict events was sporadic (i.e., a total of only 21 events for group three) and the group three individuals involved often were not consistent over the two study periods (pre-parturition and post-parturition). The most important aspect of this study's conflict data is that it indicates a relative paucity of agonistic dynamics within mother-offspring dyads. Thus, conflict behaviour appears to be a less reliable indicator of the dyadic relationship than are affiliative behavioural measures of grooming, contact and proximity.

Be596671

The data for this subject are summarized for each affiliative behaviour in table 5.2. There was only one observed instance of conflict within this dyad which occurred in the pre-parturitional study period.

Table 5.2 Be596671: Behavioural Data in Minutes by Study Period

Study Period	Grooming	Contact	Proximity	Total mins.of Observational Data
a	31.85	60.88	90.78	171.47
b	0.00	0.00	9.58	40.65

In order to descriptively compare her with data from group three, the minutes spent in each behaviour category are converted to percentages in table 5.3 using the formula given in Chapter three on page 35.

Table 5.3 Be596671: Behavioural Data in Percentages by Study Period

Study Period	Grooming	Contact	Proximity
a	18.57	35.50	52.94
b	0.00	0.00	23.57

This subject spent 18.57% of her time grooming her offspring in the pre-parturitional period. Following the arrival of the neonate, intradyadic grooming ceased, a 100% drop in the activity. Group three registered a statistically significant decrease (i.e., 19.4%) in grooming of offspring so the pattern of grooming activity for Be596671 closely resembles that of group three. The effect of sibling birth has a much greater adverse effect in the single case however (i.e., Be596671).

Intradyadic contact suffered a similar fate in the post-parturitional period, a decrease of 100%. Be596671 went from spending 35.5% of her time in contact with her offspring to none following delivery. Again, as in grooming, Be596671 closely resembles group three's highly significant decrease in intradyadic contact time following birth. The effect is even greater in this individual.

The time spent in intradyadic proximity was 52.94% during pregnancy for Be596671 and this number decreased to 23.57% following parturition, a percentage decrease of 55.5%. In a comparison, Be596671 closely resembles group three which experienced a significant 33.5% decrease in proximity following parturition.

Conflict data for Be596671 indicate that there was only one episode within the dyad during the entire study. This occurred in the pre-parturitional period. Such a behavioural rarity can only allude to a near absence of agonism within the dyad. This observation does not fall within the predictions of Trivers (1974) due to the relative absence of conflict even after the neonate arrived and also since the one conflict event that did occur took place in the pre-parturitional period when maternal care was not yet divided between the offspring and the neonate. The qualitative information provided by this single subject, Be596671, could be tested using a larger subject group of mother-offspring dyads with both an additional infant and a neonate. Further research would necessitate observations within the semi free-range, as opposed to a free-range, situation in which a one year interbirth interval is not uncommon (S.T.P.O census).

Be596671 appears to pattern her behaviour closely to group three, at least in the affiliative behaviour categories. This is a reasonable possibility since the eighteen subjects in group three also delivered neonates during the study. It appears that the presence of a one year old infant does not confound the intradyadic dynamic that occurs as a result of subsequent sibling

birth although further research is necessary in order to test this apparent phenomenon. The accessibility of a stable food source in the semi free-range situation affords females greater reproductive fecundity than in the free-range situation where food is not always readily available (Fedigan, 1992).

CHAPTER SIX

Conclusion

This research project was designed to pursue two specific goals. The first was to determine the effect of a neonatal sibling upon established mother-two year old offspring dyads. The maternal care patterns of pregnant mothers toward their two year old offspring were compared with those following parturition. The second goal was to determine whether birth season has an effect on mother-offspring relationships. In order to explore this possibility, the two groups of nonpregnant mother dyads (i.e., those with only offspring and those with an additional infant) were independently compared between pre-birth season and birth season. Statistical tests did not indicate a difference in maternal care of offspring between these two nonpregnant groups. Birth season was identified as the period characterized by the bulk of 1991 births within the whole population (S.T.P.O census).

The pregnant subjects significantly decreased the time spent with offspring following parturition. The change in time spent together is most likely due to the mother's increased parental workload which does not allow her to attend to the demands of the two year old as previously. The offspring is thereby encouraged to spend an increasing amount of time away from its mother and to establish relationships with peers . Since the mother is not motivated to attend to this older sibling, its independence is enhanced (Altmann, 1980). Births most adversely affected the contact pattern of mother-offspring dyads in this study. The single subject, Be596671, who was also pregnant, appeared to follow the pattern of decreasing offspring care associated with the arrival of her neonate. Marked decreases occurred in all affiliative behaviours. In support of those affiliative behaviour statistics, descriptive conflict data for group three indicate a tentative marginal increase in the number of intradyadic conflict episodes in the post-parturition period. The mother is less likely to expend energy on an already self-sufficient offspring, disciplining it when it attempts to utilize her resources in such activities as nursing (Trivers, 1974).

The effect of subsequent birth upon a dyad is to loosen its ties, resulting in a re-structuring of the maternal care time budget to allocate less time to two year old offspring and a great deal to the dependent neonate. The arrival of the neonate signals the termination of high caloric expenditures such as nursing of the two year old. Less energy-costly activities, such as dorsal carrying, may continue at a reduced rate. Further, the neonate's presence will accelerate natural ontogenetic processes already occurring within the two year old resulting in its increased mastery of survival skills like predator avoidance and food acquisition. This is demonstrated by the greater independence observed in offspring with neonatal siblings as

compared to those whose mothers were not pregnant. The neonate appears to be a catalyst in the inevitable re-structuring of the mother-offspring relationship as a result of ontogeny.

Whether or not the intradyadic change is permanent necessitates further study which would record the intradyadic interaction pattern over the course of the year following sibling birth. It is probable that the dyad regains some of its affiliative dynamic since Japanese macaques habitually maintain close ties to their mothers in the long-term. However, the intradyadic relationship may not fully recover with time since the offspring is becoming increasingly independent as it matures. In addition, the sex of the offspring influences the relationship in the long-term since females tend to maintain close ties with matrilineal kin whereas males peripheralize towards adolescence and eventually emigrate in free-range Japanese macaque populations (Nakamichi, 1989).

Birth season effects on nonpregnant mother dyads were not found to be significant in either those mothers of only two year olds offspring or those with additional one year old infants. Affiliative behaviour patterns were maintained over the course of the study though in group one (i.e., only two year olds), their proportions altered at birth season. Grooming time doubled but persisted as only small increment of mothers' daily time budgets while contact and proximity decreased by approximately twenty-six percent. This implies that mothers were maintaining contact, rather than the offspring. Further study could determine whether this apparent phenomenon of altered behaviour proportions is consistent at birth season. If so, perhaps the two year old who is attempting to reduce interaction with its mother, is an unwilling object of her increased maternal care behaviour at birth season.

In group two, mothers with an additional one year old infant, there was an apparent increase in all three affiliative behaviours but the results were not statistically significant and therefore inconclusive. Further research of these mothers would determine whether in fact birth season has the effect of increasing maternal care toward the two year old though this seems unlikely since these mothers also have one year old infants in their care. In addition, Ehardt (1987) found an increase in non-kin interactions between nonpregnant females and new mothers (refer to page 49).

Mother-offspring dyads enjoy stable relationships in the four months surrounding their second birthdays. Two year olds have characteristic, predictable interaction patterns with their mothers regardless of whether they have one year old siblings or not. The results from this study clearly indicate that the one year old infant is not a catalyst for mother-two year old offspring intradyadic change, at least in the early months surrounding birth season. Continuous ontogenetic processes ultimately affect the dyadic relationship (Higley and Suomi, 1986) but are not a major factor in alteration of mother-offspring relationships until the youngster is at least twenty-seven months of age (personal observations, 1991 and 1992).

Mothers who deliver neonates develop an altered behaviour pattern with offspring at parturition that results in a distancing of the dyad members who now spend less time in proximity. The type of interactions also changes, with a drop in contact being the most significant effect. The amount of time spent in intradyadic grooming decreases to a lesser degree, indicating the continuity of bond-enhancing activities and therefore of the bond.

During the second birth season following its own birth, an offspring maintains its established closeknit relationship with mother. The exception to this rule occurs if the offspring's mother delivers a neonate within this birth season. In such a case, the intradyadic relationship loosens, interactions decrease, and the offspring spends a greater amount of time alone and in the company of peers than other offspring without neonatal siblings do. However, separation does not occur between a Japanese macaque mother and her two year old offspring except during the few hours associated with the mother's labour and subsequent delivery of the neonate (Fedigan, 1992; refer to Chapter two, page 18). These findings do not appear to be affected by the sex of the two year old offspring within each dyad.

In Japanese macaques, maternal care is an ongoing, ever-changing commitment by mothers who spend considerable time interacting with any and all of their female and often, male, offspring well into adulthood and oftentimes for life (refer to Chapter two, page 12). This species-specific tendency for lifelong bonding of matrilineal kin groups (Fedigan, 1992) supports the findings of this study that indicate temporary disruptions to mother-offspring relationships only in conjunction with the arrival of a neonate. These include decreases in intradyadic affiliative behaviours and tentatively, slight increases in conflict though overall intradyadic agonism was rare and therefore not statistically treated. New additions to the family unquestionably alter the intradyadic dynamic to a significant degree but these changes do not weaken the mother-offspring bond in the long term.

Limitations of the Research

This research project is limited by a number of complications that arose both in the field and later during the stage of data analysis. Some of these problems are unavoidable, due to the nature of the semi free-range situation which allows its residents voluntary migration within and outside of the fifty-acre enclosure. Other problems could not be circumvented within the confines of the research design but could be prevented in future field studies with the additional knowledge gained by the endeavour. I will explain these limitations in some detail according to whether they were site-related or analysis-related.

Site-Related Limitations The field site is comprised of a fifty-acre fenced enclosure located within a larger, naturalistic area that is home to the splinter troop of monkeys. In addition, two supply trailers, several holding cages and a ploughed field of grain are in the immediate vicinity. The fence is regularly scaled by the monkeys who easily escape over the top and forage outside. The entire main troop often leaves the enclosure, especially during times of drought and predator menace.

Many times I had a focal animal sample in progress which was interrupted by the subject's unexpected departure from the enclosure. If possible, I continued to follow unless she moved into dense brush and became lost. The monkeys would often use this time outside of the enclosure to forage at greater distances for novel food items (i.e., prickly pear cactus). The threat of predation is greater outside and the monkeys behave accordingly, acting nervously and scanning the visual field continuously. Any unfamiliar noise will cause them to ascend into the trees where they also frequently become invisible.

The splinter troop usually responded to the main troop's exit by temporarily migrating into the enclosure. A sample of a splinter subject could be similarly disrupted by this sudden movement. The splinter troop members also frequented the space under the trailers where it was sometimes difficult to distinguish the identity of the focal animal from her companions. In these cases, samples were sometimes aborted to retain accuracy of the data.

As the spring became warmer, the adjacent field of grain sprouted and became a target foraging zone for both troops. The monkeys again were nervous to be in an unfamiliar part of the ranch, and responded by keeping a good distance (i.e., at least fifty metres) from humans. It was often difficult to assess the intradyadic proximity of a focal subject to her offspring and the sample was delayed.

Although my strategy was to sample the animals on a rotational basis, this was sometimes over-ridden by the accessibility of only a few subjects when another scheduled subject was absent for several days or longer. The basic tenets of the rotational system were adhered to but when necessary, I proceeded on to the next subject in hopes of retrieving lost time spent in fruitless searching. The absent subject would then be sampled as soon as possible to her re-entry into the troop.

The above difficulties experienced during observations should be negated by the imminent transfer of the entire monkey population in the next two years. A suitable re-location site has been aquired and enclosed by a "monkey-proof" electric fence. There is also a dependable source of fresh water and diversity and abundance of natural forage that will remove the reliance on external sources of sustenance. Predators are prevented from entering the enclosure by way of the same barrier fencing.

My method of data collection involved the use of a field computer which I found to present a number of problems. Firstly, the screen became heated by sunlight and many times the batteries went dead within a few seconds of a "hot-spot" showing up on the screen. New batteries would not simply remedy the problem since the computer itself would remain hot and any batteries inserted would immediately lose their power. The only solution was to remove the computer from the heat and bright light for at least one hour. The next section highlights computer-based analysis complications.

Analysis-Related Limitations Each evening following a day in the field, I transferred my data via disk-drive from the field computer onto a disk for later analysis. Each sample had to be transferred independently of the others from that day so this was a tedious daily process. Later on, after my return from Texas, the data had to be re-entered by each day's data into the original field computer. From there the data, again by each day's collection, was uploaded into the university computer system in order for analysis to be executed.

The data itself had been recorded into the field computer in a format which is not workable using any spreadsheet method of organization. I then manually, line by line of data, transposed the information into the appropriate form. At this point, data analysis could commence. Though I do not dismiss the field computer as a method of data collection, I strongly advise the researcher to scrutinize the software available to determine whether its potential efficiency is marred by logistical problems at the analysis stage.

The use of a computer program such as the one utilized for this study negates the recording of contextual notes. I carried a notebook into which I inserted relevant information and the time at which it occurred regarding daily environmental and social situations that could affect the quality of the data being collected. The extra time needed to record notes in a separate format (i.e., pencil and paper) from the data cancelled the efficiency advantage of computer data-inputting.

The time constraint of five months on the field site was a governing factor in the amount of data I was able to collect prior to and during birth season. Ideally, I would allow an equal amount of focal samples and therefore data minutes per subject in both study periods for direct comparison in the analysis. This would preclude the need to convert all data into percentages of total time budget spent in each activity as I have done in this study. Also, each subject who produced a neonate would be observed following parturition for the same number of samples as were collected for her during pregnancy.

In this study, pregnant mother dyads could not be compared with their non-pregnant counterparts due to the individual parturition dates of each subject and the arbitrarily set cut off date for the pre-birth season. In addition, these groups were not compared in the post-

parturitional period for the same reason. A further study could confirm the difference between offspring-directed maternal care following birth and that for nonpregnant dyads during the same study period by comparing this post-parturitional data with data from the nonpregnant subjects

It would be of interest to determine whether pregnancy itself has an effect on mother-offspring dyads. In order to accomplish this, nonpregnant mothers would necessarily be compared to those who were pregnant . A direct comparison could be performed if each nonpregnant control was compared with one pregnant subject of similar mother-type (e.g., age, rank, parity, troop membership). When a given female delivered, accumulated data on each female (i.e., subject and control) would be accepted for the analysis based on the largest data base shared by both subjects. The group of subject-control pairs (e.g., 10 non-pregnant, 10 pregnant) would then be statistically compared by utilization of the Wilcoxon matched-pairs test to determine significance of any observed difference. Each subject and control would have a given amount of data that was directly comparable to the others (e.g., eight thirty-minute samples collected between January and April, a nonpregnant control sampled right after her pregnant counterpart).

Overall, this study revealed the durability of the mother-offspring bond in the Japanese macaque, a continued affiliation which persists beyond the subsequent births of at least two younger siblings. Mother-offspring conflict, though perhaps temporarily increased at parturition, is a rare occurrence without long-term consequences for the dyad. This maternal care pattern could be factored into considerations of long-term parental investment for *Macaca fuscata*.

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APPENDIX 1 The Ethogram

*Chapter 3 has collapsed several ethogram activity codes into the larger behaviours of grooming (ethogram codes 20-22), contact (no distance between dyad members) and proximity (intradyadic distance of 0.1-5.0 metres) for the purpose of data analysis. The discussion similarly categorizes conflict (includes pinching restraining, threatening and weaning of two year old). Criteria used to differentiate juveniles and infants on the computer program apply to this study only.

*j	juvenile	-a young monkey born in 1986, 1987 or 1988.
*i	infant	-a young monkey born in 1989, 1990 or 1991 (birth year follows activity code)

Activity code:	Activity:	Definition:
1) biaf	bite adult female	-close jaws with force on body of adult female.
2) bii	bite infant	-close jaws with force on body of infant.
3) bij	bite juvenile	-close jaws with force on body of juvenile.
4) ch	chew	-manipulation of jaws repeatedly.
5) chsaf	chase adult female	-run fast in the direction of an adult female.
6) chsam	chase adult male	-run fast in the direction of an adult male.
6) chsi	chase with infant	-run fast with an infant in contact in the direction of another animal.
7) chsj	chase juvenile	-run fast in the direction of a juvenile.
8) chsv	chase vervet	-run fast in the direction of a member of the other resident primate species.
9) ci	carry infant	-locomote with an infant in contact, either riding dorsally or clinging ventrally.
10) clf	climb fence	-ascend a wire mesh barrier by using hands and/or feet.
11) clt	climb tree	-ascend tall plant by using hands and/or feet.
12) dr	drink	-ingestion of water by lowering the face to water surface with mouth open.
13) ep	eat provisions	-ingestion of food items provided by Observatory staff.
14) epaf	eat provisions adult female	-ingestion of food items provided by Observatory staff while in contact with an adult female.

15) epam	eat provisions adult male	-ingestion of food items provided by Observatory staff while in contact with an adult male.
16) epj	eat provisions juvenile	-ingestion of food items provided by Observatory staff while in contactwith a juvenile.
17) fg	forage	-moving slowly through an area, intermittently picking up and ingesting bits of plant material.
18) graf	groom adult female	-methodically comb through the fur of an adult female, extracting debris.
19) gram	groom adult male	-methodically comb through the fur of an adult male, extracting debris.
20) gri	groom infant	-methodically comb through the fur of an infant, extracting debris.
21) griam	groom infant	-methodically comb through the fur of an infant, extracting debris, while in contact with an adult male.
22) grij	groom infant	-methodically comb through the fur of an infant, extracting debris, while a juvenile is in contact.
23) grj	groom juvenile - juvenile	-methodically comb through the fur of a juvenile, extracting debris.
24) grs	groom self	-methodically comb through subject's own fur, extracting debris.
25) grsaf	groom self adult female	-methodically comb through subject's own fur, extracting debris, while in contact with an adult female.
26) grsam	groom self adult male	-methodically comb through subject's own fur, extracting debris, while in contact with an adult male.
27) grsj	groom self juvenile	-methodically comb through subject's own fur, extracting debris, while in contact with a juvenile.
28) hi	hold infant	-actively grasp infant against subject's own body, while stationary.
29) hiaf	hold infant adult female	-actively grasp infant against subject's own body, while stationary, while in contact with an adult female.
30) hiam	hold infant adult male	-actively grasp infant against subject's own body, while stationary, while in contact with an adult male.
31) nui	nurse infant	-feed milk to infant by way of its suckling.

32) nuiaf	nurse infant adult female	-feed milk to infant by way of its suckling, while an adult female is in physical contact.
33) nuiam	nurse infant adult male	-feed milk to infant by way of its suckling, while an adult male is in physical contact.
34) pij	pinch juvenile	-squeeze with force of juvenile's flesh.
35) rb	rub	-roll an object between the palms.
36) rchsaf	receive chase adult female	-(see chase) from an adult female.
37) rchsam	receive chase adult male	-(see chase) from an adult male.
38) rchsi	receive chase infant	-(see chase) from an infant.
39) rchsj	receive chase juvenile	-(see chase) from a juvenile.
40) resi	restrain infant	-pull back an infant towards subject, increasing proximity.
41) rgraf	receive groom adult female	-(see groom) from an adult female.
42) rgram	receive groom adult male	-(see groom) from an adult male.
43) rgri	receive groom infant	-(see groom) from an infant.
44) rgrij	receive groom infant, juvenile	-(see groom) from an infant and a juvenile.
45) rs	rest	-sit or lay motionless with eyes closed.
46) rsaf	rest adult female	-sit or lay motionless with eyes closed, in contact with an adult female.
47) rsafam	rest adult female, adult male	-sit or lay motionless with eyes closed, in contact with an adult female and an adult male.
48) rsafj	rest adult female, juvenile	-sit or lay motionless with eyes closed, in contact with an adult female and a juvenile.
49) rsam	rest adult male	-sit or lay motionless with eyes closed, in contact with an adult male.
50) rsj	rest juvenile	-sit or lay motionless with eyes closed, in contact with a juvenile.

51) rthaf	receive threat adult female	-(see threaten) from an adult female.
52) rtham	receive threat adult male	-(see threaten) from an adult male.
53) rthdog	receive threat dog	-(see threaten) from a resident dog.
54) rthj	receive threat juvenile	-(see threaten) from a juvenile.
55) ru	run	-quadrupedally locomote rapidly.
56) sun	suck nipple	-manipulate nipple of self with mouth and tongue.
57) sv	survey	-while sitting or standing, gaze over visual field intently.
58) svaf	survey adult female	-while sitting or standing, gaze over visual field intently, while in contact with an adult female.
59) svam	survey adult male	-while sitting or standing, gaze over visual field intently, while in contact with an adult male.
60) svj	survey juvenile	-while sitting or standing, gaze over visual field intently, while in contact with a juvenile.
61) thaf	threaten adult female	-stare with eyebrows raised at adult female.
62) tham	threaten adult male	-stare with eyebrows raised at adult male.
63) thi	threaten infant	-stare with eyebrows raised at infant.
64) thiaf	threaten, infant adult female	-while holding infant, stare with eyebrows raised at adult female.
65) thj	threaten juvenile	-stare with eyebrows raised at juvenile.
66) vo	vocalize	-emit sounds through the mouth, characteristic of the species.
67) wa	walk	-to locomote quadrupedally at a deliberate pace.
68) waj	walk juvenile	-to locomote quadrupedally at a deliberate pace, with a juvenile walking close beside.
69) wegi	wean gently infant	-a calm but determined push away of an infant who attempts to nurse.
70) weri	wean roughly infant	-an abrupt swat or pull off, given to an infant attempting to nurse.
71) ws	wet self	-partial or total immersion in water.

APPENDIX 2 Offspring and Neonates

Subject	Sex of 1989	Birthdate	Sex of 1991	Birthdate
1. Be586469	f	June 7	f	April 12
2. Be596671	f	April 13	-	May 20
3. Be596677	m	April 29	n/a	
4. Be596678	f	June 20	n/a	
5. Be596679	m	May 21		
6. Be586481	f	May 10	m	May 1
7. Be59667984	f	May 13	-	May 22
8. De6575	m(died)	May 5	n/a	
9. De6581	m	July 5	m	April 27
10. De6583	f	May 26	n/a	
11. Ki67	m	April 4	n/a	
12. Ki6782	m	May 15	f	April 19
13. Ki6783	m	?	n/a	
14. Ku6570	m	July 4	f(stillborn)	April ?
15. Ku6779	m	April 23	n/a	
16. Ku657081	f	May 26	n/a	
17. Ku6981	m	June 16	n/a	
18. Ma6068	m	April 17	n/a	
19. Ma606975	m	April 13	n/a	
20. Ma606978	m	June 9	f	May 11
21. Ma646984	f	May 12	f	May 12
22. Me7182	m	May 15	n/a	
23. Mi6471	f	June 25	m	April 27
24. Mi667284	m	May 9	f	April 12
25. No6270	m	July 1	n/a	
26. No6279	f	May 26	f	April ?
27. No627083	f	May 5	m	April 18
28. No61697583	m	June 12	n/a	
29. Pe647281	m	June 22	f	May 14
30. Pk6576	f	May 29	n/a	
31. Rh586369	m	May 14	n/a	
32. Rh5869	f	May 25	n/a	

33. Rh626775	f	June 6	n/a	
34. Rh6977	m	April 19	n/a	
35. Rh586981	m	July 4	n/a	
36. Rh697782	f	July 5	n/a	
37. Rh58636983	m	May 10	m	April 14
38. Ro69	f	May 3	m	April 23
39. Ro637380	f	June 3	f	April 13
40. Ro637382	f	May 27	f	May 3
41. Ro6684	f	June 23	m	May 12
42. Sh6479	m	May 6	f	May 13

APPENDIX 3 Raw Data Tables

Table 1 Total Data Hours by Subject

Subject	Hours	Mean(hrs/ behaviour)	Standard Dev'n	Variance	All Mother-Offspring Behaviours
Entire Population	156.00	.019	.046	.002	8318
Be5966-7984	3.50	.016	.027	.001	215
Be586469	3.45	.018	.034	.001	192
Be586481	3.50	.018	.032	.001	190
Be596671	3.54	.022	.044	.002	162
Be596677	3.40	.017	.028	.001	205
Be596678	3.09	.015	.024	.001	203
Be596679	4.05	.021	.084	.007	213
De6575	3.00	.013	.020	.000	236
De6581	4.02	.014	.024	.001	286
De6583	3.50	.021	.043	.002	168
Ki67	3.14	.019	.036	.001	167
Ki6782	4.38	.021	.061	.004	213
Ki6783	3.49	.023	.043	.002	148
Ku6570	4.67	.020	.068	.005	240
Ku657081	3.01	.033	.061	.004	92
Ku6779	3.77	.015	.026	.001	250
Ku6981	4.34	.030	.099	.010	144
Ma6068	3.50	.022	.038	.002	159
Ma606975	3.50	.016	.023	.001	225
Ma606978	3.29	.015	.026	.001	216
Ma646984	4.02	.012	.016	.000	337
Me7182	3.50	.018	.032	.001	196
Mi6471	3.39	.018	.032	.001	194
Mi667284	3.50	.025	294.	.004	138
No616975	4.40	.025	299.	.006	179
No6270	3.47	.017	304.	.000	210
No627083	4.51	.030	309.	.008	150
No6279	5.71	.018	314.	.005	316
Pe647281	4.56	.021	319.	.002	220
Pk6576	4.26	.025	324.	.002	168
Rh586369	3.50	.019	329.	.001	189
Rh5869	3.42	.020	334.	.001	176
Rh586981	4.12	.022	339.	.002	187
Rh626775	3.50	.016	344.	.001	215
Rh6977	3.59	.016	349.	.001	230
Rh697782	3.50	.015	356.	.001	234
Rh5863-6983	0.58	.028	357.	.003	21
Ro637380	3.53	.020	364.	.001	181
Ro637382	3.50	.021	369.	.001	165
Ro6684	4.51	.017	374.	.004	270
Ro69	3.36	.018	379.	.001	189
Sh6479	5.00	.022	384.	.006	229

Table 2 Group One: Behavioural Data in Minutes by Subject and Study Period

Subject	Grooming		Contact		Proximity		Total mins. data	
	a	b	a	b	a	b	a	b
Ki67	0.00	1.62	1.62	15.40	13.17	22.62	98.25	90.00
Ki6783	0.00	0.00	5.35	1.88	5.35	2.43	119.12	90.00
Ku6779	1.15	23.95	3.08	43.63	8.52	56.53	73.22	153.07
Ku65-7081	2.10	5.37	41.93	15.70	41.93	15.70	90.58	90.00
Ma6068	0.00	0.00	23.22	7.13	27.13	19.63	90.18	120.00
Me7182	0.00	0.00	2.77	0.48	14.33	2.32	120.00	90.00
Rh58-6369	0.00	19.48	12.77	30.42	27.32	41.03	90.00	120.00
Rh62-6775	2.12	0.00	37.55	6.83	67.73	8.38	120.00	89.92
Rh58-6981	0.00	0.00	0.00	0.25	0.00	6.82	102.53	144.87
Sh6479	18.65	6.18	27.98	14.82	29.05	34.15	120.00	180.28

Table 3 Group Two: Behavioural Data in Minutes by Subject and Study Period

Subject	Grooming a	Grooming b	Contact a	Contact b	Proximity a	Proximity b	Total Data Minutes a	Total Data Minutes b
Be59-6677	5.40	0.00	34.62	11.05	34.62	22.10	114.48	89.37
Be59-6678	0.00	0.00	0.45	13.03	3.35	54.93	62.50	122.90
Be59-6679	1.23	0.00	4.93	17.27	5.78	23.87	180.00	90.27
De6575	0.00	0.00	4.82	0.92	8.88	4.10	90.00	90.00
De6583	9.45	5.67	32.73	15.40	37.57	49.25	120.00	90.00
Ku6981	0.75	6.22	15.53	20.88	15.53	36.18	50.40	210.00
Ma60-6975	4.45	0.00	5.20	4.03	5.60	20.43	90.00	120.08
No6270	0.00	0.00	3.57	2.48	6.40	6.22	119.42	88.60
No6169-7583	0.00	0.00	0.00	1.77	0.00	2.38	131.02	133.07
Pk6576	6.70	6.08	18.88	18.27	18.88	26.13	99.43	155.88
Rh5869	6.68	23.98	13.78	25.78	16.50	25.88	115.47	90.00
Rh6977	5.48	16.82	8.70	22.03	19.85	32.45	90.00	125.13
Rh69-7782	0.00	4.28	0.63	25.03	0.63	42.33	90.00	120.00

Table 4 Group Three: Behavioural Data in Minutes by Subject and Study Period

Subject	Grooming a	Grooming b	Contact a	Contact b	Proximity a	Proximity b	Total mins. data a	Total mins. data b
Be58-6469	1.28	0.00	20.83	0.27	33.33	8.72	85.82	121.08
Be58-6481	8.18	7.80	40.70	17.22	44.10	26.07	120.00	90.00
Be5966-7984	9.25	0.00	32.65	0.00	43.93	0.23	180.00	30.00
De6581	16.63	4.40	43.80	4.40	51.13	9.00	150.45	90.63
Ki6782	0.30	0.00	6.05	0.00	55.42	5.45	160.35	102.47
Ku6570	2.98	0.00	8.67	0.00	31.13	0.00	280.12	0.00
Ma60-6978	0.63	0.00	5.97	2.23	26.10	4.43	137.68	59.68
Ma64-6984	0.00	0.00	0.00	0.00	0.00	0.00	181.23	59.87
Mi6471	6.33	0.00	11.12	0.98	11.12	28.38	121.40	81.98
Mi66-7284	0.00	0.00	0.35	0.00	0.35	7.15	120.38	89.90
No6279	11.28	0.00	25.00	0.00	33.38	0.50	282.48	59.85
No62-7083	2.15	20.57	40.83	20.57	108.30	32.07	181.28	89.18
Pe64-7281	1.25	0.00	15.95	0.12	31.55	5.35	182.95	90.37
Ro69	0.00	0.00	0.98	6.83	4.17	25.50	120.57	81.22
Ro63-7380	3.50	0.00	42.33	2.00	43.67	40.00	122.03	89.93
Ro63-7382	25.12	5.93	77.52	10.10	89.83	20.72	150.27	59.85
Ro6684	1.30	0.00	20.65	0.00	36.80	16.37	189.50	81.20
Rh5863-6983	0.00	0.00	0.00	0.00	0.00	0.00	4.95	30.00