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# Sexual Behavior of Immature Tibetan Macaques (Macaca thibetana)

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SEXUAL BEHAVIOR OF IMMATURE TIBETAN MACAQUES (*MACACA THIBETANA*)

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by

Anne Salow

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Tibetan macaque sociosexual behavior begins in infancy, and comprises many of their initial interactions with other group members as infants. Tibetan macaques possess a large sociosexual behavioral repertoire, including a behavior called bridging, which involves infants and juveniles, and is found in only four species. Immature macaques differ in the types, rate, and partner preferences across a variety of behaviors. This study compared rates of sexual behavior among four age and sex classes of 26 immature Tibetan macaques at Mt. Huangshan, China. A total of 643 sex behaviors were observed and evaluated for 5 parameters: total sex behavior rates, initiation rates, rates of different types of sexual behavior, partner preference, and rates within different social contexts. Nine types of sex behaviors were observed with bridging being the most common ($n$ = 179) and self-genital manipulation being the least common ($n$ = 18)($H_7 = 38.6$, $p < 0.05$). Sex behaviors occurred at the highest rate within spontaneous (2.9 sex behaviors per hour) and play (2.2 sex behaviors per hour) social contexts relative to grooming, aggressive, and self-directed contexts ($H_4 = 72.4$, $p < 0.05$). Generally, younger males

exhibited higher rates of sex behavior relative to other immature classes across all five aspects, and younger females exhibited lower rates of sex behavior relative to other immature classes across all five aspects. Immature Tibetan macaques engage in many sex behaviors with both immature and adult group members. Further studies are needed on the long-term effects of immature sexual behavior regarding its function and influence on social rank and reproductive success.

# ACKNOWLEDGMENTS

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# CHAPTER I

# INTRODUCTION AND LITERATURE REVIEW

## Introduction

Tibetan macaques are the largest sized of the 23 species in the genus *Macaca* (Thierry, 2011; Li, Zhao, & Fan, 2015). Macaques are a taxonomically diverse and geographically widespread primate group characterized by female philopatry, male dispersal, and linear dominance hierarchies in both sexes (Thierry, 2011). Tibetan macaques use social sexual behaviors including penis sucking, mounting, genital inspections and manipulations, and “bridging” behavior, in which one adult uses an infant as a buffer to mediate a social interaction with another adult (Ogawa, 1995b; Zhao, 1993; Hendershott, 2011). Despite possessing this unique sexual behavior, only observed in Tibetan (*Macaca thibetana*), Barbary (*M. sylvanus*), and Stump-tailed macaques (*M. arctoides*) (Deag & Crook, 1971; Estrada & Sandoval, 1984; Ogawa, 1995b), little research on Tibetan macaque sexual behavior has been conducted. The development of sexual behavior in immature wild Tibetan macaques has never before been studied.

Tibetan macaque infants begin to explore their surroundings around one week of age, and gradually break contact with their mothers more often across the first seven weeks of life. By the time an individual is 7-9 months old, it spends the majority of its time associating with group members other than its mother (Deng, 1993). Changes in physical appearance of fur color and hair on the forehead are drastic in the first 5 months of life. Dark hair begins to appear on the foreheads of infants around 3 months of age, and lightens before adult color appears between 4 and 5 months of age (Zhao & Deng, 1988). The onset of physiological aspects that occur during puberty such as sperm viability and first ovulation/menses in Tibetan macaques are not well known, so visible markers of puberty have been used to distinguish developmental stages in the species. Physical development in Tibetan macaques separates sub-adult and young adult males based on canine eruption and wear, body weight, age, and behavior, including ability to ejaculate (Zhao, 1993). Estrus is marked by a slight swelling between the tail and anus in females, but is not reliably detectable (Zhao, 1993). Female Tibetan macaques' first birth occurs around 5 years of age and has been used to determine the onset age of adulthood (Zhao & Deng, 1988).

## Primate Sociosexual Behavior

The idea that nonhuman animals engage in sexual behavior for strictly reproductive purposes is a common misconception of the general public and extends to the scientific community. Given primates' intricate social structure, sexual behavior often begins in infancy and serves social functions that are non-reproductive (Dixson, 2012). Non-conceptive sexual behaviors may be used as practice for reproduction, to confuse paternity, and to communicate in many social primates (*Pan paniscus, Cebus capucinus*, Manson, Perry, & Parish, 1997; *Gorilla gorilla*, Doran-Sheehy, Fernandez, & Borries, 2009; *M. fuscata*, Gunst, Leca, & Vasey, 2013). Just as non-sexual behavioral patterns are incorporated into the courtship rituals of many species, sexual behavior is sometimes also involved in social encounters that are not primarily concerned with reproduction (Dixson, 2012). Sociosexual behaviors are behaviors that are associated with sexual activity but are used socially to mediate fitness-enhancing goals (Lee, 2007). Same-sex mounts and presentations have been commonly documented in many Old World anthropoids including macaques, mandrills, talapoins, mangabeys, red colobus, proboscis monkeys, patas monkeys, langur species and great apes (Dixson, 2012). Ape sociosexual behaviors include mutual genital rubbing and grasping and appear to serve tension-reducing functions in socially volatile situations such as food sharing or intergroup interaction (Dixson, 2012). Sociosexual behaviors including bridging are exhibited by three species within the genus *Macaca* including Tibetan macaques (Deag & Crook, 1971).

Research on sexual behavior in primates including macaques has focused mainly on reproductive tactics of adults. Juvenile and infant behavior has been studied in macaques (*M. radiata*, Simonds, 1974; *M. fuscata*, Eaton, Modahl, & Johnson, 1981) but these studies have given little attention to sexual behavior. Much of what we know about macaque sexual development has come from the experimental manipulation of hormones (Goy, 1988), social environment of rhesus macaques (Harlow, Harlow, Hansen, & Suomi, 1972), observational studies of social development (Eaton, Johnson, Glick, & Worlein, 1986), and sexual development of female Japanese macaques (Leca, Gunst, & Vasey, 2014).

## Development of Sexual Behavior

Many primates begin their lives learning about social relationships through play. This social context has been extremely important in shaping behaviors, including sexual behaviors, in young rhesus macaques, as evidence by infants reared without peers their own age, which do not exhibit a full repertoire of social behaviors exhibited by adults raised with peers (Champoux, Byrne, Delizio, & Suomi, 1992). This sensitivity to early rearing conditions is indicative of the required social elements for acquiring adult sexual behavior. In immature rhesus macaques the appearance of hallmark behaviors of adult sexuality, such as female rigidity and male double-foot clasp, is predictive of adult behavior (Wallen, Zehr, Herman, & Graves, 2003). Play behavior is observed to start around one month of age in vervet monkeys (*Chlorocebus pygerythrus*), bonnet (*M. radiata*), rhesus (*M. mulatta*), and Tibetan macaques *(M. thibetana*) (Deng & Zhao, 1990). Play appears to be a uniquely immature behavior in macaques with the exception of male bonnet macaques, which continue to play in adulthood (Napier & Napier, 1967; cited in Deng, 1993).

The development of sexual behavior involves many changes surrounding puberty, including the onset of adult endocrine function, emergence of adult behavior, and an element of learning and experience (Wallen et al., 2003). Pubertal endocrine activation and the emergence of adult sexuality begin with hormonal changes that change reproductive physiology rapidly. The onset of hypothalamic-pituitary-gonadal axis activity, which remains relatively un-active during infancy and juvenility, marks the beginning of adolescence (Wallen et al., 2003). In both sexes of some species, hormonal changes associated with puberty result in increased sexual interest, solicitation, and sexual activity, in some cases at even greater than levels seen in adulthood (*M. mulatta*, Gordon, 1981; Wallen & Winston, 1984; Zehr, Tannenbaum, Jones, & Wallen, 2000; *Homo sapiens*, Halpern, Udry, & Suchindran 1997; Udry, Billy, Morris, Groff, & Raj, 1985). Adolescents mate more than juveniles and less than adults, and also play more than adults and less than juveniles (*M. fuscata*, Hanby & Brown, 1974; *M. arctoides*, Niewenhuijsen et al., 1988). Other group members often use visible markers of puberty as a signal of changing reproductive status (Wallen et al., 2003). In Stump-tailed macaques (*M. arctoides*), physical changes, such as exaggerated sexual swelling and visible testicular descent, are associated with both changes in behavior of the adolescent and changes in treatment by other adult group members (Nieuwenhuijsen et al., 1988). Prior to testicular descent, young male Stump-tailed macaques mate with adult females without interruption by adult males.

## Sex Differences in Primate Sexual Behavior

Demographic differences in sexual behavior have been documented in non-human primates (*P. paniscus, C. capucinus*, Manson et al., 1997; *M. fuscata*, Tokuda, 1961, Eaton, Johnson, Glick, & Worlein, 1985, Glick, Eaton, Johnson, & Worlein, 1986; *M. radiata*, Simonds, 1974). Many developmental differences between male and female primates are attributable to their different life histories within their society (Wallen et al., 2003). In female philopatric species such as the Tibetan macaque (Berman, Ionica, & Li, 2004), immature males and females prepare to assume different roles as adults. Young males prepare for emigration and alliance formation while young females begin to establish themselves in the matriarchal community and to raise infants (Wallen et al., 2003). In Japanese macaques, sex differences in in play behavior frequencies appear in the first year of life (Eaton et al., 1985), and sex differences in partner preference are apparent in the second year (Glick et al., 1986). Kinship plays a strong role in the partner preference of young Japanese macaques for various behaviors (Glick, Johnston, &

Worlein, 1986). Sex differences in behavior frequencies are apparent in juvenile vervet monkeys and are not predictive of adult differences (Raleigh, Flannery, & Ervin, 1979).

Although Tibetan macaques spend much of their time with their mothers as infants, they are particularly sought-after during the first year of life by other group members for their use in bridging (Ogawa, 1995c). There is a significant sex difference between male and female infants in their involvement in bridges. Adults show a strong preference for male infants, using male infants in bridges 0.43 times per hour, and using female infants 0.04 times per hour (Ogawa, 1995a). Male and female infants experience differential treatment by their mothers and other group members. Female infants are groomed and carried more by their mothers than are male infants, while male infants play more often and are cared for by other group members more often than female infants (Deng, 1993, Deng & Zhao 1991).

## Age Differences in Primate Sexual Behavior

As macaques mature, their activity budgets and frequencies of behaviors (e.g., play, grooming, and social) change. Adult Tibetan macaques spend far less time playing and the frequencies of other social behaviors including sex behaviors are variable between high, medium, and low ranking individuals (Jiang, Li, Sheeran, Sun, Xia, & Wang, 2013). Mounting behavior in particular tends to decrease in frequency with age (Jiang et al., 2013). Especially in sexual interactions, partner preference may change over time. The frequency of heterosexual and homosexual mounts in male Tibetan macaques both decrease with age, with the exception of heterosexual mounts being highest for adult males (Jiang et al., 2013). Japanese macaques gradually acquire adult-like behavioral patterns and gradually lose immature behavioral patterns as they age from juveniles to adults, with a major threshold in behavioral changes occurring at the age of 4 years for females (Leca, Gunst, & Vasey, 2014), and the frequency of mounts directed towards adult females increasing around 2 to 3 years of age for males (Gunst, Leca, & Vasey, 2013). Around puberty, males between 4 and 6 years of age may transition from play and play-related mounting of peers to increasing the frequency of reproductive sexual behavior, as has been documented in male mounting frequencies in Tibetan and Japanese macaques (*M. thibetana*, Jiang et al., 2013; *M. fuscata*, Gunst et al., 2013). The pubertal transition from juvenile to adult behavior in females may be more dependent on anatomical development allowing intromission between 3 and 5 years of age, after which females first give birth and enter adulthood (Zhao & Deng, 1988). This expected transition from play-related sexual behavior to reproductive sexual behavior may also coincide with a change in partner preference from same-sex to opposite-sex for older age classes.

## Social Aspects of Sexual Behavior

Life within a social group requires an understanding of complex individual relationships and behavior interactions. Sexual behavior in particular is controlled by and develops under many biological and environmental factors. Social context is important for many macaque species in shaping behavior and interactions with other individuals. Certain sociosexual behaviors are used for affiliative purposes and to build or maintain relationships. Particularly following aggressive encounters, many species of macaque engage in reconciliatory sexual behaviors to maintain relationships (*M. radiata*, Cooper, Aureli, & Singh, 2007; *M. tonkeana*, De Marco, Cozzolino, Dessa-Fulgheri, &Thierry, 2010; *M. arctoides*, De Waal & Johanowicz, 1993). Presentations and mounts have been linked to rank and aggression in captive Talapoin monkeys (*Miopithecus talapoin*, Dixson, Scruton, & Herbert, 1975). Up to 87% of mounts observed in the population were on lower ranking monkeys that had just been attacked, by the dominant monkeys that attacked them. Reconciliation behavior is rare in other macaque species (*M. mulatta*, De Waal & Johanowicz, 1993; Matheson, 1999). Female rhesus macaques do not spend a higher percentage of time in affiliative contact following aggression relative to percentage of time in affiliative contact following affiliative interactions (Matheson, 1999). Tibetan macaque males reconcile after aggressive encounters often with more affiliative interactions occurring after aggressive conflicts (Berman, Ionica, Dorner, & Li, 2006). In Berman and colleagues' 2006 study, reconciliation behavior was most evident in male-male dyads reflective of a despotic dominance style; however, interestingly aggressors initiated a higher proportion of affiliative interactions after a conflict relative to initiation in other social contexts. Further, males used a wider variety of specialized behaviors (embraces and same-sex mounts) in order to reconcile. (Berman, Ionica, Dorner, &Li, 2006). In Tibetan macaques, non-reproductive copulation often takes place following social conflicts that involve non-lactating females (Li, Yin, & Zhou, 2007). Non-reproductive copulation occurs at a lower frequency; with less frequent ejaculation, less harassment, and shorter mount duration than reproductive copulations occurring within the mating season (Li, Yin, & Zhou, 2007).

Since reconciliation occurs at higher rates between individuals with more valuable relationships (Aureli, 1997), it is likely that the frequency of reconciliation interactions positively correlates with age and consequent increase in societal status. Because of the nature of sexual behavior as a social tool for conflict mediation in Tibetan macaques, younger macaques may initiate and experience fewer reconciliatory sexual behaviors following aggression than their older peers.

## Current Study

This study compares different aspects of sexual behavior among immature age and sex classes in a habituated free-ranging group of Tibetan macaques at Mt. Huangshan, China. This study is structured to address five main hypotheses (Table 1). Sexual behaviors are expected to differ between age and sex classes of immature macaques; in rates of sexual behavior, partner preference, rates of initiation, and social context in which sexual behaviors occur. The hypothesis that sexual behavior should differ between age and sex classes is supported by evidence that as individuals age they begin to learn more behaviors, change their pattern of behavior, and begin to practice more reproductive directed behaviors (Wallen et al., 2003; Jiang et al. 2013). Males and females engage in different types of behavior at different frequencies from infancy to adulthood and behaviors may perform different social functions for each sex (Berman et al., 2006; Glick et al., 1986; Eaton et al., 1985). In addition, at some point in development sub-adults transition into copulating for reproductive purposes; therefore, it is expected that older immature macaques will exhibit higher rates of sexual behavior with opposite-sex individuals than with same-sex individuals, and higher rates of copulation than younger immature macaques.

Table 1

*Hypotheses of Sexual Behavior Variation Among Immature Age and Sex Classes.*

| **Hypothesis** | |
|---|---|
| 1. Total sexual behavior rate | Rate of total sexual behavior should differ between age and sex classes |
| 2. Types of sexual behavior | Rate of each type of sexual behavior should differ between age and sex classes |
| 3. Initiation rates of sexual behavior | Rates of initiation of sexual behavior should differ between age and sex classes |
| 3a. | Older immature age and sex classes should initiate sexual behavior at higher rates than younger immature age and sex classes |
| 4. Social context of sexual behavior | Social context in which the highest rates of sexual behavior occur should differ between age and sex classes |
| 4a. | Older immature classes should exhibit higher rates of sexual behavior within spontaneous contexts than younger immature classes |
| 4b. | Older immature classes should exhibit higher rates of sexual behavior within or following aggression than younger immature classes |
| 4c. | Younger immature classes should exhibit higher rates of sexual behavior within or following play than older immature classes |
| 5. Partner preference in sexual behavior | Partner preference rates should differ between age and sex classes |
| 5a. | Older immature females should prefer older immature males to other age and sex classes as partners in sexual behavior |
| 5b. | Older immature males should prefer older immature females to other age and sex classes as partners in sexual behavior |
| 5c. | Younger immature females should prefer younger immature females to other age and sex classes as partners in sexual behavior |
| 5d. | Younger immature males should prefer younger immature males to other age and sex classes as partners in sexual behavior |

CHAPTER II

JOURNAL ARTICLE

# SEXUAL BEHAVIOR OF IMMATURE TIBETAN MACAQUES (*MACACA THIBETANA*)

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Key words: Tibetan macaque, *Macaca thibetana*, sexual behavior, immature, initiation, partner preference, social context, Huangshan, China

## Abstract

Tibetan macaque sociosexual behavior begins in infancy, and comprises much of their initial interactions with other group members as infants. Tibetan macaques possess a large sociosexual behavioral repertoire, including a behavior called bridging, which involves infants and juveniles and is found in only four species. Immature macaques differ in the types, rate, and partner preferences across a variety of behaviors. This study compared rates of sexual behavior among four age and sex classes of 26 immature

Tibetan macaques at Mt. Huangshan, China. A total of 643 sexual behaviors were observed and evaluated for each class in five aspects: total sexual behavior rates, initiation rates, rates of different types of sexual behavior, partner preference, and rates within different social contexts. Nine types of sexual behaviors were observed with bridging being the most common ($n$ = 179), and self-genital manipulation being the least common ($n$ = 18). Sexual behavior occurred at the highest rate within spontaneous (2.9 sexual behaviors per hour) and play (2.2 sexual behaviors per hour) social contexts. Generally, younger males exhibited significantly higher rates of sexual behavior relative to other immature classes across all five aspects, and younger females exhibited significantly lower rates of sexual behavior relative to other immature classes across all five aspects. Older females and older males exhibited rates that were variably both higher and lower than other age classes across the five aspects.

## Introduction

The complex social structures and hierarchies of primates require an aspect of social learning that is arguably unmatched in other mammal orders. The effects of age, sex, and rank are clearly influential in the expression and use of sexual behavior especially in species with social dominance hierarchies (Aureli, 1997; Cooper, Aureli, & Singh, 2007; Berman, Ionica, Dorner, & Li, 2006, Thierry, 2011). Non-conceptive sexual behaviors may be used as practice for reproduction, to confuse paternity, and to communicate in many social primates (*Pan paniscus, Cebus capucinus*, Manson, Perry, & Parish, 1997; *Gorilla gorilla*, Doran-Sheehy, Fernandez, & Borries, 2009; *M. fuscata*, Gunst, Leca, & Vasey, 2013). Same-sex mounts and presentations have been commonly documented in many Old World anthropoids including macaques, mandrills, talapoins, mangabeys, red colobus, proboscis monkeys, patas monkeys, langur species and great apes (Dixson, 2012). Sociosexual behaviors are behaviors that are associated with sexual activity but are used socially to mediate fitness-enhancing goals (Lee, 2007). Despite possessing a unique affiliative sexual behavior first described by Ogawa in 1995 called "bridging," in which two adults touch or lick the genitals of an infant while teeth chattering, few studies exist on the sexual behavior of Tibetan macaques (Jiang, Li, Sheeran, Sun, Xia, & Wang, 2013; Li, Yin & Zhou, 1996; Ogawa, 1995a; Zhao, 1993).

Research on sexual behavior in primates including macaques has focused mainly on reproductive tactics of adults. Juvenile and infant behavior has been studied in macaques (*M. radiata*, Simonds, 1974; *M. fuscata*, Eaton, Modahl, & Johnson, 1981, Leca, Gunst, & Vasey, 2014, Gunst et al., 2013) but few of these studies examine sexual behavior. Much of what we know about primate sexual development has come from the experimental manipulation of hormones (Goy, 1988), social environment of rhesus macaques (*M. mulatta*, Harlow, Harlow, Hansen, & Suomi, 1972), and from observational studies of social development (Eaton, Johnson, Glick, & Worlein, 1986) and sexual development (Leca et al., 2014; Gunst et al., 2013) of Japanese macaques (*M. fuscata*). Even considering the complex social learning required for the acquisition of sexual behavior, few studies exist on the sexual behavior of immature wild macaques.

The social learning component of sexual behavior makes the examination of these behaviors in immature individuals particularly interesting and necessary to understanding their functions. Many primates begin their lives learning about social relationships through play (*M. fuscata*, Gunst, et. al., 2013; *Rhinopithecus roxellana*, Li, Guo, Ji, He, Wang & Li, 2011). This social context has been extremely important in shaping behaviors, including sexual behaviors, in young Rhesus macaques, as evidence by infants reared without peers their own age, which do not exhibit a full repertoire of social behaviors exhibited by adults raised with peers. (Champoux, Byrne, Delizio, & Suomi, 1992) Additionally, demographic differences have been documented in many non-human primates (*P. paniscus, C. capucinus*, Manson. et. al., 1997; *M. fuscata*, Tokuda, 1961; *M. radiata*, Simonds, 1974). In Japanese macaques, male and female differences in play and partner preference appear in the first and second years of life, respectively (Glick, Eaton, Johnson, & Worlein, 1986). Sex differences in behavior frequencies are apparent in juvenile Vervet monkeys and are not predictive of adult differences (Raleigh, Flannery, & Ervin, 1979). Immature Japanese macaques gradually acquire adult-like behavioral patterns and gradually lose less effective immature behavioral patterns as they age from juveniles to adults, with a major threshold in behavioral changes occurring at the age of 4 years for females (Leca et al., 2014), and the frequency of mounts directed towards adult females increasing around 2 to 3 years of age for males (Gunst et al., 2013). Although Tibetan macaques spend much of their time with their mothers as infants, they are particularly sought-after during the first year of life by other group members for their use in bridging (Ogawa, 1995b, 1995c). There is a significant sex difference between male and female infants in their involvement in bridges. Adults show a strong preference for male infants, using male infants in bridges 0.43 times per hour, while using female infants 0.04 times per hour (Ogawa, 1995a). Male and female infants experience differential treatment by their mothers and other group members. Female infants are groomed and carried more by their mothers than are male infants, while male infants play more often and are cared for by other group members more often than female infants (Deng, 1993; Deng & Zhao 1991). Many developmental differences between male and female primates are attributable to their different life histories within their society (Wallen, Zehr, Herman, & Graves, 2003). In female philopatric species such as the Tibetan macaque (Berman, Ionica, & Li, 2004), immature males and females prepare to assume different roles as adults. Young males prepare for emigration and alliance formation while young females begin to establish themselves in the matriarchal community and to raise infants (Wallen, et. al., 2003). The onsets of physiological aspects that occur during puberty such as sperm viability and first ovulation/menses in Tibetan macaques are not well known, so visible markers of puberty have been used to distinguish developmental stages in the species. Physical development in Tibetan macaques separates sub-adult and young adult males based on canine eruption and wear, body weight, age, and behavior, including ability to ejaculate (Zhao, 1993). Estrus is marked by a slight swelling between the tail and anus in females, but is not reliably detectable (Zhao, 1993). Female Tibetan macaques' first birth occurs around 5 years of age and has been used to determine the onset age of adulthood (Zhao & Deng, 1988).

## Methods

### *Subjects and Study Site*

Immature individuals in a group of free-ranging, habituated Tibetan macaques at a tourist park in the Valley of the Wild Monkeys at Mt. Huangshan, China served as the subjects of this study. Monkeys at the site have been habituated to human presence since its establishment in 1986 and are provisioned dry corn 3-4 times a day by park staff. The immature macaques in the group, designated YA1, served as the subjects of this study, which included 7 adult males, 9 adult females, 14 immature males, and 12 immature females. Video footage was recorded from 830h to 1700hr for forty days between August 7$^{th}$ and September 21$^{st}$, 2014.

Preliminary observations were made before collecting data for familiarization with the group's behaviors, and an intra-observer reliability rate of 1.0 was reached for behavior and individual identification from video footage before coding. For analysis, individuals were separated into four age and sex classes based on rates of copulation and ejaculation, which serve as biological markers of puberty for the species (Zhao, 1993; Zhao & Deng, 1988). Older males were characterized by the ability to copulate with observed ejaculation, distinct from younger males who were not observed to ejaculate; and older females were characterized by the observance of copulation involving intromission, distinct from younger females who were mounted with no intromission.

Table 2

*Individuals by Age, Sex, and Time Visible.*

| **Older females ID** | **Age (mo.)** | **Time visible (min)** | **Older male s ID** | **Age (mo.)** | **Time visible (min)** | **Younger females ID** | **Age (mo.)** | **Time visible (min)** | **Younger males ID** | **Age (mo.)** | **Time visible (min)** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| YCY | 64-66 | 265.61 | TRB | 78-80 | 161.89 | THX | 27-29 | 388.01 | THH | 41-43 | 132.86 |
| RYF | 64-66 | 307.60 | YRB | 78-80 | 17.23 | CLF | 22-24 | 493.37 | HXH | 38-40 | 161.42 |
| CUC | 64-66* | 232.40 | HXM | 53-55 | 311.44 | TRX | 15-17 | 438.97 | TXH | 37-39 | 551.87 |
| THY | 63-65 | 206.80 | TRG | 51-53 | 445.03 | HXW | 17-19 | 465.58 | RYM | 29-31 | 531.30 |
| YXX | 50-52 | 443.87 | YRQ | 50-52 | 306.08 | TQL | 16-18 | 356.12 | TXL | 25-27 | 658.23 |
| | | | CLM | 49-51 | 293.00 | YRL | 14-16 | 474.11 | YXK | 17-19 | 600.50 |
| | | | | | | TRI | 4-5 | 25.42 | THI | 5-7 | 446.92 |
| | | | | | | | | | YHI | 5-7 | 337.42 |

*Individual immigrated into group, age estimated based on physical appearance

*Sampling Procedure and Data Collection*

Sexual behaviors were recorded using all occurrences sampling. Video was coded to record amount of time visible for each individual, and to record each sexual behavior's social context and participants' roles as actor or recipient. An ethogram of sexual behavior is shown in Table 3 and an ethogram of social contexts is shown in Table 4.

Table 3

*Ethogram of Sexual Behaviors*

| Behavior | Description |
|---|---|
| 1. Genital inspection | An individual looks at and touches or sniffs the genitals of another |
| 2. Genital manipulation | An individual manipulates the genitals of another with its hands, or grabs the other's genitals for several seconds |
| 3. Genital manipulation (self) | An individual manipulates or grabs its own genitals with its hands for several seconds, not appearing to be grooming |
| 4. Present | An individual displays his or her rump to another |
| 5. Mount without thrust | An individual approaches from behind and positions itself into some semblance of a copulatory position with no thrusting or intromission. |
| 6. Mount with thrust | An individual approaches from behind, mounts, and thrusts his or her pelvis, without intromission. |
| 7. Orogenital | An individual sucks or licks the genitals of another |
| 8. Copulation | An individual approaches, mounts, and thrusts his pelvis, with intromission |
| 9. Bridge | A complex sequence of behavior in which an individual approaches another, alternating glances at the receiver and an infant between them, and simultaneously licks the infants genitals or body while teeth-chattering |

The type of non-sexual behaviors directly preceding the sexual behavior determined the social context of each sexual behavior. Non-sexual social behaviors preceding sexual behavior were categorized into five social contexts: aggressive, grooming, play, self-directed, and spontaneous. If sexual behavior occurred without observation of the preceding interaction, the social context was coded as "unknown." Table 4 describes each social context.

Table 4

*Social Contexts of Sexual Behaviors*

| Behavior | Description |
|---|---|
| 1. Aggressive | Sexual behavior occurred between individuals within or immediately following behaviors including aggressive chase, bite, slap, threat |
| 2. Grooming | Sexual behavior occurred between individuals within or immediately following grooming |
| 3. Play | Sexual behavior occurred between individuals within or immediately following behaviors including non-aggressive chase, wrestle, play face |
| 4. Self-directed | Genital manipulation or masturbation occurred without partner |
| 5. Spontaneous | Sexual behavior occurred between individuals that were not interacting in any apparent way immediately preceding the sex behavior |
| 6. Unknown | Sexual behavior occurred between individuals without observation of preceding interaction |

*Data Analysis*

The study group was divided into four age/sex classes based on significant biological developmental stages of adolescence for each sex. These developmental stages serve as markers for the beginning of adult reproductive capability. Females were separated into older immature (4 and 5 years, $n = 5$), those that were observed copulating; and younger immature (0-3 years, $n = 7$), those that were not observed copulating. Males were separated into older immature (4-6 years, n = 6), those that were observed regularly ejaculating in copulations, and younger immature (0-3 years, $n = 8$), those that were not observed regularly ejaculating.

A Kruskal-Wallis H test ($df = 3$) was used to measure variance between each age/sex class group for all five aspects of sexual behavior: rate of total sexual behavior, rate per dyad for partner preference, rate of each type of sexual behavior, rate of initiation, and rate within each social context. Frequencies were converted to rates of sexual behaviors per hour for each individual to account for differences in amount of time visible. Multiple paired comparisons based on mean ranks were performed to determine which classes differed significantly when the Kruskal-Wallis H test reported differences among the four classes. Partner preference for an individual was determined by examining the rates of sexual behavior with every potential partner within each age/sex class. Higher rates of total sexual behavior with partners of one age/sex class, relative to other potential age/sex class partners, indicated a preference to engage in sexual behaviors with partners of a certain age/sex class. Especially in sexual behavior, which may transition in function from play to reproduction during puberty, partner preference is likely to transition from same-sex to opposite-sex.

A secondary analysis of social network among immature monkeys based on sexual behaviors was performed using SOCPROG 2.4 (Whitehead, 2008) to determine number, strength, and composition of clusters. An estimate of social differentiation using a Poisson approximation was used to determine how well differentiated the group was by cluster. The power of the analysis to detect a true social system based on sexual behaviors was also calculated. A social network map was created using NETDRAW. Each node in the social network map represents one individual. The shape of the node represents sex of the individual, with males being shown as squares and females as circles. The size and darkness of the nodes represent age of the individual, lightest and smallest being the youngest (5 months) and darkest and biggest being the oldest (6 years). The lines between each node, called edges, represent interactions between individuals. Edges are weighted in darkness by number of sexual behaviors that occurred between two individuals, with darker lines representing a higher number of sexual behaviors than lighter lines. Clusters are created using an eigenvector centrality coefficient, which is a measure of social connectivity between individuals based on their interactions with other group members. The eigenvector centrality coefficient indicates the degree of connectedness of the individual as well as of those individuals the individual of interest is connected to (Hanneman & Riddle, 2005; Sueur & Petit, 2008; Whitehead, 2009; Zhang, 2012; cited in Kasper & Voelkl, 2009). Clustering coefficients were also calculated to determine the closeness of individuals within a cluster. When a network is a highly structured and homogenous unit the clustering coefficient is high, clustering the individual nodes closer together (Whitehead, 2009; Croft & Krause, 2008; cited in Kasper & Voelkl 2009; Hanneman & Riddle, 2005).

## Results

Video (5,468.2 minutes) was recorded across 40 days between August 7th 2014 and September 21st, 2014. Time visible ranged from 17.2 minutes to 658.2 minutes per individual (Table 1). Each actor and recipient ID and social context were recorded for each sexual behavior observed. Nine types of sexual behaviors were observed, totaling 643, with bridging being the most common (*n* = 179), accounting for 27.1% of all sexual behaviors observed, and self genital manipulation being the least common (*n* = 18), accounting for 2.8% of all sexual behaviors observed (Table 5). Rate per hour of each behavior varied within the population, and individual placement varied within quartiles across behaviors with the exception of the infant female exhibiting zero sexual behaviors, and with a clear separation between older and younger classes in rates of copulation (Figure 1).

Table 5

*Frequencies, Percent of Total, and Rate of Sexual Behaviors*

| **Sexual behavior type** | ***n*** | **% total** | **Rate per hour** |
|---|---|---|---|
| Bridging | 174 | 27.1 | 1.2(0.4-4.0) |
| Orogenital | 154 | 24 | 0.8(0.4-2.3) |
| Mount with thrust | 82 | 12.8 | 0.4(0-1.2) |
| Genital inspection | 71 | 11 | 0.6(04-1.0) |
| Copulate | 65 | 10 | 0.1(0-1.8) |
| Mount without thrust | 28 | 4.4 | 0.2(0-0.4) |

Table 5 (continued)

| **Sexual behavior type** | ***n*** | **% total** | **Rate per hour** |
|---|---|---|---|
| Genital manipulation (partner) | 26 | 4 | 0.3(0-0.4) |
| Present | 25 | 3.9 | 0.3(0-0.4) |
| Genital manipulation (self) | 18 | 2.8 | 0(0-0.2) |

Note: Numerical values for each behavior rate: median($Q_1$–$Q_3$).

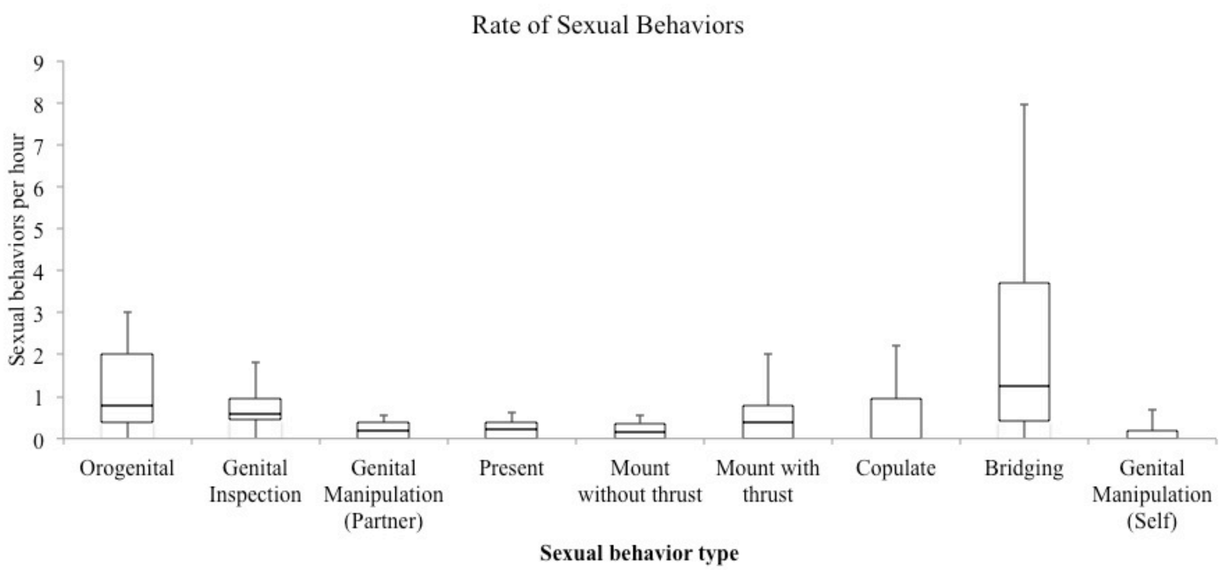


*Figure 1*. Occurrence of sexual behaviors in YA1 immature macaques.

*Total sexual behavior rates*

Total rates of sexual behavior per hour were calculated for each individual, which included all sexual behaviors an individual was observed to be involved in during the study period. Age and sex classes exhibited different rates of total sexual behavior (Table

6). Young females exhibited the lowest rates of sexual behavior, only differing significantly from young males, who exhibited the highest rates of sexual behavior ($U = 6$, $p < 0.05$, Table 6). There was no evidence for difference in all other pairwise comparisons, suggesting similar rates of sexual behavior among the four classes with the exception of younger males exhibiting higher rates than younger females.

Table 6

*Total Sexual Behavior: Hypotheses, Predictions, and Results*

| Prediction | Older females | Older males | Younger females | Younger males | Kruskal-Wallis test | Significant Pairwise Class differences | Prediction Supported |
|---|---|---|---|---|---|---|---|
| **Hypothesis #1** (Total sexual behavior rates): Rates should differ between age/sex classes | 5.2(4.5-10.3) | 6.0(5.3-6.4) | 4.0(2.3-5.6) | 8.9(7.1-12.9) | 9.0, p=0.030 | YF < YM | Yes |

Note: Numerical values for each age class: median($Q_1$–$Q_3$). In pairwise age differences, OF: older females, OM: older males, YF: younger females, and YM: younger males; N.A.: not applicable.

*Types of sexual behavior*

Age/sex classes exhibited different rates of genital manipulation, mount without thrust, copulation, orogenital, and bridging behaviors (Table 7). There was no significant difference among age/sex classes in rates of presenting, genital inspection, or mount with thrust behaviors. Except in copulations, younger males exhibited significantly higher rates than at least two other immature classes in every behavior where differences were reported. Younger males exhibited significantly higher rates than all three other immature classes in mount without thrust behavior (older females, $U= 0$, $p < 0.05$; older males, $U = 5$, $p < 0.05$; younger females, $U = 3$, $p < 0.05$; Table 7). Younger males also exhibited significantly higher rates than both female classes in genital manipulation (older females, U = 5, $p < 0.05$; younger females, U = 7, $p < 0.05$; Table 7), and significantly higher rates than both older age classes in orogenital behavior (older females, U = 4, $p < 0.05$; older males, U = 4, $p < 0.05$; Table 7). All three immature classes exhibited significantly higher rates of bridging behavior than younger females (older females, U = 4, $p < 0.05$; older males, U = 3, $p < 0.05$; younger males, U = 0, $p < 0.05$; Table 7), and younger males bridged at significantly higher rates than older females (U = 4, $p < 0.05$; Table 7). The only behavior in which classes differed and younger males did not exhibit higher rates than other age classes was copulation. Older males and older females exhibited significantly higher rates of copulation than younger males (older males, U = 7.5, $p < 0.05$; older females, U = 0, $p < 0.05$; Table 7), and younger females (older males, U = 3.5, $p < 0.05$; older females, U = 0, $p < 0.05$; Table 7).

Table 7

*Sexual Behavior Type: Hypotheses, Predictions, and Results*

| Prediction | Older females | Older males | Younger females | Younger males | Kruskal-Wallis test | Significant Pairwise Class differences | Prediction Supported |
|---|---|---|---|---|---|---|---|
| **Hypothesis #2** (Sexual behavior types): Types of sexual behavior should differ between age/sex classes | | | | | | | Yes |
| Self Genital manipulation | n.a. | 0.1(0-0.3) | 0(0-0.2) | 0(0-0.3) | 3.4, p=0.34 | n.a | |
| Present | 0.2(0.1-0.3) | 0.1(0-0.2) | 0.4(0-0.6) | 0.3(0.1-0.4) | 3.4, p=0.337 | n.a. | |
| Partner Genital manipulation | 0(0-0.2) | 0.4(0-0.4) | 0(0-0.3) | 0.5(0.3-0.6) | 9.1, p=0.028 | OF < YM<br>YF < YM | |

Table 7 (continued)

| Prediction | Older females | Older males | Younger females | Younger males | Kruskal-Wallis test | Significant Pairwise Class differences | Prediction Supported |
|---|---|---|---|---|---|---|---|
| Mount without thrust | n.a. | 0.2(0-0.4) | 0.1(0-0.3) | 0.5(0.4-0.7) | 16.1, p=0.001 | OF < YM<br>OM < YM<br>YF < YM | |
| Copulate | 1.8(1.6-3.1) | 1.7(0.2-3.1) | n.a. | 0(0-0.2) | 16.8, p=0.001 | YM < OF<br>YF < OF<br>YM < OM<br>YF < OM | |
| Genital inspection | 0.5(0.3-0.7) | 0.6(0.2-0.6) | 0.9(0.5-1.7) | 0.8(0.5-1.1) | 5.0, p=0.17 | n.a. | |
| Mount with thrust | 0.1(0-0.5) | 0.3(0-0.8) | 0.3(0-2.0) | 0.9(0.5-1.7) | 6.6, p=0.085 | n.a. | |
| Orogenital | 0.4(0.3-1.9) | 0.5(0.4-0.6) | 0.8(0.7-2.0) | 2.3(1.4-2.7) | 9.2, p=0.027 | OF < YM<br>OM < YM | |
| Bridging | 0.8(0.4-6.8) | 2.2(0.6-3.8) | 0.3(0-0.5) | 3.1(1.9-5.2) | 12.6, p=0.006 | YF < OF<br>YF < OM<br>YF < YM<br>OF < YM | |

Note: Numerical values for each age class: median($Q_1$–$Q_3$). In pairwise age differences, OF: older females, OM: older males, YF: younger females, and YM: younger males; N.A.: not applicable.

*Initiation*

Age/sex classes show significant differences in rates of initiation of sexual behavior (Table 8). Younger females initiated fewer sexual behaviors per hour than older males (U = 0, $p < 0.05$) and younger males (U = 4, $p < 0.05$). All other pairwise comparisons indicated no significant differences.

Table 8

*Initiation: Hypotheses, Predictions, and Results*

| Prediction | Older females | Older males | Younger females | Younger males | Kruskal-Wallis test | Significant Pairwise Class differences | Prediction Supported |
|---|---|---|---|---|---|---|---|
| **Hypothesis #3** (Initiation Rates): Rates should differ between age/sex classes | 1.2(0.6-6.5) | 3.5(3.5-5.8) | 1.2(0.5-1.9) | 3.7(2.8-4.7) | 24.1, $p<0.001$ | YF < YM<br>YF < OM | Yes |

Note: Numerical values for each age class: median($Q_1$–$Q_3$). In pairwise age differences, OF: older females, OM: older males, YF: younger females, and YM: younger males; N.A.: not applicable.

*Social context of sexual behaviors*

The highest proportion of sexual behaviors occurred within the spontaneous social context in which two individuals were not apparently interacting prior to engaging in a sexual behavior (39.12%, Table 9) followed by sexual behaviors occurring within or following play bouts (29.73%). Lower proportions of sexual behavior occurred within grooming (3.45%), aggressive (2.55%), and self (2.4%) contexts. Rates of sexual behavior correspond to their proportions, with sexual behavior rates being highest within spontaneous (0.048 sb/min) and play (0.036 sb/min) contexts, and within grooming (0.004 sb/min), aggressive (0.003 sb/min), and self (0.003 sb/min) being the lowest (Table 9).

Table 9

*Number and Percentage of Sexual Behaviors Occurring Within Social Contexts*

| **Social context type** | **n** | **% total** |
|---|---|---|
| Spontaneous | 261 | 39.12 |
| Play | 198 | 29.73 |
| Grooming | 23 | 3.45 |
| Aggressive | 17 | 2.55 |
| Self | 16 | 2.4 |
| Unknown | 151 | 22.67 |

Age/sex classes exhibited significant differences in rates of sexual behavior within spontaneous and play social contexts (Table 10). Younger females engage in significantly lower rates of spontaneous sexual behavior than other age/sex classes (older males, U = 3, $p < 0.05$; older females, U = 5, $p < 0.05$; younger males, U = 10, $p < 0.05$), which suggested that young females are more likely to engage in sexual behaviors with individuals with whom they are already interacting. Within or following play, young males engaged in significantly higher rates of sexual behaviors than all other age/sex classes (older males, U = 4, $p < 0.05$; older females, U = 1, $p < 0.05$; younger females, U = 9, $p < 0.05$). Additionally, younger females engaged in higher rates of sexual behaviors within or following play than older females (U = 5, $p < 0.05$). There was no evidence for significant differences in rates of sexual behavior between age/sex classes were found within grooming, aggressive, and self contexts.

Table 10

*Social Context: Hypotheses, Predictions, and Results*

| Prediction | Older females | Older males | Younger females | Younger males | Kruskal-Wallis test | Significant Pairwise Class differences | Prediction Supported |
|---|---|---|---|---|---|---|---|
| **Hypothesis #4** (Social context): Proportion of sexual behaviors within social contexts should differ between age/sex classes | | | | | | | Yes |
| Self | n.a. | 0.1(0-0.3) | 0(0-0.2) | 0(0-0.2) | 3.0, p=0.338 | n.a. | |
| Grooming | 0.3(0.1-1.1) | 0.3(0-0.5) | 0.1(0-0.2) | 0.3(0.2-0.4) | 2.6, p=0.457 | n.a. | |
| Aggressive | 0(0-0.3) | 0.2(0-0.4) | 0.2(0-0.5) | 0.2(0.1-0.5) | 1.2, p=0.754 | n.a. | |
| Play | 0.5(0.4-1.0) | 0.4(0-1.6) | 2.0(1.4-2.4) | 3.2(2.6-4.7) | 14.0, p=0.003 | OF < YM<br>OM < YM<br>YF < YM<br>OF < YF | |
| Spontaneous | 2.6(2.0-6.3) | 2.3(1.9-2.5) | 1.2(0.5-1.7) | 2.8(1.5-5.0) | 9.4, p=0.024 | YF < OF<br>YF < OM<br>YF < YM | |

Note: Numerical values for each age class: median($Q_1$–$Q_3$). In pairwise age differences, OF: older females, OM: older males, YF: younger females, and YM: younger males; N.A.: not applicable

*Partner preference*

Age/sex classes exhibited significant differences in partner preferences in sexual behavior (Table 11). Young males preferred other young males as partners in sexual behaviors above the other three age/sex classes, and younger females were the least preferred age/sex class as partners in sexual behavior for both old males and young males. Older females did not exhibit different rates of sexual behaviors among the four age/sex classes as partners in sexual behavior (Table 11). Older males exhibited higher rates with older females than with younger females ($U = 421.5$, $p < 0.05$, Table 11), and higher rates with younger males than younger females ($U = 799$, $p < 0.05$, Table 11).

Younger males exhibited higher rates of sexual behavior with other younger males than they did with any of the other three age/sex classes (older males, U = 466, $p < 0.05$; older females, U = 375.5, $p < 0.05$; younger females, U = 492.5, $p < 0.05$, Table 11) Younger females exhibited higher rates with younger males than older males (U = 861.5, $p < 0.05$, Table 11). All other pairwise comparisons were not significant.

Table 11

*Partner Preference: Hypotheses, Predictions, and Results*

| Predictions | Older females | Older males | Younger females | Younger males | Kruskal-Wallis test | Significant Pairwise Class differences | Prediction Supported |
|---|---|---|---|---|---|---|---|
| **Hypothesis #5** (Partner preference):Partner preference should differ between age/sex classes | | | | | | | Yes |
| #5a. Older females should prefer older males to other age/sex classes | 0(0-0.2) | 0.1(0-0.7) | 0(0-0.2) | 0(0-0.4) | 5.7, p=0.128 | n.a. | No |
| #5b. Older males should prefer older females to other age/sex classes | 0.1(0-0.7) | 0(0-0.3) | 0(0-0.1) | 0(0-0.5) | 8.1, p=0.043 | YF < YM<br>YF < OF | No |
| #5c. Younger males should prefer younger males to other age/sex classes | 0(0-0.4) | 0(0-0.5) | 0.8(0-1.2) | 0.1(0-0.3) | 16.4, p=0.001 | YF < YM<br>OF < YM<br>OM < YM | Yes |
| #5d. Younger females should prefer younger females to other age/sex classes | 0(0-0.4) | 0(0-0.5) | 0.1(0-0.3) | 0.1(0-0.3) | 9.2, p=0.027 | OM < YM | No |

Note: Numerical values for each age class: median($Q_1$–$Q_3$). In pairwise age differences, OF: older females, OM: older males, YF: younger females, and YM: younger males; N.A.: not applicable.

*Social Network Analysis*

A strength-of-analysis value of 0.831 was calculated using a Poisson approximation, indicating a strong representation of the social system based on sexual behavior where a value of 1 is a true representation of the social system and a value of 0 is a useless measure. A social differentiation estimate of 1.493 was also calculated using a Poisson approximation, where an estimate of less than 0.3 indicates a homogenous society, greater than 0.5 indicates a well differentiated society, and greater than 2 indicates an extremely differentiated society.  Our value of 1.493 indicates that the clusters are extremely differentiated.  In other words, individuals strongly prefer the individuals within their cluster as partners in sexual behavior to individuals in other clusters. Six distinct clusters are apparent.  Each cluster is composed of approximately same-age individuals, and is mixed-sex (Fig. 2).

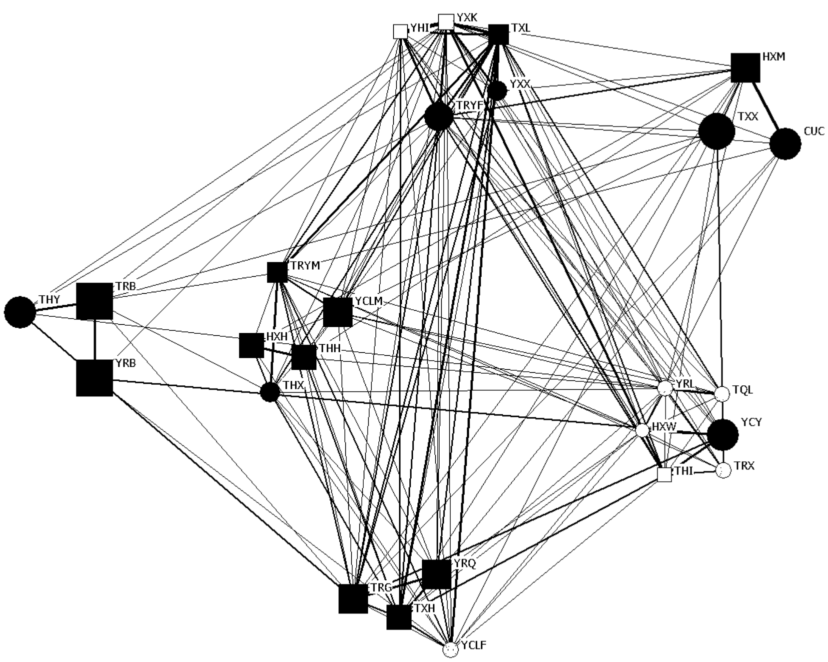


*Figure 2*.  Social network of YA1 immature macaques based on sexual behavior.

Age/sex classes differed significantly in 12 out of 20 Kruskal-Wallis H tests for different aspects of sexual behavior. For each significant result, 6 pairwise comparisons were made between the classes to determine which age classes differed from each other, for a possible 72 possible pairwise comparisons. Young males exhibited significantly higher rates than at least one other age class in 11 of the 12 Kruskal-Wallis tests reporting significant differences between age classes, and were only significantly lower than older males and older females in rates of copulation. Young females were significantly lower than other age classes in 10 out of the 12 significant Kruskal Wallis tests, and were only significantly higher than older females in social context rates of sexual behavior within or following play. Older females and older males both exhibited significantly higher rates of copulation than younger age classes. Out of 12 significant Kruskal-Wallis comparisons among age classes, both older females and older males exhibited significantly higher rates of sexual behavior than another age/sex class in 3 tests (copulation, bridging, spontaneous), and significantly lower in 4 tests (mount without thrust, orogenital, play, young male partner preference).

## Discussion

The results support the hypotheses that the sexual behavior of immature macaques differs among age/sex classes in total rate, initiation, type, social context, and partner preference.  Younger males and younger females most drastically differed from other age/sex classes, while older males and females exhibited variably higher and lower rates in multiple aspects of sexual behavior.

Younger males generally exhibited significantly higher rates within various aspects of sexual behavior relative to other immature classes. They exhibited significantly higher rates than another class in 19 pairwise comparisons across all five aspects, and significantly lower in two pairwise comparisons with older males and with older females in only one type of behavior, copulation. This high rate of sexual behavior among young males relative to other immature classes may be related to higher rates of mounting and play, and lower rates of grooming relative to females that have been documented in immature Japanese macaques (Eaton, Johnson, Glick, & Worlein, 1985) and infant Tibetan macaques (Deng, 1993, Deng & Zhao, 1990; Deng & Zhao, 1991).

Younger females generally exhibited significantly lower rates in all five aspects of sexual behavior relative to other immature classes, particularly in rates of different types of behavior, spontaneous sexual behavior, and in rates of initiation. This lower rate of sexual behavior may also be in accordance with previous research documenting immature female Japanese macaques spending significantly more time in proximity and grooming than immature males (Eaton et al., 1985). The current study observed low overall rates of sexual behavior occurring within grooming social contexts and high rates of sexual behavior occurring within play. This finding combined with past research concluding macaque females spend more time in grooming and males spend more time in play (Deng, 1993; Eaton, et. al., 1985) may supplement our understanding of the importance of sexual behavior in its social functions, and how those functions differ between sexes for some macaque species.

Differences between younger age classes and older age classes may relate to the physical and physiological changes associated with puberty, and to the social learning and development that occurs over time in immature macaques. Rates of copulations involving intromission and regular ejaculation were observed only in older age classes of immature individuals. However, the prediction that partner preference would transition from same-sex to opposite sex between younger and older age classes was not supported. This may be due to high rates among immature individuals of bridging and other sociosexual behaviors that do not necessarily serve exclusively reproductive purposes, and their tendency to involve partners of both sexes. In other words, in addition to copulating with opposite-sex partners, older age classes also engaged in high rates of sociosexual behavior with partners of the same sex. Jiang and colleagues' 2013 study documented higher rates of heterosexual mounting among adult males. The high rate of same-sex sexual behaviors in immature males in this study may be due to the inclusion of additional behaviors such as bridging, and may also be due to potential behavioral differences between pubertal and adult males.

Kinship does not appear to play a role in the partner preference of immature macaques according to the social network clusters. Only one mother's offspring all belonged to the same cluster, while all of the offspring of five different mothers belonged to different clusters that contained no siblings. Only two clusters contained any siblings, and clusters primarily contained individuals that were close in age. The partner preference rate findings are in accordance with the social network clusters. No clusters contain both older males and younger females, with older males preferring both younger males and older females to younger females as partners in sexual behavior, and younger females preferring younger males to older males. In support of the finding that young males prefer other young males above all three other immature classes as partners in sexual behavior, no younger males are found in clusters without at least two other younger males, and all younger males belong to three out of the six clusters.

The exact onset of adult physiological reproductive capabilities (e.g. sperm viability and first ovulation) in Tibetan macaques is unknown, so physical markers of puberty and adulthood have been used to separate and characterize developmental stages. A study by Zhao in 1993 separated sub-adult and young adult males based on canine eruption and wear, body weight, age, and behavior, including ability to ejaculate. Estrus is marked by a slight swelling between the tail and anus in females, but is not reliably detectable (Zhao et. al. 1993). Females are determined to enter adulthood upon first giving birth around 5 years of age (Zhao & Deng, 1988). Provisioning in this group may inadequately represent body weight as a marker of development. The behavioral traits that accompany puberty are related to physiological changes in hormonal activity and serve as pubertal markers ipso facto. Future research on body weight and canine eruption and wear in the YA1 troop would supplement developmental stage divisions of age/sex classes.

Data collection during the mating season may have influenced behaviors observed, especially copulations and behaviors by older immature macaques that may exhibit more adult-typical behavior patterns. Tibetan macaque grouping diversity, i.e., change in member composition of sub-groups, has been shown to dramatically increase during the mating season due to increased mating competition and intergroup transfer (Zhao, 1993). The rates of bridging may be inflated in older juvenile males during the mating season, when maternal care is significantly reduced and correlates to the number of infants in proximity to adult males and bridging reception rate (Zhao, 1996).

The findings that immature Tibetan macaques engage in considerable rates of sexual behavior, and that aspects of sexual behavior vary between age and sex classes, adds to the understanding of development of sexual behavior in this species. Future additional analyses on bridging roles in immature Tibetan macaques may yield results that explain the acquisition and function of this unique behavior. Older males and older females were never used in bridges by other immature macaques in this study, but exhibited higher rates of bridging as either an actor or recipient than adult males [0.35 bridges per hour (Ogawa, 1995a)] as reported in previous studies. Additionally, the three individuals younger than 7 months of age were only used in bridges in this study, but were never themselves the initiators or recipients. Further analysis is needed to determine at what age Tibetan macaques begin to bridge beyond being used by older individuals within bridging. High rates of bridging among immature macaques relative to adult bridging rates could yield information on the function of this interesting behavior in a species with a large and complex sexual behavior repertoire.

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