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The Development of Social Behavior in the Tibetan Macaque (*Macaca thibetana*)

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THE DEVELOPMENT OF SOCIAL BEHAVIOR IN THE TIBETAN MACAQUE (*MACACA THIBETANA*)

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Master of Science

Primate Behavior and Ecology

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by

Rose Margaret Amrhein

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CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

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ABSTRACT

THE DEVELOPMENT OF SOCIAL BEHAVIOR IN THE TIBETAN MACAQUE (*MACACA THIBETANA*)

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Rose Margaret Amrhein

May 2020

Social cognition is vital for the proper integration into adulthood for any highly social animal species. The development of social intelligence during the childhood and adolescence of a social organism affects the individual throughout its life. This social intelligence allows for the establishment and maintenance of bonds through the formation of empathy, the understanding of intention and emotion, and theory of mind in some species. Changes to the rate and effectiveness of social development could lead to an individual incapable of integrating into the social environment of adulthood. Yet, much still needs to be learned about the process and influences of social development. Through the study of the play and social behavior in infant and juvenile Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China, I made comparisons of these social behavioral frequencies across ages. I found consistent relationships between social behavioral frequencies, specifically grooming, bridging, and play behaviors, and the age of the individual. According to these frequency patterns, individuals around 4 years of age begin to exhibit social behaviors consistent with those of adulthood. However, I also established that the more complex behaviors of play handicapping and play signaling that are believed to be linked to a complex social understanding are not directly and solely related to age. My results suggest other influences likely play a role in the ontogeny of social behaviors including the sex of the individual and maternal rank. To gain a clearer and in depth understanding of the exact progression and influences of social development in young Tibetan macaques, longitudinal studies are required.

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CHAPTER I

INTRODUCTION

As a social animal, humans, along with other social primates, require the ability to form bonds, interact with conspecifics, and understand basic social norms to be integrated into adult society. The foundation for these abilities is largely formed during infancy, childhood, and adolescence during which social interactions are likely to be novel (Byrne & Whiten, 2002). Through these early social interactions, humans learn concepts of empathy, emotion, and intention, key factors for adult social interactions (Tousignant, Sirois, Achim, Massucotte, & Jackson, 2017). Due to its importance in adult life, the ontogenesis of social cognition has been a central research topic, especially in learning and developmental psychology, yet it still requires more study.

In the past century, scientists of different fields approached the subject of cognition from different perspectives. With anthropologists, psychologists, and biologists providing their own theories, a consensus on the processes of social cognitive development of human and non-human primates was never attained. Today, the study of cognition is increasingly multidisciplinary, yet, individual circumstances are often forgotten. Different human cultures have different social requirements for an individual to become an integrated member of society (Lancy, Bock, & Gaskins, 2010). Influences of natural and peer environments of an individual of any primate species are known to have an effect on social development, but it is still unclear if these effects are of the same degree across age groups (Kuwabara & Smith, 2012). While the process and timeline of general brain development appear consistent in humans across cultures, the vulnerability to outside influence (i.e., stressful life events and environmental pressures) of the individuals in different stages is still unclear, for which it needs to be investigated, particularly in a behavioral context with greater specificity (Choudhury, Blakemore, & Charman, 2006).

By studying social primates such as Tibetan macaques in their infant and juvenile years, we can gain critical insights into the development of social interactions and behaviors. This can allow us to understand how key biological and social factors such as age, sex, and dominance ranking affect developmental rate and behavioral patterns. With this knowledge, we may be able to locate periods where social development is highest. This, in turn, will allow us to have a more cohesive approach to understanding how social development relates to an individual's integration into adult society and what influences during development may affect the success of this integration (Gutowski, White, Liang, Diamonti, & Bernado, 2017; Kang, Boss, & Clowtis, 2016; Mcdonald, Kehler & Tough, 2018; Tousignant et al., 2017).

To assess this level of integration into adult society, it is important to investigate the degree and timing for the acquisition of important social behaviors. In Tibetan macaques, both grooming (Wang et al., 2015; Berman et al., 2008) and bridging behaviors (Xia et al., 2013; Ogawa, 2006) represent a level of social cognition as they have been found to be vital in maintaining group cohesion, establishing dominance hierarchies, and contributing to a society based on reciprocity. Additionally, play behaviors, while not common in adults of the species, are still suggestive of a growing understanding of social expectations. For example, play signaling has been found to maintain play bouts by communicating to play partners and audience members that there is no threat, thus sustaining the bout (Wright et al., 2018; Yanagi & Berman, 2014). Play handicapping also extends play bouts as individuals who increase their vulnerability by self-handicapping are less likely to intimidate a play partner (Petrů, Špinka, Charvátová, & Lhota, 2009). Thus, these behaviors constitute a fundamental framework from which social development unveils. It is for this reason that I chose to investigate the role of these key behaviors in social play to understand how infant and juvenile Tibetan macaques integrate themselves into adult society.

I hypothesize that infant and juvenile Tibetan macaques develop social cognitive abilities through a series of stages as they integrate themselves into adult society. This would suggest the ability to identify the observable stages of social development based on the age of the individual. For example, monkeys of a specific age should all show similar patterns and rates of behaviors. Any significant deviation from these behavioral norms may indicate negative influences that could affect their integration into adulthood later in life. To test my hypothesis, I make the following testable predictions involving social behaviors:

I. There will be an increase of allogrooming as macaques age.

II. Bridging behavior, especially among males, will be absent in the first years of life, but will increase closer to adulthood.

III. Rates of play will decrease as the macaques age.

IV. Frequency of play signals during play bouts will increase as the macaques age.

V. Play-handicapping will also increase as macaques age.

VI. Subsequently, duration of individual play bouts will increase.

Although several important studies have been conducted on Tibetan macaques, including those on play behaviors (Wright et al., 2018), dominance style (Balasubramaniam et al., 2012), and infant directed aggression (Self, 2013), our knowledge of infant social development and group integration in this species is still lacking. Specifically, this study is important for two reasons. First, the development of social understanding in other primates could allow us to gain evolutionary insights into the development of human infants and children. This can provide a broader understanding of how childhood experiences shape adult behavior later in life and how this can affect the ability to integrate into adulthood with minimal conflict. Through the understanding of the most at risk ages in regards to inhibited social development, further steps can be taken to ensure that children in situations that could impact their social development (e.g., disruptive home lives, poor socioeconomic status, traumatic/stressful life events) can continue to be integrated into adult life successfully (Jaffari-Bimmel, Juffer, Ijzendoorn, Bakersmans-Kranenburg, & Mooijaart, 2006). Second, this knowledge can aid in our understanding of morality in both humans and animals. While there has been much conjecture about the development of morality in humans, a consensus has yet to be reached about the presence and development of morality within the animal kingdom (Fitzpatrick, 2017).

While this study is cross sectional, it will serve as a representation of Tibetan macaque social ontogeny. Through the tracking of individuals of all ages, the average pathway of social development for the species can be produced. This study can also provide a beginning stage of data accumulation for a longitudinal study in which the actual success of adult integration is assessed. Integration into social groups is valuable to many organisms as group participation can heighten survival and reduce the risk to individuals within a social group (de Waal & Macebo, 2016). For the same reason, this study could be largely beneficial to the conservation of Tibetan macaques and other social primates. By identifying behavioral stages in which infants and juveniles are most likely to be affected by change, when social behavioral plasticity may be at its lowest, we can infer the age groups most vulnerable and at risk of having their social development negatively affected. In addition, through the study of the link of maternal rank, more knowledge can be gained about how social influences and status alter the potential success of an individual (Maestripieri, 2018; Suarez-Jimenez et al., 2013)

CHAPTER II

LITERATURE REVIEW

Social Development and Adult Life Integration

The study of social development is of great importance as sociality is extensively integrated into many aspects of life. Social behaviors can shape the outcome of an adult individual (Byrne & Whiten, 2002) and can be shaped by events during development (Mcdonald et al., 2018). The process of social development in social organisms has been linked to foraging, explorative, and mating behaviors across the animal kingdom (Lihoreau, Brepson, & Rivault, 2009; Ballen, Shine, & Olssen, 2014) and has been considered a way in which to study speciation (Wobber, Wrangham, & Hare, 2010). Social development is also closely associated with the study of morality in humans and non-human animals, especially primates (de Waal & Macebo, 2016) and has been extensively linked to concepts such as theory of mind and altruism. These connections among multiple disciplines, make studies that investigate social development and its connection to non-social behaviors vital for furthering the understanding of life processes.

The development of key social behaviors is vital for proper integration into adulthood across the primate order. Through juvenile and adolescent ages, individuals should be surrounded and interacting with peers of similar ages in order to obtain and practice skills, both social and physical, necessary for success as adults. These skills accumulate into complete social intelligence, which can be broken down into ideals of social connectivity and reciprocity in addition to something known in humans and some primates as Machiavellian intelligence (Byrne & Whiten, 2002). Machiavellian intelligence is defined by successfully participating in social groups often highlighted by personal political situations. For example, during adolescence, interactions with peers in a society with hierarchical dominance structures allows for the development of the ability to gauge one's dominance and adjust behavior based on personal rank (Pellegrini & Smith, 2005). Additionally, this understanding of rank along with the formation of close, supportive relationships can aid in a primate's ability to maintain their rank or challenge that of another (Cheney, Seyfarth, & Smuts, 1986).

Chimpanzees, macaques, and baboons are three groups of primates that express Machiavellian intelligence to great degree, likely as a result of a large brain size (Byrne & Whiten, 1992). In these primates, behaviors associated with tactical deception are often expressed in both immature and adult individuals. These behaviors require a certain degree of social understanding and planning in order to manipulate a situation to one's advantage (Byrne & Whiten, 1992). However, it is also important to note that Machiavellian intelligence in primates defers from the definition ascribed to human behavior as it does not necessarily remove cooperate behaviors from the calculation. Rather, the Machiavellian intelligence in primates allows them to make decisions on when to use deceptive or cooperative actions, thus demonstrating high social cognition (Byrne, 2018).

All species, no matter how phylogenetically related, are going to experience their own process of social development and the differences within these processes may lead to very different results (Wobber et al., 2010). It is the consistency between social developmental differences and the end result that is vital for our understanding of cognition and integration (Byrne & Whiten, 2002). For example, chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*), two closely related species phylogenetically, have somewhat different social structures. Where chimpanzees have been known to be violent and intolerant toward mistakes in social contexts, bonobos are known to be rather peaceful. Bonobos exhibit more juvenile-like behavior, playing into adulthood and performing sexual interactions without an apparent reproductive purpose. Recent research suggests that these two species are likely the partial result of developmental differences associated with social behaviors, especially those involved with social inhibition. In this case, bonobos appear to be delayed in their social development, allowing for their unique sociality. These findings lead to the implication that the ontogeny of social behaviors may be an evolutionary mechanism, subsequently leading to speciation events (Wobber et al., 2010).

Even vertebrates not previously considered social exhibit the necessity of social interaction for success. In a study of juvenile veiled chameleons (*Chamaelo calyptarus*), those prevented from having occasional interactions with conspecifics are more submissive and less successful at foraging later in life (Ballen et al., 2014). Invertebrates also show similar patterns. Gregarious cockroaches (*Blattella germanica*) prevented from socializing with others exhibit consequences from this isolation including reduced foraging and explorative abilities as well as lower quality mate choices (Lihoreau et al., 2009).

In humans, several different aspects of sociality build the framework for social cognition (Tousignant et al., 2017). This framework, if fully formed, is what allows for successful social interactions as adults in which the individual meets societal expectations of behavior. The first part of this framework is theory of mind. Theory of mind (ToM) is the ability to understand that another person has their own set of feelings, intentions, and thoughts (Wellman, 2014). This calls for the ability to integrate personal information regarding the other person in conjunction with situational knowledge (Tousignant et al., 2017). In addition, successful social organisms must have the capability of understanding emotions and the ability to recognize these emotions in other individuals (Tousignant et al., 2017). This is more complex than ToM as it requires the individual to not only acknowledge the existence of emotion, but to categorize it based on immediate information and the background of the individual. Along with this building block of sociality is the concept of empathy. Empathy is the ability to understand one's emotional and mental state and associate it with personal experiences. This can also turn into sympathy, or the ability to act based on empathy, but it is not always a requirement for successful sociality (Seyfarth & Cheney, 2013). Additionally, one must also have something known as social knowledge to successfully integrate into society. Social knowledge is a comprehension of typical social interactions and behaviors. It does not require specific information about an individual. Rather, it allows for a generalized approach to a social situation based on social norms (Achim et al., 2013).

Many studies on human and nonhuman social cognition and development have solidified the fact that most vital aspects of social development take place during childhood and adolescence and changes in social settings can influence this development (Tousignant et al., 2017). For example, studies found that infants who do not participate in any form of social group or play sessions show social and emotional deficits when they reach school age (Mcdonald et al., 2018). In the same study the researchers found that mothers who lack social support and experience postpartum depression have children with higher rates of social-emotional incompetence and behavior issues.

Successful social interactions during and after the critical period of development also have major uses in other vital areas of a social organism's life. The first social interactions of most organisms' lives are those between offspring and parent. These interactions are vital for the overall success of the individual. Studies show a strong correlation between human offspring who have had high levels of positive social interactions with their parents when infants and their rate of cognitive development as they age. Those that have not experiences the same rates of social engagement from their parents are often developmentally delayed (Kang et al., 2016). In lower income adolescents, socioeconomic stress can be a life debilitating factor as it prevents the establishment of future goals. However, when a support system of peers is present, these adolescents can use stress in a positive manner and can be actually motivated toward purpose development (Gutowski et al., 2017).

Recent findings have also shed light on the epigenetic basis of social behavioral changes. Epigenetics is the study of how gene expression (not gene sequence) changes in response to various environmental, developmental, and pathological influences (Syzf et al., 2009). Epigenetic changes take place during the affected individual's lifetime. Some of these changes may also be inherited from parents who have been affected. For example, studies in rhesus macaques (*Macaca mulatta*) show that individuals reared by competent mothers can overcome the effects of a short allele related to the serotonin transporter gene while those without mother-rearing are highly aggressive, despite having the same short allele, due to the reduced transcription of serotonin resulting from the change in gene expression. These individuals with competent mothers go on to express similar behavior with their own young and are not highly affected by deficits in serotonin (Suomi, 2009). Therefore, while current environmental and social factors may influence the behavior of an individual, there may also be changes in gene expression inherited from ancestors.

Animal Models of Morality

Animal morality, or the ability make judgements of the appropriateness of behaviors based on social norms, is rather difficult to study as we do not have the ability of exploring the inside of an animal's mind (Fitzpatrick, 2017). We can, however, witness behaviors analogous to those we see that characterize human morality. Some macaques have shown an understanding of distress in others (Ballesta & Duhamel, 2015). Canine puppies use play bows to tell others their want to play (Byosiere, Espinosa, Marshall-Pescini, Smuts, & Range, 2016) while adults continue to use signals during play to clarify intention after an event that may have been construed as aggressive (Bekoff, 1995). These signals are also similar to the use of play face in Tibetan macaques in which juveniles signal to play partners and audience members (Wright et al., 2018). Other animals show behaviors that may be altruistic. Young chimpanzees have been seen to help human caretakers obtain an object that was out of reach without verbal cues (Warneken & Tomasello, 2006). Cotton-topped tamarins also exhibit the ability to remember individuals that had altruistically given them food in the past and return the favor, while also being aware of unequal rewards and acting accordingly (Crownin & Snowdon, 2008).

Additionally, there is growing evidence of theory of mind in nonhuman primates, especially apes. Anecdotal evidence suggests that bonobos are capable of understanding when others are in danger and requesting assistance from humans on their behalf (de Waal & Macebo, 2016). A study involving chimpanzees, bonobos, and orangutans (*Pongo abelii*) highlighted their ability to understand the goals of others even when the subjects held false belief (Krupenye, Kano, Hirata, & Tomasello, 2016). The apes observed interactions in which a human agent attempted to gain an object that could have been hidden in one of two locations. The agent would watch the object as it was placed in one location, but in some trials, it would be relocated to the other location. Upon watching the human attempt to locate the object after these events, the apes would focus on the location where the human originally saw the object placed. This illustrated that the apes are capable of understanding the beliefs the human hold regarding location despite knowing the true location of the object (Krupenye et al., 2016). While most ToM is focused on apes, there is a growing body of evidence that suggests monkeys may exhibit ToM capabilities. Studies with long-tailed macaques (*M. fascicularis*) have demonstrated this potential presence of ToM in monkeys. When a submissive and dominant macaque were put in a testing apparatus with one or two food items, the submissive would retrieve the food that was out of sight of the dominant monkey, suggesting not only a knowledge of the expectations of social status, but also ability to anticipate another's visual perception (Vries, Spruijt, & Sterck, 2013). Additionally, Hayashi et al. (2020) found Japanese macaques exhibit an understanding of false beliefs in a similar manner to apes. During this study, it was found that there is likely a specific neuronal link to this understanding, suggesting that this capability may have evolved 30 million years ago and descended in both apes and old world monkeys.

ToM is not a static social component. It is believed to fluctuate with age in humans (Duval, Piolino, Benjanin, Eustache & Desgranges, 2011). Specifically, the components of human ToM including the perception of cognitive and mental states in others appear to decrease as subjects entered senescence (≥70 years). However, Duval et al. (2011) did not see significant differences between young adult and middle-aged human groups, suggesting that the structure for ToM is in place by adulthood and remains relatively stable for decades. It has been found that juvenile humans appear to acquire some of the components of ToM between 3 and 4 years of age. As with other behaviors, this acquisition has also been found to be influenced by parental investment (Vilachan-Lyra, Almeida, Hazin, & Maranhão, 2015). Additionally, the rate in which ToM capabilities are acquired has the potential to be expedited through training young children in the concepts of beliefs, desires, and perceptions in other individuals (Slaughter & Gopnik, 1996). However, the acquisition of the components of ToM can also be greatly delayed due to various factors including developmental disorders such as autism and sensory deficits, specifically seen in deaf children born to hearing parents. These factors can make it difficult for children (and sometimes adults in the case of autism) to grasp the concept of false beliefs in others (Hadwin, Baron-Cohen, Howling, & Hill, 1997).

There is an evolutionary advantage to animals that use behaviors similar to those seen in human morality. By being reciprocal and showing empathy with others, animals can strengthen bonds between group mates that lead to increased resources, protection, and reproductive opportunities (de Waal & Macedo, 2016). Through studying social development in Tibetan macaques, we may gain further insights into animal morality.

Using Models of Morality

Psychologists have attempted to describe the development of human morality by using stages to define key points in this development. Lawrence Kohlberg was one of the first to create a stage model of moral development. His model consists of stages in which an individual, most likely a human toddler or infant, undergoes changes in which they progress into having a better understanding of the wants and needs of others. This process results in an adult with the ability to make moral decisions for themselves about what right or wrong is without outside influences (Kohlberg, 1984).

Kohlberg’s model has been criticized as it assumes a constant moral struggle behind every decision, ignores emotions and outside influences (Krebs & Denton, 2005) and simplifies human decision making to a high degree (Arnold, 2000). However, this model, despite its potential flaws, may still be used as a starting point for understanding social development in nonhuman primates. By comparing behavioral frequencies related to the formation of a social foundation, especially those related to intention, reciprocity, and understanding of others, we may be able to understand what stage a macaque is in regards to integrating into adult society.

Tibetan Macaques

Tibetan macaques *(Macaca thibetana)* are located in small populations in east-central China, typically along the Yangtze River (Li & Kappeler, 2020) and are considered near threatened by the International Union for Conservation of Nature (IUCN) (Yongcheng & Richardson, 2008). Similar to other macaques, each group contains multiple males. Females remain in their natal group throughout life while males leave upon reaching maturity. Group sizes average at about forty individuals, about half of which are adults (Ogawa, 2006). Female macaques reach maturity at around 5 years of age while males may take 6 to 8 years (Zhao & Deng, 1988). Tibetan macaques have strict dominance hierarchies and are categorized as being a level II in the macaque dominance ranking due to their low levels of counter aggression, low levels of reconciliation, and relaxed parenting styles (Balasubramaniam et al., 2012; Thierry, Aureli, Nunn, Petit, Abegg, & de Waal, 2008).

While many behaviors such as male emigration upon maturity and dominance-dependent behaviors are seen across macaque species, a few behaviors are unique to Tibetan macaques, making them a novel study species (Ogawa, 2006). Unlike most other macaque species that keep their juveniles, especially males, on the outer rim of the group, juveniles are fully integrated into the group and partake in huddles, associating with individuals throughout the hierarchy (Ogawa, 2006). Tibetan macaques also exhibit bridging behavior which is uncommon in most other species (Ogawa, 2020). Males are unique compared to males of other macaque species in their use of bridging behavior as well as their affiliative interactions with other males that may include mounting and penis licking. Females form coalitions with related and unrelated females during conflict (Ogawa, 2006).

Overall, adult Tibetan macaques have been found to understand social cues and preferences (Ogawa, 1995b.), partake in reciprocal grooming (Xia et al., 2012), and adjust actions based on the rankings of others (Wang et al., 2015). Females show high levels of connectivity (Fratellone et al., 2018) and kin-biased grooming (Berman, Tin, Ionica, Li, & Ogawa, 2008). Although males are less socially connected, they participate in behaviors such as bridging and reciprocal (Xia et al., 2013) and non-reciprocal (Berman et al., 2008) grooming, perhaps to maintain peace within the group. Yet, little is known about the specifics of how young Tibetan macaques learn to follow social rules associated with behaviors such as play, bridging, and grooming and fit into their society. We know that the first few weeks of life are spent on the mother who is the sole maintainer of the infant/parent relationship (Deng, 1993). At some point, though, the infant becomes a participating member of this relationship as they become more independent. Furthermore, self and social play begin after the first month, but the extent and timeline for which social rules and cues are understood are still unknown. By studying the onset and use of social behaviors seen in adulthood, it can be illustrated how infant and juvenile Tibetan macaques learn social skills.

Notable Social Behaviors of the Tibetan Macaque

When studying social development, it is important to focus on behaviors closely linked with aspects of sociality such as the understanding of intention, reciprocity, cooperation, tolerance, and the understanding of one’s social status (Pellegrini & Smith, 2005; de Waal & Macedo, 2016). For these reasons, play, grooming, and bridging behaviors are useful ways to assess the development progress in social cognition of Tibetan macaques.

Play Behaviors

Play has been found to be a vital aspect of development in many vertebrate species (Allen & Bekoff, 2005). While definitions vary, there are five criteria typically used to categorize a behavior as play. These are described by Burghardt (2005) as:

> 1) The performance of the behavior is not fully functional in the form or context in which it is expressed; that is, it includes elements, or is directed toward stimuli, that do not contribute to current survival. 2) The behavior is spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic ("done for its own sake"). 3) It differs from the "serious" performance of ethotypic behavior structurally or temporally in at least one respect: it is incomplete (generally through inhibited or dropped final elements), exaggerated, awkward, or precocious; or it involves behavior patterns with modified form, sequencing, or targeting. 4) The behavior is performed repeatedly in a similar, but not rigidly stereotyped, form during at least a portion of the animal's ontogeny. 5) The behavior is initiated when an animal is adequately fed, healthy, and free from stress (e.g., predator threat, harsh microclimate, and social instability), or intense competing systems (e.g., feeding, mating, and predator avoidance). In other words, the animal is in a "relaxed field." (p. 71)

Play has many suggested uses. It is believed to prepare juveniles for adulthood by allowing them to acquire and build onto skills required later on in life, allow for increased fitness through exercise, develop problem-solving skills, and provide a foundation for social interactions and relationships (Bateson, 2011). Both in humans and non-human primates, play fighting has been suggested as a way to build and test social relationships. Play fighting provides the opportunity to gauge the intentions and feelings of peers and act accordingly. These skills become vital into adulthood to maintain cohesive groups and relationships (Pellis & Pellis, 2011). Additionally, the lengthened juvenile period seen in primates may suggest an extended period of learning. As play is most prevalent in this period, it is likely linked to many forms of cognition (Pellegrini & Smith, 2005).

Frequencies of play behaviors have been seen to decrease in both male and female rhesus macaques (*Macaca mulatta*) as they age (Kulik, Amici, Langos, & Widdig, 2015). However, male infants start out their lives playing more often than female infants. Furthermore, their play frequency remains higher into development than that of females. Despite the decrease of play through maturity, the duration of play bouts tends to increase as Japanese macaques (*Macaca fuscata*) age (Nahallage & Huffman, 2007). Additionally, infant and juvenile rhesus macaques tend to prefer peers of a similar age to themselves as play partners (Kulik et al., 2015).

Additionally, the despotism of a society likely affects the style of social play present during youth (Reinhart, Pellis, Thierry, Gauthier, VanderLaan, & Pellis, 2010). As macaques exhibit a scale of dominance style ranging from despotic to egalitarian, their social behaviors throughout their lives will reflect it. Juveniles of more despotic species (stage 1) such as the Japanese macaque (*M. fuscata*) show more competitive play fighting styles (Reinhart et al., 2010) marked by decreased tolerance during play (Thierry, 2004). Contrastingly, egalitarian species (stage 4) such as Tonkean macaques (*M. tonkeana*) show cooperation in play with high levels of tolerance that allows for the play session to continue (Reinhart et al., 2010). These differences in behavior as a reflection of societal structure could easily be compared to human societies. Social contexts such as religion, economic structures, and government forms produce various cultures and societies in which different behaviors are expected (Ciani, Dall'Olio, Stanyon, & Palagi, 2012). Similar to different species of macaques, children of different cultures may play at different rates and in very different contexts (Whiting & Edwards, 1973).

Research studying the relationship of play signals in Tibetan (Wright et al., 2018) and rhesus (Yanagi & Berman, 2014) macaques before, during, and after play bouts suggests that play signals are most used and most effective during play rather than directly prior and after play (Wright et al., 2018). These signals may be a way of juveniles informing to their partners their intention to continue play (Yanagi & Berman, 2014; Wright et al., 2018). Furthermore, play bouts are rarely ended by outside observers, suggesting that play signals may also serve as a way of signaling to other macaques, especially adults, assuring that there is no threat meant to the play partner (Wright et al., 2018).

Along with play signals, play handicapping also increases the duration of play (Petrů, et al., 2009). With dominant, older, or stronger individuals decreasing the intensity of their play, younger, inexperienced individuals are less threatened and are able to learn new skills through the play bout. Petrů et al. (2009) compiled a self-handicapping ethogram of five old-world monkey species assigning behaviors to three designated categories: Social self-handicapping (restricting effort, picking superior partners), kinematic self-handicapping (challenging postures or movements, carrying objects), and sensory self-handicapping (restricting perception, usually visual). These forms of self-handicapping were relatively equal in frequency across all the studied species (Petru et al., 2009). However, it is important to note that the evidence of self-handicapping behavior in Tibetan macaques is less substantial than in other species. As rhesus macaques typically pick play partners most similar in experience and size as themselves (Kulik et al., 2015), it may be that Tibetan macaques do the same.

Recent studies have indeed found some suggestion that many behaviors of other macaque species align with those of Tibetan macaques (Mayhew, Funkhauser, & Wright, 2020). For example, play most often occurs between individuals of similar age and individuals tend to spend less time playing as they reach adulthood. Both polyadic and dyadic play occur in the species, with dyadic play occurring more frequently. Additionally, it was found that maternal rank did not seem to have an influence both on the choice of play partner or the length of play itself (Mayhew et al., 2020).

Grooming

Grooming in Tibetan macaques has many implications for an individual's social situation, including reducing aggression and maintaining social connections Xia et al., 2020). Adult males groom more dominant males in exchange for reduced aggression, especially during the mating season (Xia et al., 2013). This was seen in a study taking place at Mt. Huangshan Natural Reserve in China in which Xia and colleagues studied grooming behaviors in relation to rank and time of year. Results showed that grooming reciprocity between males is the highest during the non-mating season when dominant males are less threatened by competition and will often groom submissive males in return (Xia et al., 2013). This interchange of grooming for tolerance has also been found in female dyads where one is of significantly higher rank than the other (Xia, Garber, Sun, Zhu, & Sun, 2012).

Grooming behaviors in females among the same group of macaques at Mt. Huangshan, China have also been studied. Adult females, while seen grooming all members or their natal group, often adjust time allotted for each individual depending on the group size (Berman et al., 2008). Typically, females exhibited kin bias when grooming by grooming closely related individuals more often. However, as group size increases, less time is spent grooming each individual (Berman et al., 2008). Females also exhibit reciprocal grooming more so than do males, although the extent of reciprocity is largely based on rank, with lower ranking individuals grooming those of higher rank more often (Xia et al., 2012). A study involving infant rhesus macaques aimed to understand sex differences during development by tracking social behaviors such as grooming and play behaviors. When looking at grooming during development, the authors found females tended to groom at earlier ages than males. The frequency with which they groom non-peers also increases with age (Kulik et al., 2015).

Given this knowledge on grooming, it is expected that all immature macaques will increase their grooming frequency as they age, but females will do so earlier. This increase in grooming, as well as the initiation of reciprocal grooming highlights the acquisition of adult-typical social behaviors (Xia et al., 2012; Xia et al., 2013). Through the extensive study of young macaques at all ages and both sexes, the exact onset and development of these grooming behaviors can be documented, suggesting the preparation patterns of integrating into adulthood.

Bridging

Bridging behavior is characterized by one individual picking up an infant and presenting it to another individual (Ogawa, 2006). The two macaques hold the infant together, sometimes licking or sucking on its penis if male and licking its genitals if females. Males are well known participants in this behavior and also tend to use male infants. For adult males, the bridge initiator is often a lower ranking male compared to the recipient. It is believed that this behavior is a way to maintain peace within a group with a large quantity of males (Ogawa, 2006). However, recent studies have found that juvenile and adult females also participate in bridging (Clifton et al., 2020). Unlike in males, this behavior is not necessarily linked to reducing tension, but is rather a result of interest in infants, possibly preparing young females for motherhood

(Clifton et al., 2020). Males have also been found to have a preferred infant to bridge with known as an affiliated infant (Bauer, Sheeran, Matheson, Li, & Wagner, 2014). Males understand the preferences of males they want to bridge with and will usually use this affiliated infant to initiate a bridge regardless of the distance and energy cost needed to obtain the infant. Bauer et al. found that an adult male's infant preferences are not correlated to his relationship to the mother (Bauer et al., 2014). Juveniles have been seen to attempt bridging with one another, although this is less common and has not been greatly studied (Ogawa, 2006).

There is a current lack of knowledge of the first occurrences of bridging behavior and how the frequency of this behavior increases as juvenile Tibetan macaques mature. While infants will not be active participants (aside from being held during bridges), juveniles are known to bridge with one another, likely preparing themselves for similar adult interactions (Ogawa, 2006). Through analyzing the changes in frequency of this behavior throughout the life of a young macaque, their understanding of adult interactions can be assumed.

Social Development in the genus *Macaca*

Little research has been done in regard to Tibetan macaque social development. As discussed previously, there are marked sex differences seen in social behavior frequencies in rhesus macaques (Kulik et al., 2015). These differences become most apparent at 2 years of age, suggesting that this may be a vital time for social development (Kulik et al., 2015). Some research of other macaque species provides insight into factors that possibly influence social intelligence of Tibetan macaques. A study of newborn rhesus macaques found infants use imitation of facial gestures such as lipsmacking and tongue protrusion to maintain social bonds with other individuals by imitating behaviors specific to the other individual (Simpson, Paukner, Sclafani, Suomi, & Ferrari, 2013). Comparative studies of different species with varying dominance styles have also found that mothers and group social structures play an imperative role in how infants and juveniles develop. In species with relaxed dominance styles such as Tonkean macaques (*Macaca tonkeana*) where mothers are less restrictive, infants show higher sociality at younger ages as they are permitted to interact with more group members while this is not the case for more despotic species like the rhesus macaque (Thierry, 1985; Thierry 2004). Sociality differences can also be illustrated in the same species of a single group as higher-ranking mothers tend to restrain their offspring less than lower-ranking mothers (Thierry, 1985). This can lead to an increase in play, grooming, and bridging behaviors as infants with higher ranking mothers are given the opportunity to perform these behaviors without adult intervention. Nursery-reared infant pig-tailed macaques (*Macaca nemestrina*) show steep changes in types of behaviors at several weeks old as they became more explorative and began to interact with peers, suggesting another critical time for development (Worlein & Sackett, 1997). As they mature, rhesus macaques exhibit more active forms of social behavior while behaviors used in reaction to stressful or fearful experiences remain relatively constant (Borell, Kulik, & Widdig, 2016). Social structure and development may vary across the macaque genus as well as factors such as age, ranking, and sex, which may all play important roles in determining the rate of social development.

Through the observation of behaviors that are known to be connected to social cognition, the relative onset and progression of these behaviors can be assessed. By understanding the combined frequencies of behaviors associated with social development such as grooming, play, and bridging behavior, stages of development compared to the age of an individual can be formed. These stages can serve to highlight important times in development and areas in which this development can be positively or negatively. Additionally, the effects of these influences can be illustrated through studying the correlation between maternal rank and the presentation of social behaviors. Furthermore, this study can serve as a foundation for future studies of Tibetan macaque social development and provide insights into the evolutionary understanding of morality and theory of mind.

CHAPTER III

METHODS

Study Subjects and Site

I collected data at Mt. Huangshan National Reserve, Anhui Province, China (118.3E, 30.2N, elevation 1841m). This area is a UNESCO World Heritage site and a popular tourist destination. The site is mountainous with coniferous and semi-deciduous forests in lower elevations (Berman, Ionica, & Li, 2004). Several groups of Tibetan macaques inhabit this area. Since the 1980s, these Tibetan macaques have been studied in the scientific community. Due to the drive of tourism, the macaques were relocated roughly 1 km in 1992 from their previous range to an area more suitable for tourist viewing (by the local government). This relocation led to the formation of the current macaque groups (Berman et al., 2004).

The study subjects, the members Yulingkeng A1 group (YA1), are the most frequently studied in the area. In past years, this group was also the one most viewed by tourists at viewing platforms. However, in the past few years the management of the site has changes leading to a decrease in tourism. While previously provisioned by park guards during the increase period of tourism, these macaques are now provisioned by local villagers or researchers between a few times a day to maximize visibility to tourists and researchers. While not forced to remain in this observation area, the macaques’ range is mostly limited to areas near the provisioning site. This surrounding area is largely forested and does not contain any known natural predators to the Tibetan macaques (Berman et al., 2004).

Due to the extensive research done on this group over the last few decades, the family relationship, age, sex, dominance ranking, and identity are known for each individual in the group. At the beginning of the study, the group consisted of 30 adults, 3 adolescents, 16 juveniles, and 12 infants. The adolescents were classified by the fact they had not yet emigrated out of the group and were under 8 years of age. All immature individuals were included in focal sampling. TouRongJing, a one-year old female, died in the middle of the study. Her data was not included in the final analysis.

Procedure

I spent the 2 weeks prior were spent learning to identify individuals reliably. In the following weeks, I collected data almost every day from approximately 8am - 12pm and 2pm - 5pm. Occasionally, I was unable to perform any observations due to poor weather and the absence of the study subjects, though, these days were rare and only occurred four times during data collection. I made portion of observations from the viewing platforms. However, as the macaques often dispersed into the forest, I also made many observations elsewhere, throughout the site.

I collected 10-minute focal samples (Altmann, 1974) in which I recorded the frequency of behaviors (Table 1) and durations of play. I chose samples in the order of a random sampling schedule. Each round of sampling had a new sampling schedule. I used all-occurrence sampling (Altmann, 1974) to collect data on bridging behavior as this behavior is generally less common, especially in juveniles. I recorded all observations using a Kickteck 4k camcorder to ensure a more thorough assessment of the more complicated behaviors, mainly play. Additionally, I took preliminary handwritten notes of all behaviors while in the field. As limited time was available for this study, I also analyzed previously recorded camera trap videos provided by Dr. Jessica Mayhew to find average adult male and female behavioral frequencies in order to serve as a way to gauge development.

Table 1

Ethogram

Behavior	Description
Social Play	Two or more macaques are chasing, wrestling, slapping, biting, or cuddling without clear intention of harm.
Play Signaling	Form of communication used to encourage play and increase the duration of a play bout. (See Table 2)
Play Handicapping	Individual adjusts the intensity and strength of play to match their partner. Handicapped individual increases their vulnerability. (See Table 3)
Bridging Attempt	An individual either presents an infant or juvenile to another for a bridge or tries to manipulate an already held individual for a bridge.
Bridging Success	An individual either presents an infant or juvenile to another for a bridge or tries to manipulate an already held individual for a bridge. The two hold the younger macaque together.
Groom	Combing or manipulating the hair of another individual with the hand and/or mouth.
Groom Acceptance	Another individual is combing through or manipulating the hair of the focal individual
Reciprocal Groom	The individual directly grooms an individual that had recently groomed them.

I noted play bouts when two or more individuals began chasing, wrestling, slapping, play biting, or cuddling one another without any clear intention of harm (Wright, et al., 2018). I considered the session ended when the individuals began a behavior not evident as play (as defined in Table 1) or activity ceased for more than 5 seconds through their own choice or through adult intervention (Wright et al, 2018). In the case of a play bout at the end of the focal period, I continued the focal sample until play ceased. It is likely that when a mismatched pair of macaques are playing, for example, a 1-year-old and a 5-year-old juvenile, the oldest, largest one is performing some form of self-handicapping behavior. This may include reducing their strength or allowing the smaller individual to have more power in a situation (Shimada, 2006). While there is not extensive research done on play-handicapping in the *Macaca* genus, Shimada broadly categorizes the behavior as when size or age differences between partners are significant and the smaller, younger, or more vulnerable individual is capable of continuing to play without being overwhelmed. However, it is often difficult to identify when an individual is restricting strength and intensity. Therefore, more discrete handicapping behaviors were used. The individual in the dominant position may allow themselves to be chased and, if an object is being used, would forfeit their possession of the object to the lower individual (Shimada, 2006). I created the ethogram for play handicapping using a combination of previously defined behaviors (Petru, Špinka, Charvátová, & Lhota, 2009) and personal observations once in the field prior to the start of data collection (Table 2). I recorded any occurrence of play signals during play bouts according to the definitions in Table 3. The play signals that I observed, were the most prevalent signals of young Tibetan macaques seen according to Wright et al. (2018).

Table 2

Definitions of Play Handicapping

Handicap	Definition
Posture Handicapping	Individual is in a vulnerable position such as lying down, hanging, doing a headstand
Visual Handicapping	Individual is engaged in play bout with eyes closed
Bite Allowance	Individual is allowing partner(s) to bite on/near vulnerable areas i.e., genitals, face, neck
Role reversal/Chase	Dominant opponent switches role in bout to be submissive participant (chaser becomes the chased, relinquishes object, etc.)
Manipulation Allowance	Individual is easily pushed over, rolled, or physically moved by partner(s)

Table 3

Definitions of Play Signals

Play Signal	Definition
Play face	Expression in which the brow is pulled back and open mouth in which the top lip hides the upper teeth (Levy, 1979)
Slap-and-play face	Open mouth face in conjunction with hitting a playmate's body
Crouch-and-stare	Individual maintains visual fixation of partner while limbs are fixed and ventral surface is on or near the ground (Symons, 1978)
Dangle-and-stare	Individual hangs from object by hind limbs and visually fixates on partner (Levy, 1979)
Roll-onto-back-and-stare	Individual lies on back and stares at partner (Levy, 1979)
Play threat	Individual directs a lunge within close proximity to partner and slaps ground without facial expression

Most common forms of play signals in Tibetan macaques. Adapted from Wright et al. (2018)

Since it is often difficult to determine which individual initiated a bridge, especially when looking at females with infants, I broke bridging behaviors into two categories: attempts and successes. A bridge attempt was recorded if the macaque picked up an infant or juvenile monkey and presented it to another individual by holding it out to them. I labeled it as a success if two individuals held the infant together, possibly licking its genitals or sucking its penis if male (Ogawa, 1995a). As I was using all occurrence sampling for bridging behaviors, I recorded data for both individuals participating in a bridging event.

I recorded occurrences of allogrooming in terms of acceptance, grooming, or reciprocal grooming. As self-grooming has no apparent social foundations or uses, it was not assessed in this study. I noted grooming when an individual combed through another individual's hair using their hands or mouth, looking for and picking out debris or insects for at least 5 seconds. I only considered grooming as reciprocal if the focal individual began grooming a macaque that had just groomed them. I considered grooming to be terminated if the behavior was stopped for more than fifteen seconds.

To ensure intra-rater reliability, I watched and scored muted video recordings of events taken during the previous week for all behavioral frequencies and durations. I compared this the notes taken upon the recording of the data as well as the audio of the original video. I performed these checks every week for the duration of my study.

This project was approved by Central Washington University's Institutional Animal Care and Use Committee (protocol #A111801). Approval was also granted by Anhui University to conduct the study at the site.

Data Analysis

I collected 3 hours of data for each individual. I conducted all data analyses using R software in RStudio. Data was unable to be transformed and lacked normal distribution. Therefore, I chose to perform non-parametric tests When comparing grooming, bridging success, and play behaviors against age, I conducted individual Spearman rho tests on each behavior. Additionally, I also performed Spearman rho tests comparing both play signaling and play handicapping to the average length of play bout to assess whether trends aligned with what was observed in Wright et al (2018). This test was chosen largely for its ability to evaluate the correlation of non-parametric, continuous data. Additionally, while Spearman correlations typically are used with monotonic data, they have also been found to be successful to some degree in non-monotonic relationships similar to the ones that may be seen in this study (Puth, Neuhäuser, & Ruxton, 2015). Each individual's data was used for the Spearman rho tests (n = 32). For adult male and females, 5,000-days-old was used as the age for both data sets as it is close to middle age for both sexes and was also about the average adult female age during data collection. Given the apparent adult skew regarding the age of individuals, an additional Spearman rho test was performed for each behavior omitting the adult data (n = 30).

For further assessment of the effects of combined factors, specifically, maternal rank and sex, I used a Generalized Linear Mixed Model (GLMM) through the glmmML package in Rstudio. GLMMs are highly versatile tests that do not require normality, can be used with a combination of binomial and continuous data, and control for random effects of individuals. They have become increasingly prevalent in ecological studies due to these factors and their ability to break down various relationships within datasets of few samples (Bolker et al., 2009). It is important to note, however, that model-fitting for a particular data set can be quite challenging and a more accurate, advanced model may be more suitable than the one used through the glmmML package in Rstudio. Because maternal rank was not determined for the average male and female adult data, YeQiuSe, and HuangYu, their data was omitted from the GLMM analyses (n = 28). All tests used a confidence interval of 0.95.

CHAPTER IV

RESULTS

Grooming

All occurrences of allogrooming were used for analysis. Data about reciprocal grooming were not enough to perform separate analyses. The Spearman's correlation test for grooming indicated a positive relationship with grooming and age both in analyses including (n = 32, ρ = 0.794, p = 5.86e-08) and excluding adult data (n = 30, ρ = 0.761, p = 1.07e-06). In Figure 1, it appears that grooming behaviors is near adult levels at around 4 years of age. The GLMM results (n = 28, z = 4.195, p = 2.73e-05) resembled those of the Spearman's rho. However, maternal rank and sex of groomer were not found to have a significant effect on the frequency of grooming (z = -1.027, p = 0.304; z = 1.697, p = 0.090).

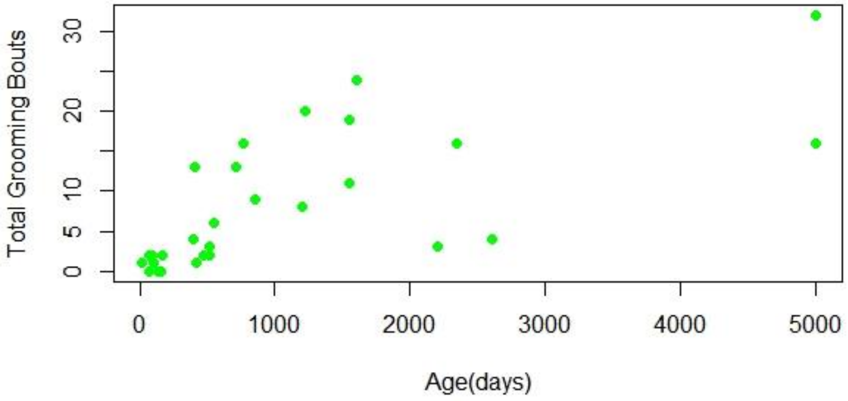

Figure 1: Total occurrences of grooming among individuals of varying ages

Bridging

Only bridging successes were used for the analysis as bridging attempts were too few. The earliest successful bridge was performed by YeQiuTian who was 554 days old at the beginning of data collection. According to the Spearman's test, the frequency of successful bridges was also correlated with age (n = 32, ρ = 0.772, p = 2.30e-07) (Figure 2). Similar results were seen when adult data was omitted (n = 30, ρ = 0.718, p = 8.08e-06). Bridging successes near adult frequencies between 4 and 5 years of age. The GLMM also indicated this relationship (n = 28, z = 5.2562, p = 1.47e-07) as well as the significant influence of maternal rank. As maternal rank rose, the occurrences of successful bridging were higher (n = 28, z = -2.39, p = 1.69e-02). The relationship of bridging and sex was not significant (z = 0.548, p = 0.583)

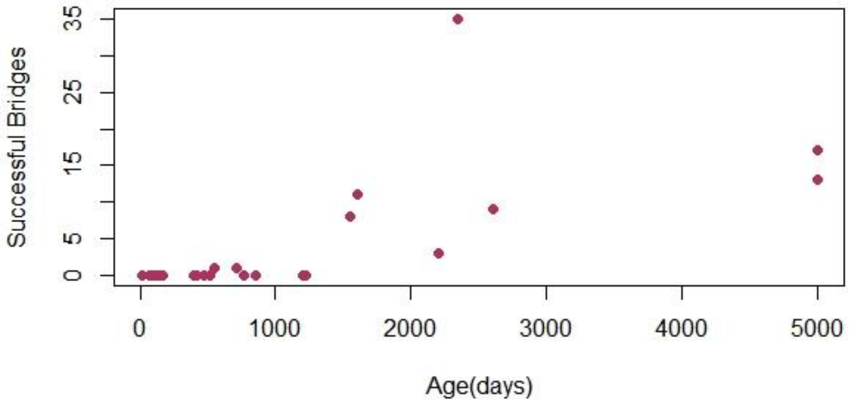

Figure 2: Occurrences of successful bridges across varying ages.

Play Behaviors

According to the significant results of the Spearman rho (*n* = 32, ρ = -0.625, *p* = 1.32e-4) and the GLMM (*n* = 28, z = -6.740, *p* = 1.58e-11), Tibetan macaques appeared to play less as they aged, with levels reaching those of adults at around 4 years as evident in Figure 3. These results were also seen in Spearman rho analyses omitting adult data (*n* = 30, ρ = -0.550, *p* = 0.002). Additionally, the GLMM also exhibited strong influences from both sex and maternal rank. Male individuals had higher frequencies of playing (*n* = 28, z = -3.652, *p* = 2.60e-04). Higher ranking individuals were also played more (*n* = 28, z = -2.004, *p* = 4.51e-02). The average length of play was also negatively correlated with age (*n* = 32, ρ = -0.367, *p* = 0.039; *n* = 28, *z* = -4.833, *p* = 0.35e-06) with younger individuals playing for longer periods of time. Maternal rank and sex did not have an influence on the average length of an individual's play bout (*p*>0.05). However, play signaling (*n* = 32, ρ = 0.938, *p* = 2.28e-15) and play handicapping (*n* = 32, ρ = 0.881, *p* = 2.91e-11) had a positive relation to the average length of a play bout (Figures 4 and 5). When adult data was omitted, play signaling and play handicapping continued to show these relationships to the average length of play bouts (*n* = 30, ρ = 0.937, *p* = 1.95e-10; *n* = 30, ρ = 0.876, *p* = 2.20e-10).

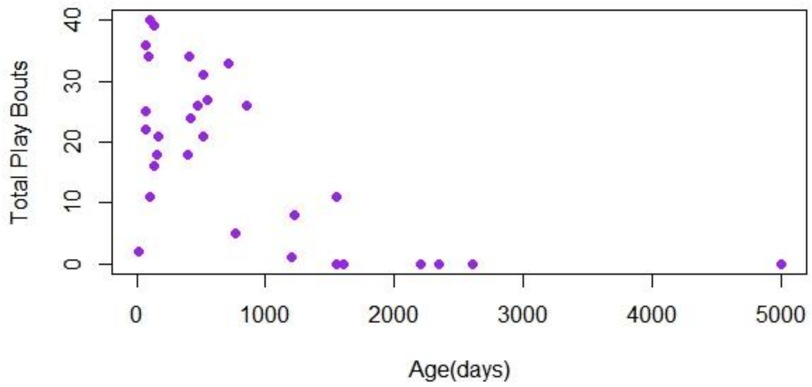

Figure 3: Total amount of play bouts per individual of varying age

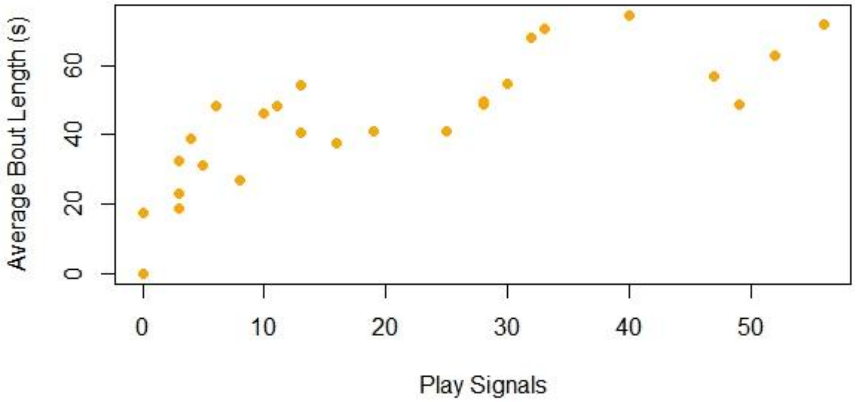

Figure 4: Effects of play signal occurrence on the average length of play bouts

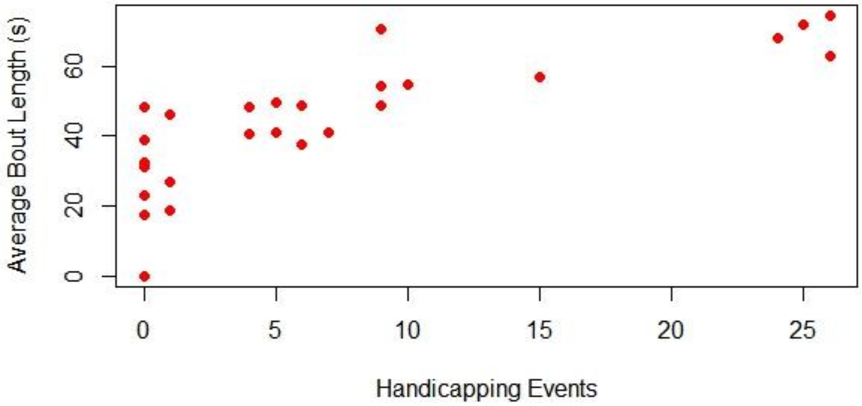

Figure 5: Effects of play handicapping on the average length of play bouts

Play behaviors related to further social understanding and successful development also showed somewhat significant results, but only in conjunction with other factors. Spearman rhos showed that play signaling (*n*= 32, ρ = -0.323, *p* = 0.071) and handicapping (*n* = 32, ρ = -0.204, *p* = 0.262) were not significantly correlated with age on their own. Analyses of data without adult data points yielded similar results for both behaviors ($n = 30$, $p > 0.05$). However, GLMM's showed that when combined with sex, trends began to be significant. For play signaling, the GLMM showed that younger ($n = 28$, $z = -3.526$, $p = 4.22e-04$) and male ($n = 28$, $z = -3.076$, $p = 2.10e-03$) individuals actually showed higher rates of play signaling. The same trends were seen with play handicapping as younger ($n = 28$, $z = -2.029$, $p = 4.28e-02$) and male ($n = 28$, $z = -3.327$, $p = 8.78e-04$) individuals were seen to handicap more than others. Of all behaviors recorded, play face was the most prevalent play signal and postural handicapping was the most frequent handicap type (Table 4). I was not capable of assessing the difference of age among play partners during handicapping events as there were often multiple partners that entered and left the play bout throughout its duration.

Table 4

Frequencies of Specific Play Signals and Handicap Types

Type of signal	**Frequency**	**Type of Handicap**	**Frequency**
Play face	407	Postural handicap	100
Slap and play face	48	Visual handicap	57
Crouch and stare	23	Bite allowance	14
Dangle and stare	37	Role reversal/chase	11
Roll onto back and stare	14	Manipulation allowance	11
Play threat	7		
Total	536	**Total**	193

CHAPTER V

DISCUSSION

To investigate the progression of social development in Tibetan macaques and gain more insight into their ability to identify and follow social rules, I conducted a cross sectional study of immature macaques at the Valley of the Wild Monkeys, Huangshan, China. Through the assessment of behavioral frequencies and durations across ages and the influences of maternal rank and sex, I found that a large portion of the data supports the predictions derived from my hypothesis.

The prediction (Prediction I) that grooming would increase during development was supported by this study. However, the expected sex difference (Kulik et al., 2015; Xia et al., 2012) in which females, regardless of age, would groom more was not supported. This is quite possibly a result of the small samples size as well as the skew between sexes. Where there was nearly an equal number of male and female individuals under the age of 2 years old, there were greater disparities in sex ratio in older age groups as well as a smaller sample size overall.

As expected, bridging success also increased with age, suggesting an increased understanding of social rules and dynamics (Ogawa, 2006). This result supports Prediction II. It is important to note, however, that the youngest, successful bridge initiator was 554 days old. This is remarkably younger than previous anecdotes that stated successful bridging occurred after the 3-year mark. Of course, not all individuals around this age participated in similar behaviors and the behavior is likely influenced by other factors. For example, maternal rank may be one of these factors as its relationship to bridging behavior was found to be significant. Individuals with mothers of higher rank were found to bridge more often than those of lower rank. This could potentially be a result of higher-ranking mothers giving their offspring more freedom than those of lower ranks (Thierry, 1985), allowing the juveniles a greater opportunity to participate in this behavior. Interestingly, no significant difference between male and female bridging behaviors was found. This is likely partially due to the small sample size. While young individuals were found to bridge, the highest proportion of bridges were in those over the age of 3, of which there were only 7 individuals used in data analysis. Four of these were females. Two of these females, YeXiaYue and HuaXiaYue, were of the same age cohort and often interacted socially. Additionally, YeXiaYue had given birth to a daughter, YeQiuSe, shortly before data collection. These two females often bridged together. It cannot be certain whether this behavior occurred before YeQiuSe's birth and was always a behavior associated with their social bond due to the lack of information regarding their behavior before observations. However, this high frequency of bridging may also be a way for both females, especially, HuaXiaYue, to practice for motherhood without risking aggression from other mothers (Clifton et al., 2020).

Predictions for play (III, IV, V, and VI) had varying levels of support. Individuals did indeed play less often as they aged according to our analysis, supporting Prediction III. As seen in previous macaque studies (Kulik et al., 2015), males were found to play more frequently than females. This coincides with the fact that females typically mature faster than males and begin to exhibit adult typical behaviors sooner (Zhao & Dheng, 1988). In addition to the influences of sex, maternal rank also appeared to have some relation to the frequency of play with those of higher rank playing more often. This is likely related to Thierry's (1985) findings that lower-ranking mothers, especially in despotic primate societies, tend to restrict their offspring's exploration and interactions more than higher ranking mothers. Therefore, offspring of higher-ranking mothers may have simply been given the opportunity to play more often than those of lower ranking mothers.

The finding that the average length of a play bout also decreased with age was surprising as it was expected that, although frequency would decrease, the length of the bouts would increase due to an increase of social understanding of how to prevent play from ending prematurely. This result indicates the rejection of Prediction VI. There are two possibilities. One is that Prediction VI was made based on the study in the Japanese macaques (Nahallage & Huffman, 2007), but it may not necessarily be the case for the Tibetan macaque for reasons that are yet to be known. Also, it is important to note that the results maybe likely to be skewed by the few individuals in older age cohorts. These data may not reflect the situation for the species as a whole. It is likely that a more evenly distributed population may have yielded difference results.

Similarly, both play signaling and handicapping did not show the expected positive correlation with age when studied independently in the Spearman rho correlations, so Predictions IV and V are not supported. This is once again likely due to the significantly higher proportion of younger individuals. GLMMs did show that, for both types of behavior, the sex of the individual had a significant impact on the frequency of the behavior. Specifically, males participated in play signaling and play handicapping more often. This aligns with the previous findings in rhesus macaques that males, in general, play more often than females (Kulik et al. 2015). While the predictions of a positive correlation between age and behavioral frequency of play signaling and handicapping were not supported, it is important to mention that both play handicapping and play signaling were found to significantly influence the average length of the play bout, making it longer, thus supporting findings found in Wright et al. (2018).

Predictions I and II that stated grooming and bridging increases with age were supported. Moreover, Prediction III was also supported as individuals played less often as they aged.

However, the more detailed predictions, Predictions IV, V, and VI, of play were not supported. It is highly possible that this was a result of a skewed sample population in which infants and 1-year-old individuals were plentiful but older juveniles and adolescents were scarce.

In general, it is also important to note that there were likely many anthropogenic influences. During data collection there were times where both tourists and researchers were present on the platforms and throughout the site. During these periods, I observed many negative interactions that led to monkeys being frightened away or forced to threaten and sometimes attack humans. In other scenarios, humans brought food to the site in which the monkeys either stole, or were eventually given, leading to other concerns about the subsequent health of these individuals. Garbage was also often left at the site and would distract from natural behaviors. All of these factors likely skewed the amount of natural behaviors I was capable of recording and, in many, interrupted focal sampling.

Additionally, the site itself led to many challenges that may have affected the results. Because the site is no longer being maintained by the Chinese government, it, in many areas, has fallen into disrepair. While the main viewing platforms are still intact, the bridge leading further into the site is nearly gone, and I had to carefully climb on the metal frame if I wanted to observe monkeys near the upper platform. This, in addition to the monkeys moving further away due to inconsistent provisioning, forced me to go off from the typical areas and into the forest. The terrain is steep and slippery and often forces humans to rely on the support of trees as they work their way up hillsides. Because of this, macaques would easily go out of view and be lost as relocating them would take time and filming would have to be stopped until I could safely navigate to the new location.

Of course, one of the largest factors that may negatively have contributed to this study was the sample size. While the summer of data collection was the summer with the highest number of births in the past years for the YA1 group, data was still greatly limited in the older age groups. This was especially seen in individuals of 2 years of age and older making up only a third of the study subjects. This skew means that the analysis of social development for older juveniles would be less thorough than those of infants and 1-year-olds. Additionally, when looking at older juveniles, I also saw a disparity in sexes with individuals of similar ages being all male or all female depending on the birth cohort (Table 5).

Table 5

Immature Macaque Roster

Macaque ID	**Sex**	**Days Old (July 11th)**	**Maternal Rank**
YeXiaKun	M	2342	2
HuangYu	M	2200	N/A Immigrated
TouXiaLong	M	2602	8
TouQiuSong	M	1556	6
HuaXiaYue	F	1606	7
YeXiaYue	F	1548	2
TouQiuYing	F	1228	10
TouFuHua	F	1205	16
YeXiaMing	M	856	9
TouXiaJun	M	713	8
YeQiuTian	M	554	1
TouQiuGuo	F	767	6
TouFuKang	M	517	16
TouHuaMeng	M	512	15
TouFuJian	M	477	14
YeXiaPeng	M	420	3
TouRongJing	F	510	17
YeXiaTong	F	409	2

Table 5 (CONTINUED)

Macaque ID	Sex	Days Old (July 11th)	Maternal Rank
HuaXiaChong	M	398	7
TouHuaWei	M	166	13
TouQiuMu	M	141	10
TouHuaZheng	M	105	19
YeQiuXiao	M	102	1
YeHuaXun	M	93	20
TouFuZhong	M	74	16
HuaQiuZhi	F	154	12
TouXiaDi	F	138	8
TouQuiZhu	F	134	6
YeXiaQin	F	68	2
TouHuaSheng	M	69	15
YeQiuSe	F	11	NA (mother is 4yrs old)

Shortcomings aside, there are some notable outcomes from this study. Interestingly, grooming, bridging, and play bouts all saw similar patterns with levels reaching those of adulthood at around 4 years of age. This may suggest that this period of time is vital for social integration as juveniles begin to make the transition into adolescence and subsequently adulthood. The 4-year mark in Tibetan macaques may be comparable to the point between 3 and 4 years of age in human children in which they begin to exhibit the components required for ToM (Vilachan-Lyra et al., 2015). Furthermore, the findings in this study support those of previous research in which the functions of play signals and play handicapping were assessed (Wright et al., 2017; Petrů, et al., 2009). This further acts to solidify the connection of play to important realms related to social development including potential components of theory of mind such as intention and empathy (Seyfarth & Cheney, 2013; Wellman, 2014).

However, while there was indeed evidence for the development of behaviors related to social rules in Tibetan macaque society, much more research must be conducted for a better understanding of the progression of social behaviors, especially those with greater complexity. Ideally, a longitudinal study is needed to complement cross sectional studies like the current one to establish the full relationship and degree of importance of each behavior to adult integration and social success. Only then will we be able to truly connect social behaviors to concepts of morality like theory of mind, while also creating a more concrete formula in which the timeline of individual social development can be obtained.

Further studies on this developmental timeline should continue to incorporate outside factors like maternal rank and individual sex as these are likely going to influence social and nonsocial behaviors. During this study, anecdotal observations regarding social deficits related to maternal age and the number of siblings were made so it is likely that a large array of familiar factors are further influencing results regarding social development.

In conclusion, this study shows that, although a definite timeline was still not entirely clear, juvenile Tibetan macaque began exhibiting adult-typical behaviors at 4 years of age. In the time prior to this point, juvenile Tibetan macaques are expected to exhibit specific behaviors in correspondence to their acquisition and understanding of social rules. Specifically, this is defined by the increase of grooming and bridging behaviors and the decrease in general play occurrences. However, this process is in no way linear, nor will it be the same for each individual as other factors such as sex and maternal rank often play a role leading to individual-specific behavioral patterns.

REFERENCES

Achim, A. M., Guitton, M., Jackson, P. L., Boutin, A., & Monetta, L. (2013). On what ground do we mentalize? Characteristics of current tasks and sources of information that contribute to mentalizing judgments. *Psychological Assessment*, *25*(1), 117-126. doi:10.1037/a0029137

Allen, C., & Bekoff, M. (2005). Animal play and the evolution of morality: An ethological approach. *Topoi, 24*(2), 125-135. doi:10.1007/s11245-005-5050-8

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3), 227-266. doi:10.1163/156853974x00534

Arnold, M. L. (2000). Stage, sequence, and sequels: Changing conceptions of morality, post-Kohlberg. *Educational Psychology Review*, *12*(4), 365-383. doi:10.1023/a:1009026230018

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., . . . Waal, F. B. (2012). Hierarchical steepness, counter-aggression, and macaque social style scale. *American Journal of Primatology, 74*(10), 915-925. doi:10.1002/ajp.22044

Ballen, C., Shine, R., & Olsson, M. (2014). Effects of early social isolation on the behaviour and performance of juvenile lizards, *Chamaeleo calyptratus*. *Animal Behaviour, 88*, 1-6. doi:10.1016/j.anbehav.2013.11.010

Ballesta, S., & Duhamel, J. (2015). Rudimentary empathy in macaques' social decision-making. *Proceedings of the National Academy of Sciences, 112*(50), 15516-15521. doi:10.1073/pnas.1504454112

Bateson, P. (2011). Theories of play. In A. D. Pellegrini (Ed.), *The Oxford Handbook of the Development of Play*. Oxford: Oxford University press.

Bauer, B., Sheeran, L. K., Matheson, M. D., Li, J., & Wagner, R. S. (2014). Male Tibetan macaques' (*Macaca thibetana)* choice of infant bridging partners. *Zoological Research, 35*(3), 222-230. doi:10.11813/j.issn.0254-5853.2014.222

Bekoff, M. (1995). Play signals as punctuation: The structure of social play in canids. *Behaviour,132*(5), 419-429. doi:10.1163/156853995x00649

Berman, C., Yin, H., Ionica, C., Li, J., & Ogawa, H. (2008). Variation in kin bias over time in a group of Tibetan macaques at Huangshan, China: Contest competition, time constraints or risk response? *Behaviour, 145*(7), 863-896. doi:10.1163/156853908784089252

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. doi: 10.1016/j.tree.2008.10.008

Borell, C. V., Kulik, L., & Widdig, A. (2016). Growing into the self: The development of personality in rhesus macaques. *Animal Behaviour, 122*, 183-195. doi:10.1016/j.anbehav.2016.10.013

Burghardt, G. (2005). Defining Play. In *The genesis of animal play: Testing the limits* (pp. 45–82). Cambridge, MA: MIT Press.

Byosiere, S., Espinosa, J., Marshall-Pescini, S., Smuts, B., & Range, F. (2016). Investigating the function of play bows in dog and wolf puppies (*Canis lupus familiaris, Canis lupus occidentalis*). *Plos One,11*(12). doi:10.1371/journal.pone.0168570

Byrne, R. W. (2018). Machiavellian intelligence retrospective. *Journal of Comparative Psychology*, *132*(4), 432–436. doi: 10.1037/com0000139

Byrne, R. W., & Whiten, A. (1992). Cognitive evolution in primates: Evidence from tactical deception. *Man*, *27*(3), 609. doi: 10.2307/2803931

Byrne, R. W., & Whiten, A. (2002). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Oxford.

Cheney, D., Seyfarth, R., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science, 234*(4782), 1361-1366. doi:10.1126/science.3538419

Choudhury, S., Blakemore, S., & Charman, T. (2006). Social cognitive development during adolescence. *Social Cognitive and Affective Neuroscience, 1*(3), 165-174. doi:10.1093/scan/nsl024

Ciani, F., Dall'Olio, S., Stanyon, R., & Palagi, E. (2012) Social tolerance and adult play in macaque societies: A comparison with different human cultures. *Animal Behavior, 84*(6), 1313-1322. doi:10.1016/j.anbehav.2012.09.002

Clifton, G., Sheeran, L., Wagner, R.S., Funkhouser, J., & Li, J.-H. (2020). Preliminary observations of female-female bridging behavior in Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China. In J.-H. Li, L. Sun, & P. Kappeler (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 173–187). SpringerOpen.

Cronin, K. A., & Snowdon, C. T. (2008). The effects of unequal reward distributions on cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour, 75*(1), 245–257. doi: 10.1016/j.anbehav.2007.04.032

Deng, Z. (1993). Social development of infants of *Macaca thibetana* at Mount Emei, China. *Folia Primatologica,60*(1-2), 28-35. doi:10.1159/000156673

Duval, C., Piolino, P., Bejanin, A., Eustache, F., & Desgranges, B. (2011). Age effects on different components of theory of mind. *Consciousness and Cognition*, *20*(3), 627–642. doi: 10.1016/j.concog.2010.10.025

Fitzpatrick, S. (2017). Animal morality: What is the debate about? *Biology & Philosophy,* 32(6), 1151-1183.

Fratellone, G. P., Li, J., Sheeran, L. K., Wagner, R. S., Wang, X., & Sun, L. (2018). Social connectivity among female Tibetan macaques (*Macaca thibetana*) increases the speed of collective movements. *Primates*. doi:10.1007/s10329-018-0691-6

Gutowski, E., White, A. E., Liang, B., Diamonti, A., & Berado, D. (2017). How stress influences purpose development: The importance of social support. *Journal of Adolescent Research, 33*(5), 571-597. doi:10.1177/0743558417737754

Hadwin, J., Baron-Cohen, S., Howlin, P., & Hill, K. (1997). Does teaching theory of mind have an effect on the ability to develop conversation in children with autism? *Journal of Autism and Developmental Disorders, 27*(5), 519-537.

Hayashi, T., Akikawa, R., Kawasaki, K., Egawa, J., Minamimoto, T., Kobayashi, K., . . . Hasegawa, I. (2020). Macaques exhibit implicit gaze bias anticipating others' false-belief-driven actions via medial prefrontal cortex. *Cell Reports, 30*(13), 4433-4444.e5.

Jaffari-Bimmel, N., Juffer, F., Ijzendoorn, M. H., Bakermans-Kranenburg, M. J., & Mooijaart, A. (2006). Social development from infancy to adolescence: Longitudinal and concurrent factors in an adoption sample. *Developmental Psychology*, *42*(6), 1143-1153. doi:10.1037/0012-1649.42.6.1143

Kang, D., Boss, L., & Clowtis, L. (2016). Social support and cognition: Early childhood versus older adulthood. *Western Journal of Nursing Research, 38*(12), 1639-1659.

Kohlberg, L. (1984). *Essays on moral development / the psychology of moral development* (Vol. 2). San Francisco, CA: Harper & Row.

Krebs, D. L., & Denton, K. (2005). Toward a more pragmatic approach to morality: A critical evaluation of Kohlberg's model. *Psychological Review, 112*(3), 629-649. doi:10.1037/0033-295x.112.3.629

Krupenye, C., Kano, F., Hirata, S., Call, J., & Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science, 354*(6308), 110-114. doi:10.1126/science.aaf8110

Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015). Sex differences in the development of social relationships in Rhesus macaques (*Macaca mulatta*). *International Journal of Primatology, 36*(2), 353-376. doi:10.1007/s10764-015-9826-4

Kuwabara, M., & Smith, L. B. (2012). Cross-cultural differences in cognitive development: Attention to relations and objects. *Journal of Experimental Child Psychology, 113*(1), 20-35. doi:10.1016/j.jecp.2012.04.009

Lancy, D. F., Bock, J., & Gaskins, S. (2010). Putting learning in context. In D.F. Lancy, J.C. Bock, & S. Gaskin (Eds.), *The Anthropology of Learning in Childhood* (pp. 3-10). Plymouth, UK: AltaMira Press.

Levy, J. (1979). Play behavior and its decline during development in rhesus monkeys (*Macaca mulatta*). Ph.D. thesis, University of Chicago

Li, J.-H., & Kappeler, P. (2020). Social and life history strategies of Tibetan macaques at Mt. Huangshan. In J.-H. Li, L. Sun, & P. Kappeler (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 17–46). SpringerOpen.

Lihoreau, M., Brepson, L., & Rivault, C. (2009). The weight of the clan: Even in insects, social isolation can induce a behavioural syndrome. *Behavioural Processes, 82*(1), 81-84. doi:10.1016/j.beproc.2009.03.008

Maestripieri, D. (2018). Maternal influences on primate social development. *Behavioral Ecology and Sociobiology*, 72(8), 1-12.

Mayhew, J., Funkhouser, J., & Wright, K. (2020). Considering social play in primates: A case study in juvenile Tibetan macaques (*Macaca thibetana*). In J.-H. Li, L. Sun, & P. Kappeler (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 93-117). SpringerOpen.

Mcdonald, S. W., Kehler, H. L., & Tough, S. C. (2018). Risk factors for delayed social-emotional development and behavior problems at age two: Results from the All Our Babies/Families (AOB/F) cohort. *Health Science Reports, 1*(10). doi:10.1002/hsr2.82

Nahallage, C. A., & Huffman, M. A. (2007). Age-specific functions of stone handling, a solitary-object play behavior, in Japanese Macaques (*Macaca fuscata*). *American Journal of Primatology, 69*(3), 267-281. doi:10.1002/ajp.20348

Ogawa, H. (1995a). Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). *International Journal of Primatology,16*(5), 707-729. doi:10.1007/bf02735716

Ogawa, H. (1995b). Recognition of social relationships in bridging behavior among Tibetan macaques (*Macaca thibetana*). *American Journal of Primatology, 35*(4), 305-310. doi:10.1002/ajp.1350350406

Ogawa, H. (2006). *Wily monkeys: Social Intelligence of Tibetan macaques* (A. Yanagi, Trans.). Kyoto, Japan: Kyoto University Press.

Ogawa, H. (2020). Bridging behavior and male-infant interactions in *Macaca thibetana* and *M. assemensis*: Insight into the evolution of social behavior in the *sinica* species-group of macaques. In J.-H. Li, L. Sun, & P. Kappeler (Eds.), *The behavioral ecology of the Tibetan macaque*. SpringerOpen.

Pellegrini, A. D., & Smith, P. K. (2005). *The nature of play: Great apes and humans*. New York: Guilford.

Pellis, S. M. & Pellis V. C. (2011). Rough and tumble play: Training and using the social brain. In A. D. Pellegrini (Ed.), *The Oxford Handbook of the Development of Play*. Oxford: Oxford University press.

Petrů, M., Špinka, M., Charvátová, V., & Lhota, S. (2009). Revisiting play elements and self-handicapping in play: A comparative ethogram of five Old World monkey species. *Journal of Comparative Psychology,123*(3), 250-263. doi:10.1037/a0016217

Puth, M.-T., Neuhäuser, M., & Ruxton, G. D. (2015). Effective use of Spearmans and Kendalls correlation coefficients for association between two measured traits. *Animal Behaviour, 102*, 77–84. doi: 10.1016/j.anbehav.2015.01.010

Reinhart, C. J., Pellis, V. C., Thierry, B., Gauthier, C., VanderLaan, D. P., Vasey, P. L., & Pellis, S. M. (2010). Targets and tactics of play fighting: Competitive versus cooperative styles of play in Japanese and Tonkean macaques. *International Journal of Comparative Psychology, 23*(2), 166-200.

Self, S., Sheeran, L. K., Matheson, M. D., Li, J., Pelton, O. D., Harding, S., & Wagner, R. S. (2013). Tourism and infant-directed aggression in Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China. *Anthrozoös, 26*(3), 435-444. doi:10.2752/175303713x13697429463790

Seyfarth, R., & Cheney, D. (2013). Affiliation, empathy, and the origins of theory of mind. *Proceedings of the National Academy of Sciences of the United States of America*, 110 (Supplement 2), 10349-10356.

Shimada, M. (2006). Social object play among young Japanese macaques (*Macaca fuscata*) in Arashiyama, Japan. *Primates,47*(4), 342-349. doi:10.1007/s10329-006-0187-7

Simpson, E. A., Paukner, A., Sclafani, V., Suomi, S. J., & Ferrari, P. F. (2013). Lipsmacking imitation skill in newborn macaques is predictive of social partner discrimination. *PLoS ONE, 8*(12). doi:10.1371/journal.pone.0082921

Slaughter, V., & Gopnik, A. (1996). Conceptual coherence in the child's theory of mind: Training children to understand belief. *Child Development, 67*(6), 2967-2988.

Suarez-Jimenez, B., Hathaway, A., Waters, C., Vaughan, K., Suomi, S., Noble, P., . . . Nelson, E. (2013). Effect of mother's dominance rank on offspring temperament in infant rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology*, 75(1), 65-73.

Suomi, S. (2009). How gene-environment interactions shape biobehavioural development: Lessons from studies with rhesus monkeys. In R. Tremblay, W. Koops, & M. van Aken (Eds.), *Development and Prevention of Behavior Problems* (pp. 7–23). New York, NY: Psychology Press.

Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. New York, NY: Columbia University Press.

Szyf, M., Provencal, N., McGowan, P., Tremblay, R., & Meaney, M. (2009). Epigenetics and behavior. In R. Tremblay, M. van Aken, & W. Koops (Eds.), *Development and preventions of behavior problems: From genes to social policy* (pp. 25–60). New York, NY: Psychology Press.

Thierry, B. (1985). Patterns of agonistic interactions in three species of macaque *(Macaca mulatta, M fascicularis, M tonkeana*). *Aggressive Behavior, 11*(3), 223-233. doi:10.1002/1098-2337(1985)11:33.0.co;2-a

Thierry, B. (2004). Social epigenesis. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies: A model for the study of social organization* (pp. 267-290). Cambridge: Cambridge University Press.

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & Waal, F. B. (2008). A comparative study of conflict resolution in macaques: Insights into the nature of trait covariation. *Animal Behaviour, 75*(3), 847-860. doi:10.1016/j.anbehav.2007.07.006

Tousignant, B., Sirois, K., Achim, A. M., Massicotte, E., & Jackson, P. L. (2017). A comprehensive assessment of social cognition from adolescence to adulthood. *Cognitive Development*, *43*, 214-223. doi:10.1016/j.cogdev.2017.05.001

Villachan-Lyra, P., Almeida, E., Hazin, I., & Maranhão, S. (2015). Styles of attachment and acquisition of the theory of mind. *Estudos De Psicologia*, *20*(3). doi: 10.5935/1678-4669.20150016

Vries, A. M. O.-D., Spruijt, B. M., & Sterck, E. H. M. (2013). Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation. *Animal Cognition*, *17*(1), 77–84. doi: 10.1007/s10071-013-0639-6

de Waal, F. B., & Macedo, S. (2016). *Primates and Philosophers: How Morality Evolved*. Princeton; Oxford: Princeton University Press.

Wang, X., Sun, L., Li, J., Xia, D., Sun, B., & Zhang, D. (2015). Collective movement in the Tibetan macaques (*Macaca thibetana*): Early joiners write the rule of the game. *Plos One, 10*(5). doi:10.1371/journal.pone.0127459

Warneken, F., & Tomasello, M. (2006). Altruistic helping in human infants and young chimpanzees. *Science*, *311*(5765), 1301-1303.

Wellman, H. M. (2015). Introduction: Theory of mind, development, and foundational human cognition. In *Making minds: How theory of mind develops* (pp. 1–14). New York City, NY: Oxford University Press. doi: DOI:10.1093/acprof:oso/9780199334919.003.0015

Whiting, B., & Edwards, C. P. (1973). A cross-cultural analysis of sex differences in the behavior of children aged three through 11. *The Journal of Social Psychology*, *91*(2), 171-188. doi:10.1080/00224545.1973.9923040

Wobber, V., Wrangham, R., & Hare, B. (2010). Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. *Current Biology, 20*(3), 226-230. doi:10.1016/j.cub.2009.11.070

Worlein, J. M., & Sackett, G. P. (1997). Social development in nursery-reared pigtailed macaques *(Macaca nemestrina*). *American Journal of Primatology, 41*(1), 23-35. doi:10.1002/(sici)1098-2345(1997)41:13.0.co;2-1

Wright, K. R., Mayhew, J. A., Sheeran, L. K., Funkhouser, J. A., Wagner, R. S., Sun, L., & Li, J. (2018). Playing it cool: Characterizing social play, bout termination, and candidate play signals of juvenile and infant Tibetan macaques (*Macaca thibetana*) . *Zoological Research, 39*(4), 272-283.

Xia, D., Li, J., Garber, P. A., Matheson, M. D., Sun, B., & Zhu, Y. (2013). Grooming reciprocity in male Tibetan macaques. *American Journal of Primatology, 75*(10), 1009-1020. doi:10.1002/ajp.22165

Xia, D.., Garber, P.A., Sueur, C., R.S., & Li, J.-H. (2020). Behavioral exchange and interchange as strategies to facilitate social relationships in Tibetan macaques. In J.-H. Li, L. Sun, &

P. Kappeler (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 60-77). SpringerOpen.

Xia, D., Li, J., Garber, P. A., Sun, L., Zhu, Y., & Sun, B. (2012). Grooming reciprocity in female Tibetan macaques (*Macaca thibetana)*. *American Journal of Primatology*, *74*(6), 569-579. doi:10.1002/ajp.21985

Yanagi, A., & Berman, C. M. (2014). Functions of multiple play signals in free-ranging juvenile rhesus macaques (*Macaca mulatta*). *Behaviour*, *151*(14), 1983-2014. doi:10.1163/1568539x-00003227

Yongcheng, L. & Richardson, M. 2008. *Macaca thibetana*. *The IUCN Red List of Threatened Species* 2008. doi:10.2305/IUCN.UK.2008.RLTS.T12562A3359510.en

Zhao, Q., & Deng, Z. (1988). *Macaca thibetana* at Mt. Emei, China: III. Group composition. *American Journal of Primatology,16*(3), 269-273. doi:10.1002/ajp.1350160308