

Spring 2021

## Playing with Relatives: Genetic Kinship and Play Behavior in Juvenile Tibetan Macaques

Riley Derby

Central Washington University, derbyr@cwu.edu

Follow this and additional works at: <https://digitalcommons.cwu.edu/etd>



Part of the [Animal Studies Commons](#), and the [Biological and Physical Anthropology Commons](#)

---

### Recommended Citation

Derby, Riley, "Playing with Relatives: Genetic Kinship and Play Behavior in Juvenile Tibetan Macaques" (2021). *All Master's Theses*. 1502.

<https://digitalcommons.cwu.edu/etd/1502>

This Thesis is brought to you for free and open access by the Master's Theses at ScholarWorks@CWU. It has been accepted for inclusion in All Master's Theses by an authorized administrator of ScholarWorks@CWU. For more information, please contact [scholarworks@cwu.edu](mailto:scholarworks@cwu.edu).

PLAYING WITH RELATIVES: GENETIC KINSHIP AND PLAY BEHAVIOR IN JUVENILE  
TIBETAN MACAQUES

---

A Thesis  
Presented to  
The Graduate Faculty  
Central Washington University

---

In Partial Fulfillment  
of the Requirements for the Degree  
Master of Science  
Primate Behavior

---

by  
Riley Nicholas Derby

May 2021

CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

We hereby approve the thesis of

Riley Nicholas Derby

Candidate for the degree of Master of Science

APPROVED FOR THE GRADUATE FACULTY

---

---

Dr. Jessica Mayhew, Committee Chair

---

---

Dr. Lori Sheeran

---

---

Dr. Lixing Sun

---

---

Dean of Graduate Studies

## ABSTRACT

# PLAYING WITH RELATIVES: GENETIC KINSHIP AND PLAY BEHAVIOR IN JUVENILE TIBETAN MACAQUES

by

Riley Nicholas Derby

May 2021

This thesis is composed of a journal-ready article and an accompanying appendix containing data and figures. In this thesis, I statistically analyzed the relationship between player age, player sex, genetic kinship and social play duration in juvenile Tibetan macaques.

Chapter I provides a general introduction and addresses current and past literature on the behavior, ecology and play among macaque genera and Tibetan macaques within this study. I review the fitness benefits of play behavior and the influence of kin selection on macaque social life. Additionally, I review the existing literature on Tibetan macaque play and how the current study will contribute to the literature.

Chapter II expands upon current literature on Tibetan macaque social play by considering the influence of genetic kinship on total play duration. Obtained from calculating the kinship coefficient of each juvenile within the group (through known pedigree data), the results indicated that there was a significant positive correlation between total play duration and genetic kinship of play partners. I propose that kin biased selection among the juveniles within this group is facilitated through social play events. This is supported both by the significant correlation found in this study and the existing literature on social partner development during juvenile life.

Chapter III provides general conclusions drawn from this study and how it contributes to the understanding of Tibetan macaque play behavior. Lastly, future studies are considered to continue the expansion knowledge surrounding macaque and primate play.

## ACKNOWLEDGMENTS

I would like to thank Dr. Jessica Mayhew, my thesis committee chair, for her support, encouragement, flexibility, guidance, and mentorship throughout the past two years of my graduate education. I also thank Dr. Lori Sheeran, Dr. Lixing Sun, and Courtney Martinez for their time, advice, data and expertise in this research area. I'd like to thank my fiancé, Katherine, for her support and encouragement of my research and the pursuit of my goals. I'd like to thank my older brother Andrew for inspiring me and pushing me to strive for better. Thank you to my parents, Richard and Wendy, for always supporting my academic goals. Thank you to all of my friends and family that have supported and will continue to support my academic journey. Finally, I would like to thank the following entities for their generous support: the Debra and Arlen Prentice Award through the CWU Primate Behavior Program for this research, and the CWU School of Graduate Studies and Research. The previously collected data used in this project was approved by the Central Washington University Institutional Animal Care and Use Committee (IACUC) board (protocol: #A031608; #A051602; #M061603; #A051702).

## TABLE OF CONTENTS

Chapter		Page
I	GENERAL INTRODUCTION AND LITERATURE REVIEW.....	1
	Introduction .....	1
	What is Play?.....	2
	Adaptive Value of Play .....	2
	Social Play.....	3
	Macaque Sociality .....	5
	Macaque Play .....	6
	Altruism and Macaque Kin Selection .....	7
	Tibetan Macaque Sociality.....	8
	Tibetan Macaque Play.....	9
	Current Investigation.....	10
II	PLAYING WITH RELATIVES: GENETIC KINSHIP AND PLAY BEHAVIOR I N JUVENILE TIBETAN MACAQUES.....	12
	Abstract .....	13
	Keywords .....	13
	Introduction.....	14
	Methods.....	18
	Results.....	20
	Discussion .....	24
	Future Considerations .....	28
	Acknowledgements .....	28
	References .....	30
III	GENERAL CONCLUSIONS.....	42
	COMPREHENSIVE REFERENCES.....	44
	APPENDIX A.....	59
	Appendix A—Chapter II Supplemental Tables and Figures .....	59

## LIST OF TABLES

Table		Page
1	Total Individual Social Play Durations.....	22
A1	Matrilineal Player Dyads (Tou = 37; Ye = 11; Hua = 3).....	59
A2	Kinship Coefficients between Player Dyads .....	60

## LIST OF FIGURES

Figure		Page
1	Kinship Coefficient vs Individual Play Bout Durations ( $n = 3,305$ ) .....	21
2	Positive Correlation ( $r = 0.137$ ) between Kinship Coefficient and Total Durations .....	24
A1	2016 Negative Trend between Age and Play Frequency .....	63
A2	2016 Negative Correlation between Age and Individual total Play Durations .....	64
A3	2017 Negative Trend between Age and Play Frequency .....	65
A4	2017 Negative Trend between Age and Individual total Play Durations ...	66

## CHAPTER I

### GENERAL INTRODUCTION AND LITERATURE REVIEW

#### Introduction

The juvenile period in primates is defined as the time between weaning and sexual maturity, and fitness has direct ties to this period of life (Altmann, 1962; Cenni & Fawcett, 2018; Chase et al., 2002; Symons, 1978; Thierry, 2004). However, even within some of the most well studied genera such as *Macaca*, close analysis of juvenile sociality has been relatively overlooked. *Macaca* species are distributed across varying ecologies, resulting in variable social styles. This variation has generated research interest in conducting large-scale comparisons of the genus (Thierry, 2000, 2007; Thierry et al., 2000). Macaques typically display strict hierarchies based on matrilineal power in females and competitive power in males (Thierry, 1985, 2000, 2007; Thierry et al., 2000). Tibetan macaques (*Macaca thibetana*) are a despotic species that display this type of strict hierarchy (Berman et al., 2004; Funkhouser et al., 2018). Juvenile Tibetan macaques participate in varying amounts of social behavior, including play, with other individuals within the group (Li & Kappeler, 2020; Wright et al., 2018). Social play can include mutual forceful behaviors, such as wrestling and play biting, but is defined as multiple conspecifics engaging and influencing each other's actions or behaviors (Burghardt, 2005; Fagen, 1981). Juvenile Tibetan macaques have been observed to play with individuals of the same age cohort (Mayhew et al., 2020; Wright et al., 2018). These social behaviors and resulting relationships can have a lasting impact on the development and success of an individual in the future (Altmann, 1962; Cenni & Fawcett, 2018; Chase et al., 2002; Symons, 1978; Thierry, 2004). This study considers the play behavior of juvenile Tibetan macaques in the YA1

group at Mt. Huangshan, China, and asks how the genetic kinship between juveniles influences their social relationships and choice of play partner.

### **What is Play?**

Play has been defined in multiple ways with a focus on either the function or structure of the behavior (Bekoff & Allen, 1997; Fagen, 1981; Martin & Caro, 1985). Burghardt (2005) established specific criteria to distinguish play behavior from other common behaviors. These parameters state that for a behavior to be considered play, it must (1) have limited immediate function, (2) be endogenous, (3) have structural or temporal properties that are different from “serious” behaviors, (4) be flexibly exercised and not stereotypical, and (5) be performed in a relaxed field (i.e., free of stress or social/physical pressures).

There are three overlapping categories of play: solitary, object, and social (Bekoff & Byers, 1981; Fagen, 1981). Solitary play is characterized by high intensity or long durations of locomotor movements performed alone. Object play is characterized by the manipulation of any object with no immediate benefit in either a social or solitary environment (Burghardt, 2005). Social play is characterized as an interaction between two or more conspecifics that potentially influence each other’s behaviors or actions (Burghardt, 2005; Fagen, 1981). Social play typically includes reciprocal and forceful behaviors, such as wrestling and play biting between conspecifics (Burghardt, 2005; Fagen, 1981).

### **Adaptive Value of Play**

The evolutionary origin of play behavior in animals is a complicated topic involving development, connection to cognition, and overall adaptive value. Play is considered extremely difficult to study due to its characterization as an intricate form of communication (Bekoff, 1972; Bekoff & Allen, 1997; Burghardt, 2005; Fagen, 1981; Pellis & Pellis, 2009). Fagen (1981)

suggested six overlapping hypotheses on the beneficial aspects of play: (1) play facilitates the growth of stamina, skills, and overall strength; (2) play determines development; (3) play generates specified information of conspecifics; (4) play advances cognitive skills required for adaptable, flexible, versatile and innovative behavior; (5) play includes behaviors used in intraspecific competition; and (6) play creates and reaffirms social bonds and cohesion between group members. Bekoff and Byers (1981) suggested that the function of play involves motor skills development, socialization, and cultivation of cognitive abilities. Smith (1982) added that play is important to the development of strength and endurance. The repetition of motor patterns in addition to the vigorous setting in which play occurs leads to the development of physical fitness and the advancement of particular behavioral and physical skills. Play may also establish and strengthen social bonds and relationships between conspecifics (Bekoff, 1977; 1984). Overall, play is considered multi-functional due to the significant costs required in order to participate in the activity. Without benefits such as the enhancement of physicality, social relationships, and cognition, individuals that participate in play would be at a disadvantage compared to individuals that do not play (Fagen, 1993, Palagi, 2006, 2018; Symons, 1978).

### **Social Play**

Social play requires many flexible behavioral abilities, including partner cooperation, communication, learning, and the social development of juveniles (Bekoff & Allen, 1997; Palagi et al., 2007). Play functions to increase the physical fitness of individuals (Byers & Walker, 1995; Fontaine, 1994; Martin & Caro, 1985), but it additionally creates and improves social connections and flexible behavior (Baldwin & Baldwin, 1974; Brown, 1988; Fagen, 1984). Social play can function as an opportunity for juveniles to hone adult social skills (Baldwin &

Baldwin, 1974; Brown, 1988; Fagen, 1984) and include behavioral analogues from a range of social situations, including agonism and mating (Burghardt, 2005; Wright et al., 2018).

Unlike juveniles, adult primates engage in social interactions through affiliative behaviors such as grooming or alliance forming (Kanngiesser et al., 2011; Lehmann & Boesch, 2009). Across many taxa, juveniles engage in social play more frequently than adults (Mayhew et al., 2020; Shimada & Sueur, 2014). Social play interactions among juveniles help increase social cohesion and form affiliations among conspecifics, thereby helping facilitate the social relationships among young animals (Bjorklund & Pellegrini, 2002; Clark, 2011; Fagen, 1981; Maestriperieri & Ross, 2004; Mayhew et al., 2020; Palagi, 2006; Palagi & Paoli, 2007; Shimada & Sueur, 2014; Smith et al., 2013).

Play is expected to occur between individuals of similar skill (Kulik et al., 2015), age, and conspecifics that will likely be encountered into adulthood (Maestriperieri & Ross, 2004). For example, Pellis and Pellis (1996) reviewed social play behavior across multiple taxa and hypothesized that social play bouts influence the power relationships between subadult juveniles, especially in male-male bouts. The aggressive behaviors performed during play can serve as practice for future aggressive interactions and potentially enhance a juvenile's success when exhibiting affiliative or agonistic behaviors during adulthood. Additionally, future social partners, relationships, and behavioral contexts can be predicted from play between juveniles (Maestriperieri & Ross, 2004; Pellis et al., 2019). This continuation of a social relationship established through play can be the result of the social skills (reciprocal actions between players, communication, and partner selection) built during play bouts (Mayhew et al., 2020; Yanagi & Berman, 2014b).

## **Macaque Sociality**

*Macaca* live in both temperate and tropical regions throughout Asia and Africa and have the widest geographical range among non-human primates (Thierry, 2007). *Macaca* as a genus is defined by its unity through evolutionarily conserved traits, such as female philopatry, and its diversity due to a broad range of ecological variation (Thierry, 2000, 2007; Thierry et al., 2000). To better understand this genus, we must consider both evolutionary and ecological factors that have led to the persistence of their unique, but variable social styles across time and environment (Thierry, 2007).

Macaques share the same basic group structure, social system, and dispersal pattern (Thierry, 2007). They are mainly frugivorous, semi-terrestrial primates that form groups containing multiple males and females with their offspring. Macaques have female-biased sex ratios within groups and are female philopatric, meaning females remain in their natal groups whereas males disperse at sexual maturity (Thierry, 2000, 2007; Thierry et al., 2000). Females typically establish and maintain lasting relationships with relatives within their group. These matrilineal relationships are foundational to group structure as well as the power dynamics between individuals (Thierry, 2007).

Dominance style is determined by the agonistic interactions between dyads (Thierry, 2000; Thierry et al., 2000), and macaques are placed on a four-grade scale of dominance style. Species within the first grade are considered nepotistic and hierarchical, whereas species within the fourth grade are considered egalitarian and tolerant of one another (Thierry, 2000; Thierry et al., 2000). This dominance scale, established by Thierry (2000), is based on the highly unidirectional aggression contests in grade one species. These contests result in a loser who flees or submits with the potential for severe biting. Additionally, reconciliation after these events in

grade one species is rare. However, in grade four species, the majority of aggressive contests are met with protest or counterattack with a low chance of biting. Reconciliatory behaviors after contests are also much more common, occurring almost 50% of the time in unrelated individuals (Thierry, 2000). Species that fall under grade one (highly nepotistic) include rhesus macaques (*Macaca mulatta*) and Japanese macaques (*Macaca fuscata*). The grade four species (more egalitarian) include Tonkean macaques (*Macaca tonkeana*) and Sulawesi crested macaques (*Macaca nigra*) (Thierry, 2000). Tibetan macaques were originally placed in grade three due to their display of submissive behaviors, but further research has shown that Tibetan macaques fall under the second, more despotic, grade due to similar agonistic rates to grade one species and lower reconciliatory rates than other grade three species (Berman et al., 2004; Mayhew et al., 2020; Thierry, 2000; Thierry et al., 2000).

### **Macaque Play**

Macaque social play can be characterized in multiple ways depending on the species and type of social style present. Social play in despotic species, like the rhesus macaques, is described as competitive, unlike the cooperative play style observed in less despotic species (Petit et al., 2008; Reinhart et al., 2010). Competitive play styles tend to involve more risk as more vulnerable areas like the face or genitals are targeted and attacked during the bout. Attacking these sensitive areas can create miscommunication between conspecifics and end the play bout prematurely (Reinhart et al., 2010; Scopa & Palagi, 2016; Yanagi & Berman, 2014b). To prolong interactions in competitive species, formalized play signals are frequently used to indicate playful intent (Scopa & Palagi, 2016; Wright et al., 2018; Yanagi & Berman, 2014a). The use of signals within despotic species can potentially minimize the risk of misinterpretation and interference by a third party (Scopa & Palagi, 2016; Thierry et al., 2000; Wright et al., 2018;

Yanagi & Berman, 2014b). However, in tolerant species, the signals can be redundant and simply communicate the beginning and end of play (Pellis et al., 2011; Scopa & Palagi, 2016).

### **Altruism and Macaque Kin Selection**

Altruism is an important evolutionary concept that provides support for gregarious living and cooperation with other individuals. Hamilton (1964) provided the mechanism of kin selection, which suggests that individuals selectively choose interactions among kin that would help facilitate the evolution of cooperative behaviors. Although kin selection is not the only strategy through which cooperation can develop (Axelrod & Hamilton, 1981; Dugatkin, 1997; Trivers, 1971), some macaque species, especially despotic species, provide an example of high rates of kin selection through nepotistic behaviors (Berman, 1983c; Silk, 1982; 2002; Silk et al., 1981).

Matrilineal kinship is the foundation of many aspects of macaque sociality and regulates female philopatry, social networks, and power hierarchies. Kinship bias has immense impact, especially on the females within a macaque group (Silk, 2002). Female kin remain in their birth groups for their entire lives and allocate most of their activity budget to resting, grooming, feeding, and caring for their infants near maternal kin (Altmann, 1980; Chapais, 1983; Cheney, 1978; DeFler, 1978; Gouzoules, 1984; Gouzoules & Gouzoules, 1987; Kapsalis & Berman, 1996; Kurland, 1977; Missakian, 1974; Sade, 1965; Silk, 1982, 1999; Silk et al., 1981). Additionally, coalitionary support is more likely to be offered to females with matrilineal kin ties during interactions with conspecifics (Berman, 1983a, b, c; Bernstein & Ehardt, 1985, 1986; Chapais, 1983; Datta, 1983a, b; de Waal, 1977; Kaplan, 1977, 1978; Kurland, 1977; Massey, 1977; Silk, 1982). Although there may be other ways in which macaques gain support from non-kin (grooming for social and feeding site tolerance), kin selection plays a large role in the sociality of

despotic species (Cords, 1997; de Waal, 1991; Hemelrijk, 1994; Perry, 1996; Seyfarth, 1977; Silk, 1992 a, b).

### **Tibetan Macaque Sociality**

Tibetan macaques (*Macaca thibetana*) are genetically related the most to Assamese macaques (*Macaca assamensis*) but resemble the stump-tailed macaque (*Macaca arctoides*) in appearance (Berman et al., 2004; de Waal, 2001). Ecologically, they are most similar to Barbary macaques (*Macaca sylvanus*), living within montane habitats on the subtropical boundary. Female macaques reach adulthood between 4-5 years of age, whereas males reach maturity around 7-8 years (Wright et al., 2018; Xia et al., 2012; Zhao & Deng, 1988).

Tibetan macaques live in multi-male, multi-female groups comprising of up to 50 individuals with the sex ratio being relatively even or slightly favoring females (Berman et al., 2004; Funkhouser et al., 2018; Mayhew et al., 2020; Thierry, 2000; Thierry et al., 2000). Female Tibetan macaque social organization is characterized by strict, linear dominance styles with strong kin bias and coalition formation (Berman et al., 2004; Funkhouser et al., 2018). Bias for female kin in activities such as grooming, infant handling, and coalitionary support highlight the nepotistic and despotic sociality of Tibetan macaque (Berman et al., 2004; Funkhouser et al., 2018; Thierry, 2000; Thierry et al., 2000; Xia et al., 2012; Xia et al., 2013), Female rank is matrilineal, in that females obtain ranks below their mother but above older siblings (Berman et al., 2004; Funkhouser et al., 2018; Thierry, 2011; Zhao, 1997). The connection of maternal kinship and dominance within a group influences the social interactions between both kin and non-kin (Berman et al., 2008; Xia et al., 2012).

Male Tibetan macaques also form linear dominance hierarchies and have a strict, despotic style of dominance (Berman et al., 2004; Xia et al., 2013). Both aggression and

tolerance by high-ranking individuals are important tactics affecting social status and relationships (Xia et al., 2012; Xia et al., 2013). Adult males are also thought to obtain the highest rank among all individuals within the group, but in some cases, females can outrank some males (Berman et al., 2004). Similar to most macaque species, male Tibetan macaques disperse at sexual maturity (7-8 years old) and can transfer between groups throughout their lives (Thierry, 2000; Thierry et al., 2000; Zhao, 1997). Due to dispersal at sexual maturity, the males within a group are generally unrelated (Thierry, 2000, 2007; Thierry et al., 2000; Xia et al., 2013). Tibetan macaques are seasonal breeders resulting in high mating competition that corresponds with increased levels of aggression. Additionally, coalitionary action increases as males defend against extra-group males attempting to immigrate into the group (Xia et al., 2010; Xia et al., 2013).

### **Tibetan Macaque Play**

In the beginning of life, an infant monkey remains with and is centered around its mother. However, as age increases, young primates gain independence from their mothers and engage in social interactions with other group members, specifically individuals of the same age, through social play (Berman, 1980,1982; Nakamichi, 1989, 1996; Rhine & Hendy-Neely, 1978). Tibetan macaque juveniles participate in fast, rough-and-tumble dyadic and polyadic play bouts, similar to other macaque species (Wright et al., 2018). Juveniles within this species more frequently engage in solitary play as infants and move toward social play with similarly aged individuals that peaks at 2.5 years of age (Batts, 2012; Mayhew et al., 2020; Wright et al., 2018). The majority of juveniles within the group participate in play bouts with variation in frequency, duration, and play signaling (Wright et al., 2018). Wright et al. (2018) found nine play signals in this species, including crouch and stare signal. Six of the play signals expressed are also

expressed in the formalized signaling of rhesus macaques (Yanagi & Berman, 2014a). The adult social relationships within a grade two despotic species, like the Tibetan macaque, generally show high amounts of kin bias and likely influence over the socialization of juveniles (Berman et al., 2004; Thierry, 2011). Mothers in despotic macaque species are more restrictive with their offspring and may interfere during play bouts with the offspring of other individuals that are of different ranking or matriline (Maestriperi, 2004). Therefore, the social organization would be expected to affect juvenile play behavior due to third-party interference (aggressive or affiliative behaviors) by adults (Maestriperi, 2004; Thierry, 2011). Although this hypothesis was not supported due to a lack of data in Wright et al. (2018), signaling behavior may provide insight as more than just a reliable indicator of play. Wright et al. (2018) found that having individuals in proximity during a play bout impacted the signaling behavior of the individuals involved (i.e., signals increased when audience members increased from 0 to 2 individuals). This study will continue to pursue this topic to help provide better understanding of the relationships between juveniles that are formed and strengthened during play.

### **Current Investigation**

In the current investigation, I intend to understand the relationship between genetic kinship and play behavior in juvenile Tibetan macaques at Mt. Huangshan, China. This study will provide insight into the social development of juvenile Tibetan macaques by considering factors such as kin bias and tolerance of conspecifics. The development of social relationships among Tibetan macaque juveniles has long-term fitness consequences for both males and females (Altmann, 1962; Cenni and Fawcett, 2018; Chase et al., 2002; Symons, 1978; Thierry, 2004). Macaque play has been studied among a variety of species (Petit et al. 2008; Reinhart et al., 2010; Scopa & Palagi, 2016; Wright et al., 2018; Yanagi & Berman, 2014b); however, the

connection between play behavior and genetic kinship has been overlooked in this species and well-studied group. This project will provide insight into social development and relationships within Tibetan macaques and provide a foundation for future studies of other macaque species.

**CHAPTER II****PLAYING WITH RELATIVES: GENETIC KINSHIP AND PLAY BEHAVIOR IN  
JUVENILE TIBETAN MACAQUES**

**Riley N. Derby <sup>1,\*</sup>, Jessica A. Mayhew <sup>1,2</sup>, Lixing Sun <sup>1,2</sup>, Courtney Martinez <sup>1</sup>,  
and JinHua Li <sup>3</sup>**

<sup>1</sup> Central Washington University, Primate Behavior Program, Ellensburg, 98926, USA

<sup>2</sup> Central Washington University, Department of Anthropology & Museum Studies, 98926, USA

<sup>3</sup> Anhui University, School of Resource & Environmental Engineering, 551, China

\* Riley.Derby@cwu.edu

**Abstract**

Juvenile development has direct ties to the overall fitness in primates. Even in well-studied genera such as *Macaca*, juvenile sociality has been relatively overlooked. However, juvenile macaques participate in varying amounts of social behavior, including play. Three categories of play behavior are exhibited among juvenile macaques: solitary play, object play, and social play. Play is hypothesized to increase physical abilities, determine developmental rates, advance cognitive abilities, and improve social skills. Social play requires many flexible behavioral abilities such as partner cooperation, communicative abilities, learning, and social development. In this paper, we investigated the relationship between social play, player age, player sex, and genetic kinship in juvenile Tibetan macaques. We used previously collected focal, scan, and video data from 2016-2017 and known pedigree information from the Yulingkeng A1 (YA1) Tibetan macaque group. We analyzed all social play bouts and calculated the kinship coefficient between play partners. This resulted in 3,305 play bouts, 60,190 seconds of play, and 159 distinct dyadic player configurations across the two years. Our results indicate that social play duration is regulated by player age, sex, and genetic kinship between play partners. Overall, we suggest that kin-biased selection occurs between the juvenile Tibetan macaques within this group during social play events.

**Keywords: Social play, kinship, juvenile Tibetan macaque, fitness**

## Introduction

The fitness level of an individual in many primate species has a direct connection to experiences during juvenile development (Altmann, 1962; Cenni and Fawcett, 2018; Chase et al., 2002; Symons, 1978; Thierry, 2004). Even within some of the most well studied genera such as *Macaca*, close analysis of juvenile sociality has been relatively overlooked. Juvenile Tibetan macaques (*Macaca thibetana*) participate in varying amounts of social behavior, including play, with other individuals in the group (Li & Kappeler, 2020; Wright et al., 2018). Play has been defined in varying ways depending on a focus of either the function or structure of the behavior (Bekoff & Allen, 1997; Fagen, 1981; Martin & Caro, 1985). Burghardt (2005) established specific criteria to determine and distinguish play behavior from other common, more “serious” behaviors. These parameters state that for a behavior to be considered play, it must (1) have limited immediate function, (2) be endogenous, (3) have structural or temporal properties that are different from “serious” behaviors, (4) be flexibly exercised and not stereotypical, and (5) be performed in a relaxed field (i.e., free of stress or social/physical pressures).

The evolutionary origin of play behavior in animals is a complicated topic involving development, its connection to cognitive development, and its overall adaptive value (Bekoff, 1972; Bekoff & Allen, 1997; Burghardt, 2005; Fagen, 1981; Pellis & Pellis, 2009). However, play is hypothesized to improve physical condition and fitness (Bekoff & Byers, 1981; Byers & Walker 1995; Fontaine, 1994; Martin & Caro, 1985; Smith, 1982), advance cognitive skills (Fagen, 1981), and facilitate social bonds and relationships between conspecifics (Bekoff, 1977; 1984; Fagen, 1981). Improved social skills and flexible behavioral abilities, including partner cooperation, communication, learning, and social development, are required for social play (Baldwin & Baldwin, 1974; Bekoff & Allen, 1997; Brown, 1988; Fagen, 1984; Palagi et al.,

2007). Social play can function as an opportunity for juveniles to hone adult social skills (Baldwin & Baldwin, 1974; Brown 1988; Fagen, 1984). It includes behavioral analogues from a range of social situations including agonism and mating (Burghardt, 2005; Wright et al., 2018). Without fitness benefits, such as the enhancement of physicality, cognition, and social relationships, individuals that participate in play would be at a disadvantage to individuals that do not play (Fagen, 1993; Palagi, 2006, 2018; Symons, 1978).

Social play can include mutual aggressive behaviors, such as wrestling and play biting but is defined as multiple conspecifics engaging and influencing each other's actions or behaviors (Burghardt, 2005; Fagen, 1981). These social behaviors and resulting relationships can have a lasting impact on the development and success of an individual in the future (Altmann, 1962; Cenni & Fawcett, 2018; Chase et al., 2002; Symons, 1978; Thierry, 2004). Although play can occur between individuals of varying ages, juveniles participate in social play much more frequently than adults. Play is expected to occur between individuals of similar skill (Kulik et al., 2015), age, and conspecifics that will likely be encountered into adulthood (Maestriperieri & Ross, 2004). Future social partners, behavioral contexts, social cohesion, affiliations, and strength of relationships between individuals can be predicted from social play (Bjorklund & Pellegrini, 2002; Clark, 2011; Fagen, 1981; Maestriperieri & Ross, 2004; Palagi, 2006; Palagi & Paoli, 2007; Pellis et al., 2019; Shimada & Sueur, 2014; Smith et al., 2013). For example, Pellis & Pellis (1996) hypothesized that social play bouts influence the power relationships between subadult juveniles, especially in male-male bouts. The aggressive behaviors performed during play can serve as practice for future aggressive interactions and potentially enhance a juvenile's success when exhibiting affiliative or agonistic behaviors during adulthood. Juvenile Tibetan macaques have been observed to play with individuals of a similar age (Mayhew et al., 2020; Wright et al.,

2018). Although previous studies have considered the effect of age and sex on social play behavior in Tibetan macaques, this study provides insight on the effect of genetic kinship between play partners.

Tibetan macaques are a grade two despotic species that live in multi-male, multi-female groups of up to 50 individuals with the sex ratio being relatively even or slightly favoring females (Berman et al., 2004; Funkhouser et al., 2018; Mayhew et al., 2020; Thierry, 2000; Thierry et al., 2000). Tibetan macaque social organization is characterized by strict, linear dominance styles with strong kin bias and coalition formation (Berman et al., 2004; Funkhouser et al., 2018). Matrilineal kinship is the foundation for many aspects of Tibetan macaque sociality and regulates female philopatry, social networks, and power hierarchies. Kin selection has considerable impact, especially on the females within a despotic macaque group (Hamilton, 1964; Silk, 2002). Female kin remain in their natal groups for their entire lives and spend the most time resting, grooming, feeding, and handling their infants near maternal kin (Altmann, 1980; Chapais, 1983; Cheney, 1978; DeFler, 1978; Gouzoules, 1984; Gouzoules & Gouzoules, 1987; Kapsalis & Berman, 1996; Kurland, 1977; Missakian, 1974; Sade, 1965; Silk, 1982, 1999; Silk et al., 1981). Additionally, they are more likely to provide coalitionary support to matrilineal kin during interactions with other conspecifics (Berman, 1983a,b,c; Bernstein & Ehardt, 1985, 1986; Chapais, 1983; Datta, 1983a,b; de Waal, 1977; Kaplan, 1977, 1978; Kurland, 1977; Massey, 1977; Silk, 1982). Female kin bias across contexts, such as grooming, infant handling, and coalitionary support, highlights the underlying nepotistic and despotic essence of Tibetan macaque sociality (Berman et al., 2004; Funkhouser et al., 2018; Thierry, 2000; Thierry et al., 2000; Xia et al., 2012; Xia et al., 2013).

Tibetan macaque juveniles participate in fast, rough-and-tumble dyadic and polyadic play bouts, similar to other macaque species (Wright et al. 2018). A competitive social play style, common in despotic macaques, involves more risk, as more vulnerable areas such as the face or genitals are targeted and attacked during the bout. Attacking these sensitive areas can create miscommunication between conspecifics and end the play bout prematurely (Reinhart et al., 2010; Scopa & Palagi, 2016; Yanagi & Berman, 2014). Juveniles within this species more frequently engage in solitary play as infants and transition toward social play with similarly aged individuals that peaks in frequency at 2.5 years of age (Batts, 2012; Mayhew et al., 2020; Wright et al., 2018). Most juveniles within the group also participate in social play bouts with variation in frequency, duration, and play signaling (Wright et al., 2018).

Although the play behavior of multiple macaque species has been studied (Petit et al., 2008; Reinhart et al., 2010; Scopa & Palagi, 2016; Wang et al., 2021; Wright et al. 2018; Yanagi & Berman, 2014), the connection between play behavior and genetic kinship has been overlooked in this species and within this well-studied genus. In the current investigation, we intend to understand the relationship between play behavior and age, sex, and genetic kinship in juvenile Tibetan macaques at Mt. Huangshan, China. This study provides insight into the social development of juvenile Tibetan macaques by considering kin selection, which remains unexplored. We continue to explore the social development within Tibetan macaques and provide a foundation for both the continued study of this population, and future studies of other macaque species by addressing the following three hypotheses: 1) If player age influences social play behavior, then older individuals will play less frequently than younger individuals; 2) If player sex influences social play behavior, then same sex dyads will play more frequently and for

longer than mixed sex dyads; and 3) If genetic kinship influences social play behavior, then more closely related individuals will play with each other for longer (total duration).

## **Methods**

We conducted this study with the Yulingkeng A1 (YA1) group at the Valley of the Wild Monkeys in the Huangshan Scenic District, Anhui Province, China. The YA1 group is provisioned with corn three to four times a day by park staff and is free ranging across the provisioning zone, the manufactured platforms and bridges, a stream and waterfall, forests, and cliffs (Funkhouser et al., 2018). Additionally, YA1 has been habituated to human researchers since 1986 and tourism since 1994 (Berman et al., 2004; Funkhouser et al., 2018, Li & Kappeler, 2020). We used previously collected social play data spanning July-August 2016 and July-August 2017, collected between 06:30 and 17:30. During the 2016 field season, group YA1 had 47 individuals: 13 adult females and 8 adult males (between the ages of 6 and 31) and 26 juveniles/infants between the ages of 0 and 5. During the 2017 field season, the group had 46 individuals: 15 adult females and 10 adult males (between the ages of 6 and 31) and 21 juveniles/infants between the ages of 0 and 5. This project used previously collected data that was approved by the Central Washington University Institutional Care and Use Committee (IACUC) board (protocol: #A031608; #A051602; #M061603; #A051702)

Social play data from 2016 were collected using both focal and scan follows (Altmann, 1974), and any video footage of play bouts was recorded using a Sony Handycam camcorder. Social play data from 2017 were collected using all-occurrence sampling. For both years, the data collectors monitored infant and juvenile interactions until social play was initiated, and video footage (i.e., Sony Handycam) of the play bout was recorded. The play bout was followed until both individuals ceased to participate in playful behavior for more than 10 seconds. We

then coded play videos using VLC media player (version 3.0.3, Vetinari) and Microsoft Excel (version 16.14) for player identity, age, sex, matriline, duration of play bout, and total number of players involved (see Mayhew et al. 2020 for methods). We recorded the ages of individuals in days at the beginning of data collection each year, and play duration was recorded in seconds (s).

We reviewed all social play interactions and converted polyadic play bouts into dyadic interactions to determine the duration of play between all dyads. This resulted in 3,305 play bouts with 159 distinct dyads. We calculated play duration for each dyad by totaling the seconds (s) of play from the 2016 and 2017 datasets. We used pedigree information for this study group (Li & Kappeler, 2020) to determine genetic kinship between juveniles using kinship coefficients (Wright, 1922), which represent the probability that a random allele from individual A is identical by descent (IBD) with a random allele from individual B at the same locus. We conducted statistical analyses using Jamovi (1.6.15) and R (4.0.0). We ran the *pedtools* and *ribd* packages (Vigeland, 2020) in R allowing for cases of founder inbreeding, generalized kinship coefficients, IBD coefficients, and standard kinship coefficients. Because of the lack of genomic data on these monkeys, only standard kinship coefficients were calculated using accessible pedigree information (mother, father, grandmother, etc.). The scale used for kinship coefficients ranged from 0-1, with a kinship coefficient of 0 indicating no genetic relationship between dyad members and a value of 1 indicating an identical twin.

We assessed both datasets for normality. Due to the non-normal distribution of the data, we applied non-parametric tests, including Spearman rank correlation, Mann-Whitney U and Kruskal-Wallis tests, and chi-squared goodness of fit test. We conducted Spearman rank correlations to address whether player age affected social play duration. We used chi-square goodness of fit and Mann-Whitney U tests to determine the effect of player and partner sex on

play duration. We also addressed matrilineal variation using a Kruskal-Wallis test. Lastly, we used a Spearman rank test to analyze the relationship between genetic kinship and both the total and individual bout play durations.

## Results

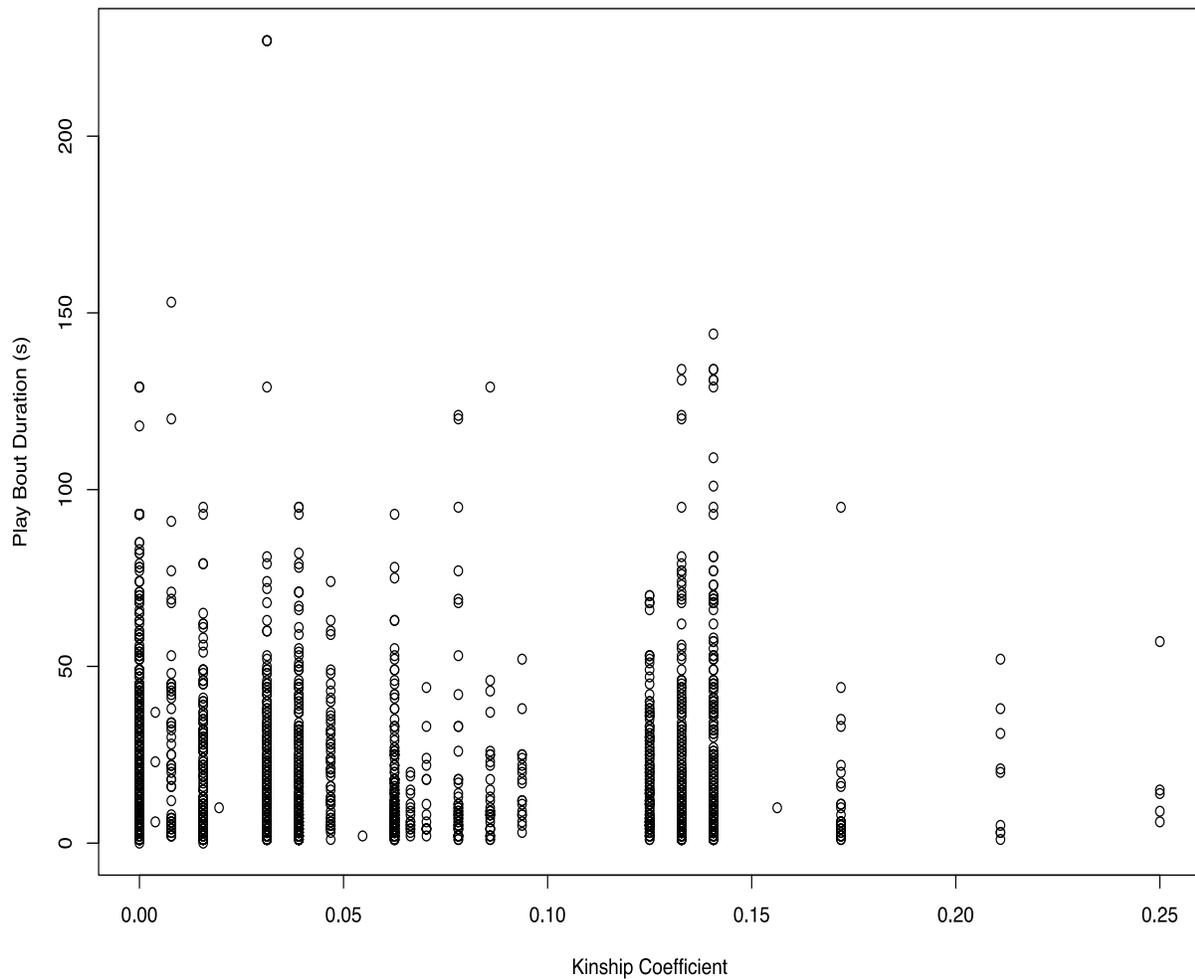
Overall, we analyzed 3,305 social play bouts (60,190 s) across the two field seasons (mean  $\pm$  *SD* = 18.21  $\pm$  20.72 s; max = 227 s) (See Figure 1). Play duration was summed for each of the 159 distinct player dyads (mean dyadic duration = 378.55  $\pm$  554.97 s; max = 4,155 s), which were then categorized based on sex (MM, FF, and FM). In total, there were 29 distinct MM dyads (mean = 582.83  $\pm$  644.66 s), 58 distinct FF dyads (mean = 267.19  $\pm$  412.68 s), and 72 distinct FM dyads (mean = 385.97  $\pm$  597.94 s). Total bout frequencies (the number of play bouts participated in) and durations (total number of seconds played) were then summed for each individual player. Across both field seasons, TQS (M), THN (M), and YXYue (F) participated most frequently overall playing in 1,172, 842, and 741 bouts, respectively. TQS (M), YXYue (F), and THN (M) were also the three individuals that played the longest overall (17,713, 11,534, and 11,757s, respectively) (see Table 1).

We then separated the data by field season and analyzed each year independently to examine the dynamics of play within the group. In 2016, juveniles engaged in 38,133 s of play across 1,443 play bouts (mean = 26.43  $\pm$  22.51 s; max = 153 s). In 2017, the juveniles engaged in 22,057 s of play across 1,862 bouts (mean = 11.85  $\pm$  16.63 s). Total individual durations per monkey were also determined. In 2016, YXC (M), TQS (M), TFH (F), THN (M), and YXYue (F) played the most (7,926, 7,502, 7,419, 5,214, and 5,987 s, respectively). However, in 2017, TQS (M), THN (M), and YXYue (F) were the most playful (10,211, 6,320, and 5,770 s, respectively) (See Table 1). Individual frequency of play was also calculated per year. In 2016,

TQS (M) ( $n = 356$  bouts), YXYue (F) ( $n = 246$  bouts), and YXC (M) ( $n = 243$  bouts) participated in the most play bouts. In 2017, TQS (M) ( $n = 816$  bouts), THN (M) ( $n = 634$  bouts), and YXYue (F) ( $n = 495$  bouts) participated in the most play bouts.

### Figure 1

*Kinship Coefficient vs Individual Play Bout Durations ( $n = 3,305$ )*



The age of each juvenile was calculated in days (d) based on the first day of data collection each season (7/14/16 and 7/7/17). The mean age in 2016 was younger than in 2017 (764 and 1012 d, respectively). There was a significant negative relationship between player age and total play duration in 2016 ( $r = -0.416$ ,  $p < 0.05$ ); however, there was no significant

relationship between player age and duration in 2017 ( $r = -0.135, p > 0.05$ ) (See Appendix A).

Additionally, there was no significant relationship between player age and play bout frequency

for either year (2016:  $r = -0.229, p > 0.05$ ; 2017:  $r = -0.053, p > 0.05$ ).

**Table 1**

*Total Individual Social Play Durations*

<b>Individual</b>	<b>2016 Total Duration (s)</b>	<b>2017 Total Duration (s)</b>	<b>Total Duration (s)</b>
<b>HXW (F)</b>	1946	385	<b>2331</b>
<b>HXYue (F)</b>	6226	1213	<b>7439</b>
<b>HXYun (F)</b>	N/A	948	<b>948</b>
<b>HY (M)</b>	4305	586	<b>4891</b>
<b>TFH (F)</b>	7419	1165	<b>8584</b>
<b>THL (F)</b>	2497	3869	<b>6366</b>
<b>THN (M)</b>	5214	6320	<b>11534</b>
<b>THX (F)</b>	N/A	154	<b>154</b>
<b>TQG (F)</b>	N/A	180	<b>180</b>
<b>TQL (F)</b>	1470	1684	<b>3154</b>
<b>TQS (M)</b>	7502	10211	<b>17713</b>
<b>TQY (F)</b>	7096	1418	<b>8154</b>
<b>TRX (F)</b>	693	1820	<b>2513</b>
<b>TRY2 (M)</b>	4112	1532	<b>5644</b>
<b>TXH_I (F)</b>	1733	N/A	<b>1733</b>
<b>TXL (M)</b>	2447	188	<b>2635</b>
<b>YCH (F)</b>	2055	36	<b>2091</b>
<b>YCLong (M)</b>	288	790	<b>1078</b>
<b>YH_I (M)</b>	2516	N/A	<b>2516</b>
<b>YRLan (F)</b>	506	4	<b>510</b>
<b>YXC (M)</b>	7926	N/A	<b>7926</b>
<b>YXDuo (F)</b>	N/A	1220	<b>1220</b>
<b>YXK (M)</b>	4328	1670	<b>5998</b>
<b>YXMing (M)</b>	N/A	1660	<b>1660</b>
<b>YXYue (F)</b>	5987	5770	<b>11757</b>
<b>YXYun (F)</b>	N/A	1291	<b>1291</b>

Play duration and frequency were also analyzed by sex for 2016 and 2017. In 2016, the mean total play duration was  $4,293.11 \pm 2,423.43$  s for males and  $3,420.73 \pm 2,672.68$  s for females. The mean duration was lower for both males and females in 2017 (males =  $2,869.63 \pm 3,529.94$  s; females =  $1,410.47 \pm 1,550.76$  s). There was no significant difference between total play durations per individual of male and female players ( $H = 2.025$ ,  $df=1$ ,  $p > 0.05$ ). Dyad compositions differed significantly from the expected values ( $\chi^2(2) = 228$ ,  $p < 0.001$ ) with mixed sex (FM) play bouts occurring most frequently ( $n = 1,484$ , 45%) followed by MM ( $n = 1,037$ , 31%) and then FF play ( $n = 784$ , 24%).

Play frequency per matriline varied greatly, with members of the Tou matriline ( $n = 3,952$ , 63%) participating in the most play bouts followed by the Ye ( $n = 1,791$ , 28%) and Hua matriline ( $n = 561$ , 9%), and this was significantly different from the expected values ( $\chi^2(2) = 2805$ ,  $p < 0.001$ ). Of all the matriline, Tou had the longest mean play duration ( $506.27 \pm 660.9$  s) and the largest number of distinct dyads ( $n = 37$ ). In the Hua matriline, 3 distinct dyads emerged, and players played a mean of  $354.33 \pm 443.57$  s. Individuals in the Ye matriline played a mean of  $329.82 \pm 261.2$  s in 11 distinct dyad configurations (See Appendix A). However, these matriline differences in total play durations were not statistically significant (Kruskal-Wallis:  $H = 0.26$ ,  $df = 2$ ,  $p > 0.05$ ).

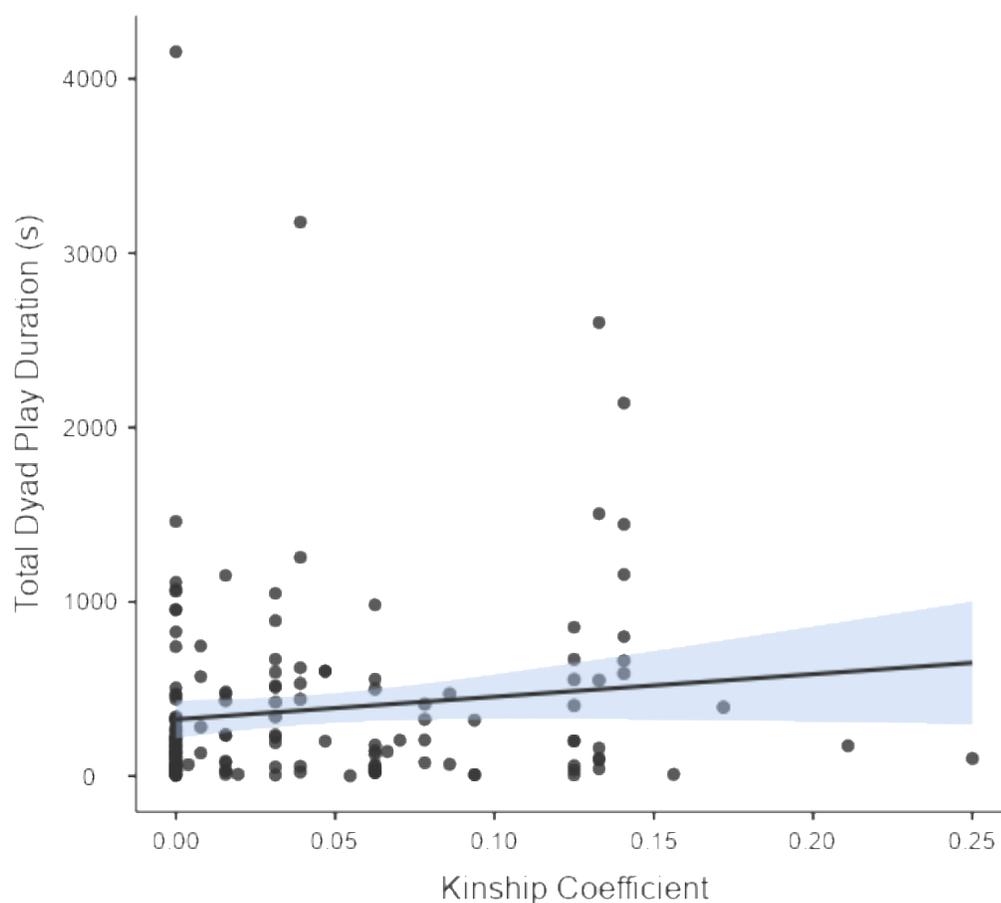
The average kinship coefficient for players was 0.048 (min = 0; max = 0.25). A Spearman rank test indicated no relationship between kinship coefficient and individual bout duration ( $r < 0.001$ ,  $p > 0.05$ ); however, there was a significant positive correlation between the total bout duration and kinship coefficient ( $r = 0.137$ ,  $p < 0.05$ ) (See Figure 2).

## Discussion

The play behavior of the YA1 juvenile macaques at Mt. Huangshan was previously examined, but the role of genetic kinship was not well documented. This study further

### Figure 2

*Positive Correlation ( $r = 0.137$ ) between Kinship Coefficient and Total Durations*



characterizes juvenile play, while building upon previous research at the same site (Mayhew et al., 2020; Wang et al., 2021; Wright et al., 2018). Although the correlation between genetic kinship and an individual play bout duration was not significant, genetic kinship did influence total play duration per dyad, emphasizing the importance of playing with specific individuals during this period of development. This finding supports our hypothesis that overall, play

duration between individuals is positively correlated with increased genetic kinship. The overall kinship between juveniles included both maternal and paternal relatives. Of the 26 juveniles considered in this study, 17 have known paternity. Paternity data showed high genetic kinship across matrilineal lines for both male and female juveniles. The high degree of kinship between juveniles across matrilineal lines supports the conclusion that playing with maternal and paternal kin is potentially a mechanism that enables juveniles within this group to navigate development effectively. In despotic macaque species, such as the grade two Tibetan macaque, kin selection plays a significant role in adult social associations and relationships (Cords, 1997; de Waal, 1991; Hemelrijk, 1994; Perry, 1996; Seyfarth, 1977; Silk, 1992 a,b). This study suggests that kin-biased selection begins in the early stages of life during social play events. Kin-biased play, especially in females, supports previous evidence that future social partners and relationships can be predicted from social play during juvenilehood (Pellis et al., 2019). Within this group, males likely also benefit from a kin-biased play system. Across 2016-2017, multiple natal males (YeRongBing, TouGui, and HuaXiaMing) occupied top-ranking positions among the male dominance hierarchy. Although expected to disperse at maturity (Thierry, 2000; Thierry et al., 2000), these males may have remained in their group due to altruistic and kin-biased relationships established during their own early development. This reasoning also suggests that highly playful males (particularly, TQS and THN) with many play partners could potentially delay dispersal as other natal males have done in the past (Mayhew et al., 2020).

Although we found no significant difference between the individual male and female play totals, we found that among the 159 distinct player configurations, MM dyads played for more than double the total time of FF dyads and over 1.5 the total time of FM dyads (MM mean = 582.83 s; FF mean = 267.19 s; FM mean = 385.97 s). These findings support previous research

about how play helps establish social dynamics between males who will likely be encountered in the future (Pellis & Pellis, 1996; Maestripieri & Ross, 2004). One function of increased duration of play between males is that it allows them to determine other individuals' strengths and abilities, as well as improve their individual physical abilities (Pellis & Pellis, 1996). We also expected that play should occur more often between dyads of the same sex; however, this prediction was not supported as the FM dyad configuration ( $n = 1484$ ) accounted for nearly 45% of all play bouts observed. This result can be due to the female-biased sex ratio between juveniles within this group (2016 = 11:9; 2017 = 15:8).

We analyzed matrilineal play duration and found no significant difference between the total play duration of each matriline. However, an uneven and variable number of matriline members was likely influential—the Hua matriline contained three juveniles, the Ye matriline contained 9 juveniles, and the Tou matriline contained 12 juveniles. Overall, matriline size likely has some influence on early play behavior as we observed 37 distinct play dyads among Tou juveniles but only 11 dyads within Ye and 3 dyads within Hua.

We also found a large difference in mean play duration per year, resulting in an overall mean of 18.21 s across both years. When considering other variables, such as mean age and demographics across years, the vast difference in play duration is unsurprising. The mean age of the players observed increased from 764 d in 2016 to 1012 d in 2017 (a difference of 248 days or ~ 8 months). The sex ratio of the group also drastically changed between years, resulting in an almost 2:1 ratio of females to males in 2017. Both age and sex impacted play duration as supported by the significant negative correlation between age and play duration in 2016 and relationship of age and play duration in 2017.

Similar to previous research at this site (Mayhew et al. 2020; Wang et al., 2021), we found a significant negative correlation between increasing age and play duration in the 2016 dataset. Although this relationship was not significant in 2017, the relationship trended in this negative direction, which supports existing literature, suggesting that play decreases and eventually ceases in adult despotic species. Less time is spent playing later in the life course due to the entrance into adult social dynamics and the readjustment of activity budgets. By 2.5 years old, juveniles have likely used play to establish social relationships with both kin and non-kin alike. As juveniles continue to age, they begin to engage in and prioritize other types of affiliation, using other social strategies to establish and maintain a variety of social relationships as they enter the adult social hierarchies.

Even with a significant relationship between total play duration and genetic kinship, we found the trio of TQS, THN, and YXYue participated in the longest play duration across these two years. Surprisingly, these individuals have low kinship coefficients, namely, because YXYue is the first offspring of YH and an immigrant male (BT), and the father of THN is unknown. With more complete pedigree information on the father of THN, there is a possibility that his genetic kinship with TQS or YXYue increases. Additionally, the death of YXC likely also impacted the data between 2016 and 2017, as he played the most total time in 2016 but was not present in 2017. YXC had a high kinship coefficient with individuals like TFH and TQY (~0.14) due to shared paternity. In 2016, both TFH and TQY played more than 7,000 s, but in 2017, both individuals played less than 1,500 s. The death of a paternal half-sibling and member of the same birth cohort likely contributed to the lower overall play observed during 2017.

## **Future Considerations**

This study emphasizes the need for more complete data collection within all age and sex categories of primate groups. Creating and recording complete pedigrees, supported by genetic information, is necessary to truly understand the impact of kin selection during play and development. Additional paternity data could enhance future studies by providing more evidence of paternal kin influence on juvenile behavior. Furthermore, when considering play, factors such as player choice and individual personality or playfulness should be considered. Long-term studies should also be conducted across the entire juvenile period of life. These long-term studies will allow for activity budgets of juveniles to be considered across many different ages. This will help determine where time and energy are spent resulting in play duration decrease and eventual discontinuation. Additionally, tools such as social network analysis can be used to determine the strength of relationships between juveniles (see Mayhew et al., 2020) and to examine how individual positions within the social network change over time. For example, the death of YXC could have impacted the social network of multiple individuals, thus resulting in less play overall following his death. If YXC was a key central individual to the social play network, the resulting loss of connectivity between other individuals may have been widespread. Similarly, certain central juveniles may act as scaffolding for new juveniles to be introduced to the social play network. These social bridges may provide critical introductions for less experienced juveniles into the juvenile social network. Continued attention on the developmental stages of primate social life can help us better capture a holistic view of primate sociality.

## **Acknowledgements**

We thank all of our collaborators at both Central Washington University, Anhui University and Mt. Huangshan, China. R.N.D received support from the Debra and Arlen

Prentice Award through the CWU Primate Behavior Program for this research. This research was partially supported by the CWU School of Graduate Studies and Research. This project used data approved by the Central Washington University Institutional Care and Use Committee (IACUC) board (protocol: #A031608; #A051602; #M061603; #A051702)

## References

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3-4), 227–266. <https://doi.org/10.1163/156853974x00534>
- Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press.
- Altmann, S. A. (1962). A field study of the sociology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Sciences*, 102(2), 338–435. <https://doi.org/10.1111/j.1749-6632.1962.tb13650.x>
- Baldwin, J. D., & Baldwin, J. I. (1974). Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist*, 14(1), 303–315. <https://doi.org/10.1093/icb/14.1.303>
- Batts, C. (2012) The impact of eco-tourism on infant and juvenile play behaviors in Tibetan macaques (*Macaca thibetana*). Central Washington University., WA.
- Bekoff, M. (1977). Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *The American Naturalist*, 111(980), 715–732. <https://doi.org/10.1086/283201>
- Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: an ethological perspective. *The Quarterly Review of Biology*, 47(4), 412–434. <https://doi.org/10.1086/407400>
- Bekoff, M. (1984). Social play behavior. *BioScience*, 34(4), 228–233. <https://doi.org/10.2307/1309460>
- Bekoff, M., & Allen, C. (1997) Intentional communication and social play: how and why animals negotiate and agree to play. In M. Bekoff., & J.A Byers, (Eds.), *Animal play:*

*evolutionary, comparative, and ecological perspectives* (pp. 97–114). Cambridge University Press.

Bekoff, M., & Byers, J. A. (1981) A critical reanalysis of the ontogeny of mammalian social and locomotor play, an ethological hornet's nest. In K. Immelmann, G.W. Barlow, L. Petrino, M. Main, (Eds.), *Behavioral development, the bielefeld interdisciplinary project* (pp. 296–337). Cambridge University Press.

Berman, C. M. (1983a). Matriline differences and infant development. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 132–134). Sinauer Associates.

Berman, C. M. (1983b). Early differences in relationships between infants and other group members based on the mother's status: Their possible relationship to peer–peer rank acquisition. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 154–156). Sinauer Associates.

Berman, C. M. (1983c). Influence of close female relations on peer–peer rank acquisition. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 157–159). Sinauer Associates.

Berman, C. M., Ionica, C. S., & Li, J. (2004). Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology*, 25(6), 1283–1312.  
<https://doi.org/10.1023/b:ijop.0000043963.77801.c3>

Bernstein, I. S., & Ehardt, C. L. (1985). Agonistic aiding: Kinship, rank, age, and sex influences. *American Journal of Primatology*, 8(1), 37–52. <https://doi.org/10.1002/ajp.1350080105>

- Bernstein, I. S., & Ehardt, C. (1986). The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour*, *34*(3), 739–747.  
[https://doi.org/10.1016/s0003-3472\(86\)80057-4](https://doi.org/10.1016/s0003-3472(86)80057-4)
- Bjorklund, D. F., & Pellegrini, A. D. (2002). Evolutionary developmental psychology. *The Origins of Human Nature: Evolutionary Developmental Psychology*. 3–10.  
<https://doi.org/10.1037/10425-001>
- Brown, S. G. (1988). Play behaviour in lowland gorillas: Age differences, sex differences, and possible functions. *Primates*, *29*(2), 219–228. <https://doi.org/10.1007/bf02381123>
- Burghardt, G. M. (2005). *The genesis of animal play: testing the limits*. MIT.
- Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *The American Naturalist*, *146*(1), 25–40. <https://doi.org/10.1086/285785>
- Cenni, C., & Fawcett, T. W. (2018). The coevolution of juvenile play-fighting and adult competition. *Ethology*, *124*(5), 290–301. <https://doi.org/10.1111/eth.12732>
- Chapais, B. (1983). Dominance, relatedness, and the structure of female relationships in rhesus monkeys. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 209–219). Sinauer Associates.
- Chase, I. D., Tovey, C., Spangler-Martin, D., & Manfredonia, M. (2002). Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences*, *99*(8), 5744–5749.  
<https://doi.org/10.1073/pnas.082104199>

- Cheney, D. L. (1978). Interactions of immature male and female baboons with adult females. *Animal Behaviour*, *26*, 389–408. [https://doi.org/10.1016/0003-3472\(78\)90057-x](https://doi.org/10.1016/0003-3472(78)90057-x)
- Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, *135*(1-2), 1–12. <https://doi.org/10.1016/j.applanim.2011.10.010>
- Cords, M. (1997). Friendship, alliances, reciprocity and repair. In A. Whiten., & R.W. Byrne, (Eds.), *Machiavellian Intelligence II* (pp. 24–49). Cambridge University Press.
- Datta, S. B. (1983a). Relative power and the acquisition of rank. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 93–103). Sinauer Associates.
- Datta, S. B. (1983b). Relative power and the maintenance of dominance. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 103–112). Sinauer Associates.
- de Waal, F.B.M. (1977). The organization of agonistic relations within two captive groups of Java-monkeys (*Macaca fascicularis*). *Zeitschrift für Tierpsychologie*, *44*: 225-282. <https://doi.org/10.1111/j.1439-0310.1977.tb00995.x>
- de Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: A sociometric analysis. *Animal Behaviour*, *41*(3), 383–395. [https://doi.org/10.1016/s0003-3472\(05\)80839-5](https://doi.org/10.1016/s0003-3472(05)80839-5)
- Defler, T. R. (1978). Allogrooming in two species of macaque (*Macaca nemestrina* and *Macaca radiata*). *Primates*, *19*(1), 153–167. <https://doi.org/10.1007/bf02373232>
- Fagen, R. (1981). *Animal play behavior*. Oxford University Press.

- Fagen, R. (1984) Play and behavioural flexibility. In P.K. Smith (Ed.), *Play in animals and humans* (pp. 159–173). Basil Blackwell.
- Fagen, R. (1993). Primate juveniles and primate play. In M. E. Pereira, & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 183 – 196). Oxford University Press.
- Fontaine, R. P. (1994). Play as physical flexibility training in five ceboid primates. *Journal of Comparative Psychology*, 108(3), 203–212. <https://doi.org/10.1037/0735-7036.108.3.203>
- Funkhouser, J. A., Mayhew, J. A., Sheeran, L. K., Mulcahy, J. B., & Li, J.-H. (2018). Comparative investigations of social context-dependent dominance in captive chimpanzees (*Pan troglodytes*) and wild Tibetan macaques (*Macaca thibetana*). *Scientific Reports*, 8(1). <https://doi.org/10.1038/s41598-018-32243-2>
- Gouzoules, S. (1984). Primate mating systems, kin associations, and cooperative behavior: Evidence for kin recognition? *American Journal of Physical Anthropology*, 27(S5), 99–134. <https://doi.org/10.1002/ajpa.1330270506>
- Gouzoules, S., & Gouzoules, H. (1987). Kinship. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, (Eds.), *Primate societies* (pp. 299–305). University of Chicago Press.
- Hamilton, W. D. (1964). The genetical evolution of social behavior: I and II. *Journal Theoretical Biology*. 7, 1–52.

- Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, 48(2), 479–481. <https://doi.org/10.1006/anbe.1994.1264>
- Kaplan, J. R. (1977). Patterns of fight interference in free-ranging rhesus monkeys. *American Journal of Physical Anthropology*, 47(2), 279–287.  
<https://doi.org/10.1002/ajpa.1330470208>
- Kaplan, J. R. (1978). Fight interference and altruism in rhesus monkeys. *American Journal of Physical Anthropology*, 49(2), 241–249. <https://doi.org/10.1002/ajpa.1330490212>
- Kapsalis, E., & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). *Behaviour*, 133(15-16), 1235–1263.  
<https://doi.org/10.1163/156853996x00387>
- 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. <https://doi.org/10.1007/s10764-015-9826-4>
- Kurland, J. A. (1977). Kin selection in the Japanese monkey. In *Contributions to primatology* (Vol. 12.). Karger.
- Li, J.-H., & Kappeler, P. M. (2020). Social and life history strategies of Tibetan macaques at Mt. Huangshan. In J.-H. Li, L. Sun, P.M. Kappeler, (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 17–46). [https://doi.org/10.1007/978-3-030-27920-2\\_2](https://doi.org/10.1007/978-3-030-27920-2_2)
- Maestriperi, D., & Ross, S. R. (2004). Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure.

*American Journal of Physical Anthropology*, 123(1), 52–61.

<https://doi.org/10.1002/ajpa.10295>

Martin, P., & Caro, T. M. (1985) On the functions of play and its role in behavioral development.

In J.S. Rosenblatt, C. Beer, M.C. Busnel, P.J.B. Slater, (Eds.), *Advances in the study of behavior* (Vol 15., pp 59–103). Academic.

Massey, A. (1977). Agonistic aids and kinship in a group of pigtail macaques. *Behavioral*

*Ecology and Sociobiology*, 2(1), 31–40. <https://doi.org/10.1007/bf00299286>

Mayhew, J. A., Funkhouser, J. A., & Wright, K. R. (2020). Considering social play in primates:

A case study in juvenile Tibetan macaques (*Macaca thibetana*). In J.-H. Li, L. Sun, P.M. Kappeler, (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 93–117).

[https://doi.org/10.1007/978-3-030-27920-2\\_6](https://doi.org/10.1007/978-3-030-27920-2_6)

Missakian, E. A. (1974). Mother-offspring grooming relations in rhesus monkeys. *Archives of*

*Sexual Behavior*, 3(2), 135–141. <https://doi.org/10.1007/bf01540997>

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*):

Implications for natural social systems and interindividual relationships. *American*

*Journal of Physical Anthropology*, 129(3), 418–426. <https://doi.org/10.1002/ajpa.20289>

Palagi, E. (2018). Not just for fun! Social play as a springboard for adult social competence in

human and non-human primates. *Behavioral Ecology and Sociobiology*, 72(6).

<https://doi.org/10.1007/s00265-018-2506-6>

- Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of social play in juvenile lowland gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology*, *49*(4), 433–445.  
<https://doi.org/10.1002/dev.20219>
- Palagi, E., & Paoli, T. (2007). Play in adult bonobos (*Pan paniscus*): Modality and potential meaning. *American Journal of Physical Anthropology*, *134*(2), 219–225.  
<https://doi.org/10.1002/ajpa.20657>
- Pellis, S. M., & Pellis, V. C. (1996). On knowing it's only play: The role of play signals in play fighting. *Aggression and Violent Behavior*, *1*(3), 249–268. [https://doi.org/10.1016/1359-1789\(95\)00016-x](https://doi.org/10.1016/1359-1789(95)00016-x)
- Pellis, S. M., Pellis, V. C. (2009) *The playful brain*. OneWorld Publications.
- Pellis, S. M., & Pellis, V. C., Pelletier, A., & Leca, J.-B. (2019). Is play a behavior system, and, if so, what kind? *Behavioural Processes*, *160*, 1–9.  
<https://doi.org/10.1016/j.beproc.2018.12.011>
- Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, *40*(2), 167–182.  
[https://doi.org/10.1002/\(sici\)1098-2345\(1996\)40:2<167::aid-ajp4>3.0.co;2-w](https://doi.org/10.1002/(sici)1098-2345(1996)40:2<167::aid-ajp4>3.0.co;2-w)
- Petit, O., Bertrand, F., & Thierry, B. (2008). Social play in crested and japanese macaques: Testing the covariation hypothesis. *Developmental Psychobiology*, *50*(4), 399–407.  
<https://doi.org/10.1002/dev.20305>

- 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). Retrieved from <https://escholarship.org/uc/item/13n9f7t5>
- Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology*, 23(1), 1–17. <https://doi.org/10.1002/ajpa.1330230115>
- Scopa, C., & Palagi, E. (2016). Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*). *Journal of Comparative Psychology*, 130(2), 153–161. <https://doi.org/10.1037/com0000028>
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698. [https://doi.org/10.1016/0022-5193\(77\)90015-7](https://doi.org/10.1016/0022-5193(77)90015-7)
- Shimada, M., & Sueur, C. (2014). The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *American Journal of Primatology*, 76(11), 1025–1036. <https://doi.org/10.1002/ajp.22289>
- Silk, J. B. (1982). Altruism among female *Macaca radiata*: Explanations and analysis of Patterns of grooming and coalition formation. *Behaviour*, 79(2-4), 162–188. <https://doi.org/10.1163/156853982x00238>

- Silk, J. B. (1992a). Patterns of intervention in agonistic contests among male bonnet macaques. In Harcourt, S., and de Waal, F. B. M. (eds.), *Coalitions and Alliances in Humans and Other Animals*, Oxford University Press, Oxford, pp. 215–232. <sup>[1]</sup><sub>[SEP]</sub>
- Silk, J. B. (1992b). The Patterning of Intervention among Male Bonnet Macaques: Reciprocity, Revenge, and Loyalty. *Current Anthropology*, 33(3), 318–325.  
<https://doi.org/10.1086/204073>
- Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, 57(5), 1021–1032.  
<https://doi.org/10.1006/anbe.1998.1065>
- Silk, J. B. (2002). Kin selection in primate groups. *International Journal of Primatology*, 23(4).
- Silk, J. B., Samuels, A., & Rodman, P. S. (1981). The Influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour*, 78(1-2), 111–137. <https://doi.org/10.1163/156853981x00284>
- Smith, P. K. (1982). Does play matter? Functional and evolutionary aspects of animal and human play. *Behavioral and Brain Sciences*, 5(1), 139–155.  
<https://doi.org/10.1017/s0140525x0001092x>
- Smith, J. E., Chung, L. K., & Blumstein, D. T. (2013). Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots. *Animal Behaviour*, 85(4), 715–725.  
<https://doi.org/10.1016/j.anbehav.2013.01.008>
- Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. Columbia University Press.

- Thierry B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, F.B.M. de Waal, (Eds.), *Natural conflict resolution* (pp. 106–128). University of California Press.
- Thierry, B. (2004). Social epigenesis. In B. Thierry, S. Mewa, & W. Kaumanns, (2004). *Macaque societies: A model for the study of social organization*. Cambridge University Press.
- Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The Influence of phylogeny on the Social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, *106*(8), 713–728. <https://doi.org/10.1046/j.1439-0310.2000.00583.x>
- Vigeland, M. D. (2020). Relatedness coefficients in pedigrees with inbred founders. *Journal of Mathematical Biology*, *81*(1), 185–207. <https://doi.org/10.1007/s00285-020-01505-x>
- Wang, T., Wang, X., Garber, P. A., Sun, B.-H., Sun, L., Xia, D.-P., & Li, J.-H. (2021). Sex-specific variation of social play in wild immature Tibetan macaques, *Macaca thibetana*. *Animals*, *11*(3), 805. <https://doi.org/10.3390/ani11030805>
- Wright, K. R., Mayhew, J. A., Sheeran, L. K., Funkhouser, J. A., Wagner, R. S., Sun, L.-X., & Li, J.-H. (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. <https://doi.org/10.24272/j.issn.2095-8137.2018.048>
- Wright, S. (1922). Coefficients of inbreeding and relationship. *The American Naturalist*, *56*(645), 330–338. <https://doi.org/10.1086/279872>

- Xia, D.-P., Li, J.-H., Garber, P. A., Sun, L., Zhu, Y., Sun, B.-H. (2012). Grooming reciprocity in female Tibetan macaques *Macaca thibetana*. *American Journal of Primatology*, 74(6), 569–579. <https://doi.org/10.1002/ajp.21985>
- Xia, D.-P., Li, J.-H., Garber, P. A., Matheson, M. D., Sun, B.-H., & Zhu, Y. (2013). Grooming reciprocity in male Tibetan macaques. *American Journal of Primatology*, 75(10), 1009–1020. <https://doi.org/10.1002/ajp.22165>
- Yanagi, A., & Berman, C. M. (2014). Functions of multiple play signals in free-ranging juvenile rhesus macaques (*Macaca mulatta*). *Behaviour*, 151(14), 1983–2014. <https://doi.org/10.1163/1568539x-00003227>

### CHAPTER III

#### GENERAL CONCLUSIONS

The aim of the study presented in Chapter II was to better understand the relationship between play duration and frequency and player age, sex, and genetic kinship between players. Using multiple analyses including Spearman rank tests, I found a significant negative correlation between player age and total play duration in 2016. Although there was not a significant correlation between play frequency and age for each year and play duration and age in 2017, the data trended negatively which supports previous studies at this site. I expected that same sex dyadic pairs would play longer and more often with one another. Male-male dyads played with each other for over 2x the total time of female-female dyads and over 1.5x the total time of female-male dyads. However, I found that female-male dyads played together for more total time than female-female dyads. Another unexpected result was female-male dyads playing the most frequently (45%) over the two-year study. I found a positive significant correlation between genetic kinship and total play duration, supporting our hypothesis. This finding suggests that kin selection plays a significant role in player partner choice and helps facilitate juvenile social relationships. Kin-biased play supports previous evidence that future social partners and social relationships can be influenced and predicted by social play. Within this group, males also potentially benefit from preferentially playing more with kin. Multiple natal males occupied the top-ranking positions in the dominance hierarchy during the study period. The altruistic, kin-biased relationships that begin and are reinforced during play events would suggest highly playful males could potentially delay dispersal as other natal males have done previously. Long-term studies should be conducted across the entirety of the juvenile development. This would allow for researchers to determine the differences in activity budgets, play network position, and

play partners across years. This data could then be utilized to help create a better understanding of the sociality and behavior of adult individuals within this group and across species.

**COMPREHENSIVE REFERENCES**

- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49(3-4), 227–266. <https://doi.org/10.1163/156853974x00534>
- Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press.
- Altmann, S. A. (1962). A field study of the sociology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Sciences*, 102(2), 338–435. <https://doi.org/10.1111/j.1749-6632.1962.tb13650.x>
- Axelrod, R., and Hamilton, W. D. (1981). The evolution of cooperation. *Science* 211, 1390–1396.
- Baldwin, J. D., & Baldwin, J. I. (1974). Exploration and social play in squirrel monkeys (*Saimiri*). *American Zoologist*, 14(1), 303–315. <https://doi.org/10.1093/icb/14.1.303>
- Batts, C. (2012) The impact of eco-tourism on infant and juvenile play behaviors in Tibetan macaques (*Macaca thibetana*). Central Washington University.
- Bekoff, M. (1977). Mammalian Dispersal and the Ontogeny of Individual Behavioral Phenotypes. *The American Naturalist*, 111(980), 715–732. <https://doi.org/10.1086/283201>
- Bekoff, M. (1972). The development of social interaction, play, and metacommunication in mammals: An ethological perspective. *The Quarterly Review of Biology*, 47(4), 412–434. <https://doi.org/10.1086/407400>
- Bekoff, M. (1984). Social play behavior. *BioScience*, 34(4), 228–233. <https://doi.org/10.2307/1309460>

- Bekoff, M., & Allen, C. (1997) Intentional communication and social play: how and why animals negotiate and agree to play. In M. Bekoff., & J.A Byers, (Eds.), *Animal play: evolutionary, comparative, and ecological perspectives* (pp. 97–114). Cambridge University Press.
- Bekoff, M., & Byers, J. A. (1981) A critical reanalysis of the ontogeny of mammalian social and locomotor play, an ethological hornet's nest. In K. Immelmann, G.W. Barlow, L. Petrinovich, M. Main, (Eds.), *Behavioral development, the bielefeld interdisciplinary project* (pp. 296–337). Cambridge University Press.
- Berman, C. M. (1980). Mother-infant relationships among free-ranging rhesus monkeys on Cayo Santiago: A comparison with captive pairs. *Animal Behaviour*, 28(3), 860–873.  
[https://doi.org/10.1016/s0003-3472\(80\)80146-1](https://doi.org/10.1016/s0003-3472(80)80146-1)
- Berman, C. M. (1982). The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys I. Social networks and differentiation. *Animal Behaviour*, 30(1), 149–162. [https://doi.org/10.1016/s0003-3472\(82\)80250-9](https://doi.org/10.1016/s0003-3472(82)80250-9)
- Berman, C. M. (1983a). Matriline differences and infant development. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 132–134). Sinauer Associates.
- Berman, C. M. (1983b). Early differences in relationships between infants and other group members based on the mother's status: Their possible relationship to peer–peer rank acquisition. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 154–156). Sinauer Associates.

- Berman, C. M. (1983c). Influence of close female relations on peer–peer rank acquisition. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 157–159). Sinauer Associates.
- Berman, C. M., Ionica, C. S., & Li, J. (2004). Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology*, 25(6), 1283–1312.  
<https://doi.org/10.1023/b:ijop.0000043963.77801.c3>
- Berman, C., Yin, H., Ogawa, H., Li, J., & Ionica, C. (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.  
<https://doi.org/10.1163/156853908784089252>
- Bernstein, I. S., & Ehardt, C. L. (1985). Agonistic aiding: Kinship, rank, age, and sex influences. *American Journal of Primatology*, 8(1), 37–52. <https://doi.org/10.1002/ajp.1350080105>
- Bernstein, I. S., & Ehardt, C. (1986). The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour*, 34(3), 739–747.  
[https://doi.org/10.1016/s0003-3472\(86\)80057-4](https://doi.org/10.1016/s0003-3472(86)80057-4)
- Bjorklund, D. F., & Pellegrini, A. D. (2002). Evolutionary developmental psychology. *The Origins of Human Nature: Evolutionary Developmental Psychology*. 3–10.  
<https://doi.org/10.1037/10425-001>
- Brown, S. G. (1988). Play behaviour in lowland gorillas: Age differences, sex differences, and possible functions. *Primates*, 29(2), 219–228. <https://doi.org/10.1007/bf02381123>

- Burghardt, G. M. (2005). *The genesis of animal play: testing the limits*. MIT.
- Byers, J. A., & Walker, C. (1995). Refining the motor training hypothesis for the evolution of play. *The American Naturalist*, *146*(1), 25–40. <https://doi.org/10.1086/285785>
- Cenni, C., & Fawcett, T. W. (2018). The coevolution of juvenile play-fighting and adult competition. *Ethology*, *124*(5), 290–301. <https://doi.org/10.1111/eth.12732>
- Chapais, B. (1983). Dominance, relatedness, and the structure of female relationships in rhesus monkeys. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 209–219). Sinauer Associates.
- Chase, I. D., Tovey, C., Spangler-Martin, D., & Manfredonia, M. (2002). Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences*, *99*(8), 5744–5749. <https://doi.org/10.1073/pnas.082104199>
- Cheney, D. L. (1978). Interactions of immature male and female baboons with adult females. *Animal Behaviour*, *26*, 389–408. [https://doi.org/10.1016/0003-3472\(78\)90057-x](https://doi.org/10.1016/0003-3472(78)90057-x)
- Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, *135*(1-2), 1–12. <https://doi.org/10.1016/j.applanim.2011.10.010>
- Cords, M. (1997). Friendship, alliances, reciprocity and repair. In A. Whiten., & R.W. Byrne, (Eds.), *Machiavellian Intelligence II* (pp. 24–49). Cambridge University Press.

- Datta, S. B. (1983a). Relative power and the acquisition of rank. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 93–103). Sinauer Associates.
- Datta, S. B. (1983b). Relative power and the maintenance of dominance. In R.A. Hinde, (Ed.), *Primate social relationships: An integrated approach* (pp. 103–112). Sinauer Associates.
- de Waal, F. B. M. (1991). Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis. *Animal Behaviour*, *41*(3), 383–395.  
[https://doi.org/10.1016/s0003-3472\(05\)80839-5](https://doi.org/10.1016/s0003-3472(05)80839-5)
- de Waal, F.B.M. (2001). *The ape and the sushi master: cultural reflections by a primatologist*. Basic Books.
- de Waal, F.B.M. (1977), The organization of agonistic relations within two captive groups of Java-monkeys (*Macaca fascicularis*). *Zeitschrift für Tierpsychologie*, *44*, 225-282. <https://doi.org/10.1111/j.1439-0310.1977.tb00995.x>
- Defler, T. R. (1978). Allogrooming in two species of macaque (*Macaca nemestrina* and *Macaca radiata*). *Primates*, *19*(1), 153–167. <https://doi.org/10.1007/bf02373232>
- Dugatkin, L. A. (1997). *Cooperation among animals: an evolutionary perspective*. Oxford University Press.
- Fagen, R. (1981). *Animal play behavior*. Oxford University Press.
- Fagen, R. (1984) Play and behavioural flexibility. In P.K. Smith (Ed.), *Play in animals and humans* (pp. 159–173). Basil Blackwell.

- Fagen, R. (1993). Primate juveniles and primate play. In M. E. Pereira, & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 183 – 196). Oxford University Press.
- Fontaine, R. P. (1994). Play as physical flexibility training in five ceboid primates. *Journal of Comparative Psychology*, *108*(3), 203–212. <https://doi.org/10.1037/0735-7036.108.3.203>
- Funkhouser, J. A., Mayhew, J. A., Sheeran, L. K., Mulcahy, J. B., & Li, J.-H. (2018). Comparative investigations of social context-dependent dominance in captive chimpanzees (*Pan troglodytes*) and wild Tibetan macaques (*Macaca thibetana*). *Scientific Reports*, *8*(1). <https://doi.org/10.1038/s41598-018-32243-2>
- Gouzoules, S. (1984). Primate mating systems, kin associations, and cooperative behavior: Evidence for kin recognition? *American Journal of Physical Anthropology*, *27*(S5), 99–134. <https://doi.org/10.1002/ajpa.1330270506>
- Gouzoules, S., & Gouzoules, H. (1987). Kinship. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker, (Eds.), *Primate societies* (pp. 299–305). University of Chicago Press.
- Hamilton, W. D. (1964). The genetical evolution of social behavior: I and II. *Journal Theoretical Biology*, *7*, 1–52.
- Hemelrijk, C. K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, *48*(2), 479–481. <https://doi.org/10.1006/anbe.1994.1264>

- Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, *73*, 758–773. <https://doi.org/10.1002/ajp.20914>
- Kaplan, J. R. (1977). Patterns of fight interference in free-ranging rhesus monkeys. *American Journal of Physical Anthropology*, *47*(2), 279–287. <https://doi.org/10.1002/ajpa.1330470208>
- Kaplan, J. R. (1978). Fight interference and altruism in rhesus monkeys. *American Journal of Physical Anthropology*, *49*(2), 241–249. <https://doi.org/10.1002/ajpa.1330490212>
- Kapsalis, E., & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). *Behaviour*, *133*(15-16), 1235–1263. <https://doi.org/10.1163/156853996x00387>
- 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. <https://doi.org/10.1007/s10764-015-9826-4>
- Kurland, J. A. (1977). Kin selection in the Japanese monkey. In *Contributions to primatology* (Vol. 12.). Karger.
- Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, *77*(2), 377–387. <https://doi.org/10.1016/j.anbehav.2008.09.038>

- Li, J.-H., & Kappeler, P. M. (2020). Social and life history strategies of Tibetan macaques at Mt. Huangshan. In J.-H. Li, L. Sun, P.M. Kappeler, (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 17–46). [https://doi.org/10.1007/978-3-030-27920-2\\_2](https://doi.org/10.1007/978-3-030-27920-2_2)
- Maestriperi, D. (2004) Maternal behavior, infant handling, and socialization. In Thierry B et. al, (Eds.), *Macaque societies: A model for the study of social organization* (pp. 231–234). Cambridge University Press..
- Maestriperi, D., & Ross, S. R. (2004). Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: Implications for adult behavior and social structure. *American Journal of Physical Anthropology*, 123(1), 52–61.  
<https://doi.org/10.1002/ajpa.10295>
- Martin, P., & Caro, T. M. (1985) On the functions of play and its role in behavioral development. In J.S. Rosenblatt, C. Beer, M.C. Busnel, P.J.B. Slater, (Eds.), *Advances in the study of behavior* (Vol 15., pp 59–103). Academic.
- Massey, A. (1977). Agonistic aids and kinship in a group of pigtail macaques. *Behavioral Ecology and Sociobiology*, 2(1), 31–40. <https://doi.org/10.1007/bf00299286>
- Mayhew, J. A., Funkhouser, J. A., & Wright, K. R. (2020). Considering social play in primates: A case study in juvenile Tibetan macaques (*Macaca thibetana*). In J.-H. Li, L. Sun, P.M. Kappeler, (Eds.), *The behavioral ecology of the Tibetan macaque* (pp. 93–117).  
[https://doi.org/10.1007/978-3-030-27920-2\\_6](https://doi.org/10.1007/978-3-030-27920-2_6)

Missakian, E. A. (1974). Mother-offspring grooming relations in rhesus monkeys. *Archives of Sexual Behavior*, 3(2), 135–141. <https://doi.org/10.1007/bf01540997>

Nakamichi, M. (1989). Sex differences in social development during the first 4 years in a free-ranging group of Japanese monkeys, *Macaca fuscata*. *Animal Behaviour*, 38(5), 737–748. [https://doi.org/10.1016/s0003-3472\(89\)80106-x](https://doi.org/10.1016/s0003-3472(89)80106-x)

Nakamichi, M. (1996). Proximity relationships within a birth cohort of immature Japanese monkeys (*Macaca fuscata*) in a free-ranging group during the first four years of life. *American Journal of Primatology*, 40(4), 315–325. [https://doi.org/10.1002/\(sici\)1098-2345\(1996\)40:4<315::aid-ajp2>3.0.co;2-0](https://doi.org/10.1002/(sici)1098-2345(1996)40:4<315::aid-ajp2>3.0.co;2-0)

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, 129(3), 418–426. <https://doi.org/10.1002/ajpa.20289>

Palagi, E. (2018). Not just for fun! Social play as a springboard for adult social competence in human and non-human primates. *Behavioral Ecology and Sociobiology*, 72(6). <https://doi.org/10.1007/s00265-018-2506-6>

Palagi, E., Antonacci, D., & Cordoni, G. (2007). Fine-tuning of social play in juvenile lowland gorillas (*Gorilla gorilla gorilla*). *Developmental Psychobiology*, 49(4), 433–445. <https://doi.org/10.1002/dev.20219>

- Palagi, E., & Paoli, T. (2007). Play in adult bonobos (*Pan paniscus*): Modality and potential meaning. *American Journal of Physical Anthropology*, *134*(2), 219–225.  
<https://doi.org/10.1002/ajpa.20657>
- Pellis, S. M., & Pellis, V. C. (1996). On knowing it's only play: The role of play signals in play fighting. *Aggression and Violent Behavior*, *1*(3), 249–268. [https://doi.org/10.1016/1359-1789\(95\)00016-x](https://doi.org/10.1016/1359-1789(95)00016-x)
- Pellis, S. M., Pellis, V. C. (2009) *The playful brain*. OneWorld Publications.
- Pellis, S. M., Pellis, V. C., Pelletier, A., & Leca, J.-B. (2019). Is play a behavior system, and, if so, what kind? *Behavioural Processes*, *160*, 1–9.  
<https://doi.org/10.1016/j.beproc.2018.12.011>
- Pellis, S. M., Pellis, V. C., Reinhart, C. J., Thierry, B. (2011). The use of the bared-teeth display during play fighting in Tonkean macaques (*Macaca tonkeana*): Sometimes it is all about oneself. *Journal of Comparative Psychology*, *125*(4), 393–403.  
<https://doi.org/10.1037/a0024514>
- Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, *40*(2), 167–182.  
[https://doi.org/10.1002/\(sici\)1098-2345\(1996\)40:2<167::aid-ajp4>3.0.co;2-w](https://doi.org/10.1002/(sici)1098-2345(1996)40:2<167::aid-ajp4>3.0.co;2-w)
- Petit, O., Bertrand, F., & Thierry, B. (2008). Social play in crested and Japanese macaques: Testing the covariation hypothesis. *Developmental Psychobiology*, *50*(4), 399–407.  
<https://doi.org/10.1002/dev.20305>

- 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). Retrieved from <https://escholarship.org/uc/item/13n9f7t5>
- Rhine, R. J., & Hendy-Neely, H. (1978). Social development of stumptail macaques (*Macaca arctoides*): Synchrony of changes in mother-infant interactions and individual behaviors during the first 60 days of life. *Primates*, 19(4), 681–692.  
<https://doi.org/10.1007/bf02373635>
- Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology*, 23(1), 1–17. <https://doi.org/10.1002/ajpa.1330230115>
- Scopa, C., & Palagi, E. (2016). Mimic me while playing! Social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*). *Journal of Comparative Psychology*, 130(2), 153–161. <https://doi.org/10.1037/com0000028>
- Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65(4), 671–698. [https://doi.org/10.1016/0022-5193\(77\)90015-7](https://doi.org/10.1016/0022-5193(77)90015-7)
- Shimada, M., & Sueur, C. (2014). The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *American Journal of Primatology*, 76(11), 1025–1036. <https://doi.org/10.1002/ajp.22289>

- Silk, J. B. (1982). Altruism among female *Macaca radiata*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, 79(2-4), 162–188.  
<https://doi.org/10.1163/156853982x00238>
- Silk, J. B. (1992a). Patterns of intervention in agonistic contests among male bonnet macaques. In Harcourt, S., and de Waal, F. B. M. (eds.), *Coalitions and Alliances in Humans and Other Animals*, Oxford University Press, Oxford, pp. 215–232. <sup>[1]</sup><sub>SEP</sub>
- Silk, J. B. (1992b). The patterning of intervention among male bonnet macaques: Reciprocity, revenge, and loyalty. *Current Anthropology*, 33(3), 318–325.  
<https://doi.org/10.1086/204073>
- Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, 57(5), 1021–1032.  
<https://doi.org/10.1006/anbe.1998.1065>
- Silk, J. B. (2002). Kin Selection in Primate Groups. *International Journal of Primatology*, 23(4).
- Silk, J. B., Samuels, A., & Rodman, P. S. (1981). The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behaviour*, 78(1-2), 111–137. <https://doi.org/10.1163/156853981x00284>
- Smith, P. K. (1982). Does play matter? Functional and evolutionary aspects of animal and human play. *Behavioral and Brain Sciences*, 5(1), 139–155.  
<https://doi.org/10.1017/s0140525x0001092x>

- Smith, J. E., Chung, L. K., & Blumstein, D. T. (2013). Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots. *Animal Behaviour*, 85(4), 715–725.  
<https://doi.org/10.1016/j.anbehav.2013.01.008>
- Symons, D. (1978). *Play and aggression: A study of rhesus monkeys*. Columbia University 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.  
[https://doi.org/10.1002/1098-2337\(1985\)11:3<223::aid-ab2480110305>3.0.co;2-a](https://doi.org/10.1002/1098-2337(1985)11:3<223::aid-ab2480110305>3.0.co;2-a)
- Thierry B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, F.B.M. de Waal, (Eds.), *Natural conflict resolution* (pp. 106–128). University of California Press.
- Thierry, B. (2004). Social epigenesis. In B. Thierry, S. Mewa, & W. Kaumanns, (2004). *Macaque societies: A model for the study of social organization*. Cambridge University Press.
- Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and Reviews*, 16(6), 224–238.  
<https://doi.org/10.1002/evan.20147>
- Thierry, B. (2011) The macaques: a double-layered social organization. In C.J. Campbell et. Al, (Eds.), *Primates in perspective* (2nd ed., pp. 229–241). Oxford University Press.
- Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, 106(8), 713–728. <https://doi.org/10.1046/j.1439-0310.2000.00583.x>

- Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46(1), 35–57. <https://doi.org/10.1086/406755>
- Vigeland, M. D. (2020). Relatedness coefficients in pedigrees with inbred founders. *Journal of Mathematical Biology*, 81(1), 185–207. <https://doi.org/10.1007/s00285-020-01505-x>
- Wang, T., Wang, X., Garber, P. A., Sun, B.-H., Sun, L., Xia, D.-P., & Li, J.-H. (2021). Sex-specific variation of social play in wild immature Tibetan macaques, *Macaca thibetana*. *Animals*, 11(3), 805. <https://doi.org/10.3390/ani11030805>
- Wright, K. R., Mayhew, J. A., Sheeran, L. K., Funkhouser, J. A., Wagner, R. S., Sun, L.-X., & Li, J.-H. (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. <https://doi.org/10.24272/j.issn.2095-8137.2018.048>
- Wright, S. (1922). Coefficients of inbreeding and relationship. *The American Naturalist*, 56(645), 330–338. <https://doi.org/10.1086/279872>
- Xia, D.-P., Li, J.-H., Garber, P. A., Sun, L., Zhu, Y., Sun, B.-H. (2012). Grooming reciprocity in female Tibetan macaques *Macaca thibetana*. *American Journal of Primatology*, 74(6), 569–579. <https://doi.org/10.1002/ajp.21985>
- Xia, D.-P., Li, J.-H., Garber, P. A., Matheson, M. D., Sun, B.-H., & Zhu, Y. (2013). Grooming reciprocity in male Tibetan macaques. *American Journal of Primatology*, 75(10), 1009–1020. <https://doi.org/10.1002/ajp.22165>

- Xia, D.-P., Li, J.-H., Zhu, Y., Sun, B.-H., & Sheeran, L. K. (2010). Seasonal variation and synchronization of sexual behaviors in free-ranging male Tibetan macaques (*Macaca thibetana*) at Huangshan, China. *Zoological Research*, *31*(5), 509–515.  
<https://doi.org/10.3724/SP.J.1141.2010.05509>
- Yanagi, A., & Berman, C. M. (2014a). Body signals during social play in free-ranging rhesus macaques (*Macaca mulatta*): A systematic analysis. *American Journal of Primatology*, *76*(2), 168–179. <https://doi.org/10.1002/ajp.22219>
- Yanagi, A., & Berman, C. M. (2014b). Functions of multiple play signals in free-ranging juvenile rhesus macaques (*Macaca mulatta*). *Behaviour*, *151*(14), 1983–2014.  
<https://doi.org/10.1163/1568539x-00003227>
- Zhao, Q., & Deng, Z. (1988). *Macaca thibetana* at Mt. Emei, China: III. Group composition. *American Journal of Primatology*, *16*(3), 269–273.  
<https://doi.org/10.1002/ajp.1350160308>
- Zhao, Q.-K. (1997). Intergroup interactions in Tibetan macaques at Mt. Emei, China. *American Journal of Physical Anthropology*, *104*(4), 459–470. [https://doi.org/10.1002/\(sici\)1096-8644\(199712\)104:4<459::aid-ajpa3>3.0.co;2-n](https://doi.org/10.1002/(sici)1096-8644(199712)104:4<459::aid-ajpa3>3.0.co;2-n)

## APPENDIX A

## CHAPTER II SUPPLEMENTAL TABLES AND FIGURE

Table A1

*Matrilineal Player Dyads* (Tou = 37; Ye = 11; Hua = 3)

<b>Tou Matriline Player Configurations</b>	<b>Ye Matriline Player Configurations</b>
TFH - THL	YH_I - YXC
TFH - THN	YH_I - YXYue
TFH - TQL	YXC - YXYue
TFH - TQS	YXDuo - YXYun
TFH - TQY	YXK - YCLong
TFH - TRX	YXK - YRLan
TFH - TXH_I	YXK - YXYue
THL - THN	YXMing - YXDuo
THL - TQG	YXMing - YXYun
THL - TQL	YXYue - YXMing
THL - TQS	YXYue - YXYun
THL - TQY	
THL - TRX	
THL - TXH_I	
THN - THX	
THN - TQL	
THN - TQS	
THN - TQY	
THN - TRX	
THN - TRY2	<b>Hua Matriline Player Configurations</b>
THN - TXL	HXW - HXYue
THX - THL	HXYue - HXYun
THX - TQS	HXYun - HXW
THX - TRX	
TQL - TQS	
TQL - TQY	
TQL - TRX	
TQS - TQY	
TQS - TRX	
TQS - TRY2	
TQS - TXH_I	
TQS - TXL	
TQY - TRX	
TQY - TXH_I	
TRX - TRY2	
TRY2 - TQL	
TRY2 - TXL	

**Table A2***Kinship Coefficients between Player Dyads*

	<b>HXW</b>	<b>HXYue</b>	<b>HXYun</b>	<b>HY</b>	<b>TFH</b>	<b>THL</b>	<b>THN</b>	<b>THX</b>	<b>TQG</b>
<b>HXW</b>	0.5	0.125	0.125	0	0.07813	0.03125	0.03125	0.03125	0.07031
<b>HXYue</b>	0.125	0.5	0.125	0	0.125	0	0	0	0.0625
<b>HXYun</b>	0.125	0.125	0.5	0	0	0	0	0	0.0625
<b>HY</b>	0	0	0	0.5	0	0	0	0	0
<b>TFH</b>	0.07813	0.125	0	0	0.5	0.03125	0.07813	0.07813	0.00781
<b>THL</b>	0.03125	0	0	0	0.03125	0.5	0.03125	0.09375	0.03906
<b>THN</b>	0.03125	0	0	0	0.07813	0.03125	0.5	0.125	0.00781
<b>THX</b>	0.03125	0	0	0	0.07813	0.09375	0.125	0.5	0.07031
<b>TQG</b>	0.07031	0.0625	0.0625	0	0.00781	0.03906	0.00781	0.07031	0.5
<b>TQL</b>	0.13281	0	0	0	0.08594	0.07031	0.03906	0.10156	0.07031
<b>TQS</b>	0.13281	0	0	0	0.08594	0.03906	0.03906	0.03906	0.13281
<b>TQY</b>	0.00781	0.125	0	0	0.13281	0.03906	0.00781	0.07031	0.0625
<b>TRX</b>	0.0625	0	0	0	0.0625	0.0625	0.0625	0.0625	0.07813
<b>TRY2</b>	0.0625	0	0	0	0.0625	0.0625	0.0625	0.0625	0.07813
<b>TXH_I</b>	0.00781	0	0	0	0.00781	0.00781	0.00781	0.00781	0.125
<b>TXL</b>	0.14063	0	0	0	0.09375	0.04688	0.04688	0.04688	0.07031
<b>YCH</b>	0	0	0	0	0	0	0	0	0
<b>YCLong</b>	0	0.03125	0	0	0.03125	0.0625	0	0.125	0.0625
<b>YH_I</b>	0	0.01563	0	0	0.01563	0	0	0	0
<b>YRLan</b>	0.125	0.0625	0	0	0.14063	0.03125	0.03125	0.03125	0.00781
<b>YXC</b>	0	0.14063	0	0	0.14063	0	0	0	0.03125
<b>YXDuo</b>	0	0.01563	0	0	0.01563	0	0	0	0.03125
<b>YXK</b>	0.125	0.01563	0	0	0.09375	0.03125	0.03125	0.03125	0.00781
<b>YXMing</b>	0.0625	0.01563	0	0	0.05469	0.01563	0.01563	0.01563	0.00391
<b>YXYue</b>	0	0.01563	0	0	0.01563	0	0	0	0
<b>YXYun</b>	0	0.01563	0	0	0.01563	0	0	0	0
	<b>HXW</b>	<b>HXYue</b>	<b>HXYun</b>	<b>HY</b>	<b>TFH</b>	<b>THL</b>	<b>THN</b>	<b>THX</b>	<b>TQG</b>

Table A2 (Continued)

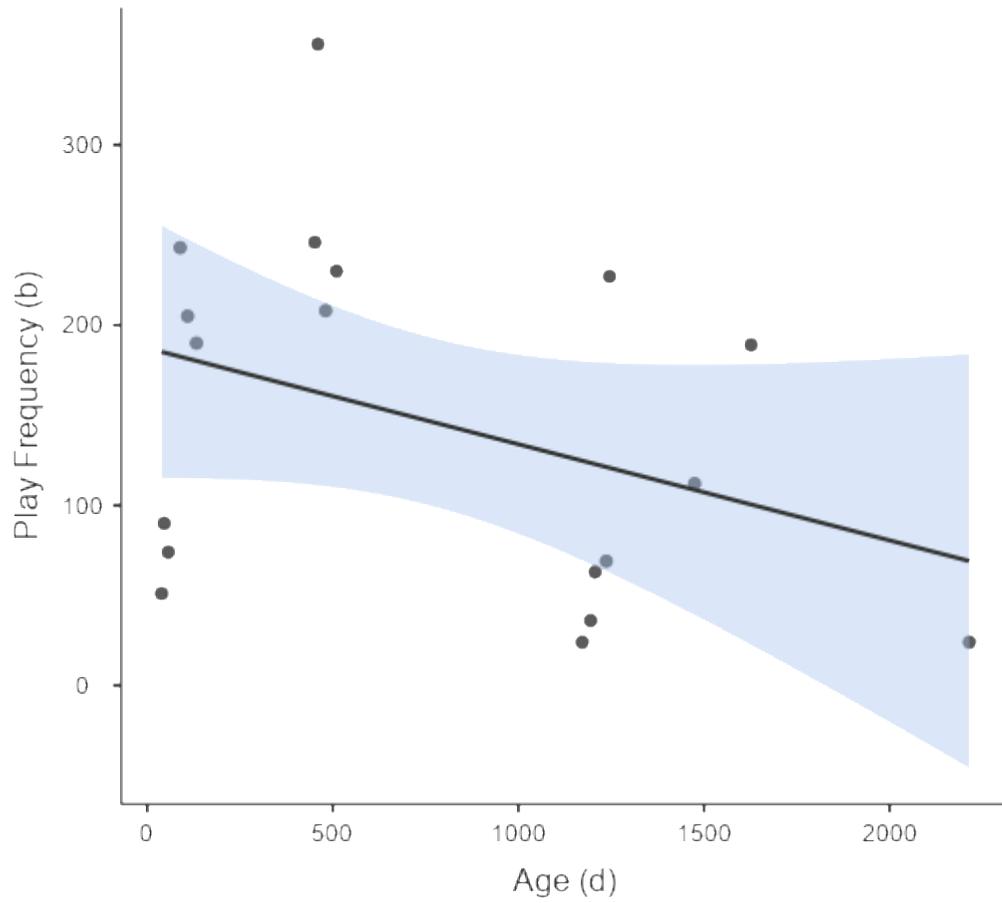
	<b>TQL</b>	<b>TQS</b>	<b>TQY</b>	<b>TRX</b>	<b>TRY2</b>	<b>TXH_I</b>	<b>TXL</b>	<b>YCH</b>	<b>YCLong</b>
<b>HXW</b>	0.13281	0.13281	0.00781	0.0625	0.0625	0.00781	0.14063	0	0
<b>HXYue</b>	0	0	0.125	0	0	0	0	0	0.03125
<b>HXYun</b>	0	0	0	0	0	0	0	0	0
<b>HY</b>	0	0	0	0	0	0	0	0	0
<b>TFH</b>	0.08594	0.08594	0.13281	0.0625	0.0625	0.00781	0.09375	0	0.03125
<b>THL</b>	0.07031	0.03906	0.03906	0.0625	0.0625	0.00781	0.04688	0	0.0625
<b>THN</b>	0.03906	0.03906	0.00781	0.0625	0.0625	0.00781	0.04688	0	0
<b>THX</b>	0.10156	0.03906	0.07031	0.0625	0.0625	0.00781	0.04688	0	0.125
<b>TQG</b>	0.07031	0.13281	0.0625	0.07813	0.07813	0.125	0.07031	0	0.0625
<b>TQL</b>	0.51563	0.17188	0.13281	0.07813	0.07813	0.03906	0.21094	0	0.0625
<b>TQS</b>	0.17188	0.51563	0.03906	0.14063	0.14063	0.13281	0.21094	0	0
<b>TQY</b>	0.13281	0.03906	0.5	0.01563	0.01563	0.03125	0.07031	0	0.09375
<b>TRX</b>	0.07813	0.14063	0.01563	0.5	0.25	0.07813	0.09375	0	0
<b>TRY2</b>	0.07813	0.14063	0.01563	0.25	0.5	0.07813	0.09375	0	0
<b>TXH_I</b>	0.03906	0.13281	0.03125	0.07813	0.07813	0.5	0.07031	0	0
<b>TXL</b>	0.21094	0.21094	0.07031	0.09375	0.09375	0.07031	0.53125	0	0
<b>YCH</b>	0	0	0	0	0	0	0	0.5	0
<b>YCLong</b>	0.0625	0	0.09375	0	0	0	0	0	0.5
<b>YH_I</b>	0	0	0.01563	0	0	0	0	0	0.0625
<b>YRLan</b>	0.13281	0.13281	0.07031	0.0625	0.0625	0.00781	0.14063	0	0.0625
<b>YXC</b>	0	0.03125	0.14063	0.0625	0.0625	0.03125	0	0	0.09375
<b>YXDuo</b>	0	0.03125	0.01563	0.0625	0.0625	0.03125	0	0	0.0625
<b>YXK</b>	0.13281	0.13281	0.02344	0.0625	0.0625	0.00781	0.14063	0	0.0625
<b>YXMing</b>	0.06641	0.06641	0.01953	0.03125	0.03125	0.00391	0.07031	0	0.0625
<b>YXYue</b>	0	0	0.01563	0	0	0	0	0	0.0625
<b>YXYun</b>	0	0	0.01563	0	0	0	0	0	0.0625
	<b>TQL</b>	<b>TQS</b>	<b>TQY</b>	<b>TRX</b>	<b>TRY2</b>	<b>TXH_I</b>	<b>TXL</b>	<b>YCH</b>	<b>YCLong</b>

Table A2 (Continued)

	<b>YH_I</b>	<b>YRLan</b>	<b>YXC</b>	<b>YXDuo</b>	<b>YXK</b>	<b>YXMing</b>	<b>YXYue</b>	<b>YXYun</b>
<b>HXW</b>	0	0.125	0	0	0.125	0.0625	0	0
<b>HXYue</b>	0.01563	0.0625	0.14063	0.01563	0.01563	0.01563	0.01563	0.01563
<b>HXYun</b>	0	0	0	0	0	0	0	0
<b>HY</b>	0	0	0	0	0	0	0	0
<b>TFH</b>	0.01563	0.14063	0.14063	0.01563	0.09375	0.05469	0.01563	0.01563
<b>THL</b>	0	0.03125	0	0	0.03125	0.01563	0	0
<b>THN</b>	0	0.03125	0	0	0.03125	0.01563	0	0
<b>THX</b>	0	0.03125	0	0	0.03125	0.01563	0	0
<b>TQG</b>	0	0.00781	0.03125	0.03125	0.00781	0.00391	0	0
<b>TQL</b>	0	0.13281	0	0	0.13281	0.06641	0	0
<b>TQS</b>	0	0.13281	0.03125	0.03125	0.13281	0.06641	0	0
<b>TQY</b>	0.01563	0.07031	0.14063	0.01563	0.02344	0.01953	0.01563	0.01563
<b>TRX</b>	0	0.0625	0.0625	0.0625	0.0625	0.03125	0	0
<b>TRY2</b>	0	0.0625	0.0625	0.0625	0.0625	0.03125	0	0
<b>TXH_I</b>	0	0.00781	0.03125	0.03125	0.00781	0.00391	0	0
<b>TXL</b>	0	0.14063	0	0	0.14063	0.07031	0	0
<b>YCH</b>	0	0	0	0	0	0	0	0
<b>YCLong</b>	0.0625	0.0625	0.09375	0.0625	0.0625	0.0625	0.0625	0.0625
<b>YH_I</b>	0.5	0.03125	0.04688	0.03125	0.125	0.03125	0.125	0.125
<b>YRLan</b>	0.03125	0.5	0.09375	0.03125	0.15625	0.09375	0.03125	0.03125
<b>YXC</b>	0.04688	0.09375	0.53125	0.14063	0.04688	0.04688	0.04688	0.04688
<b>YXDuo</b>	0.03125	0.03125	0.14063	0.5	0.03125	0.03125	0.03125	0.03125
<b>YXK</b>	0.125	0.15625	0.04688	0.03125	0.5	0.09375	0.125	0.125
<b>YXMing</b>	0.03125	0.09375	0.04688	0.03125	0.09375	0.5	0.03125	0.03125
<b>YXYue</b>	0.125	0.03125	0.04688	0.03125	0.125	0.03125	0.5	0.125
<b>YXYun</b>	0.125	0.03125	0.04688	0.03125	0.125	0.03125	0.125	0.5
	<b>YH_I</b>	<b>YRLan</b>	<b>YXC</b>	<b>YXDuo</b>	<b>YXK</b>	<b>YXMing</b>	<b>YXYue</b>	<b>YXYun</b>

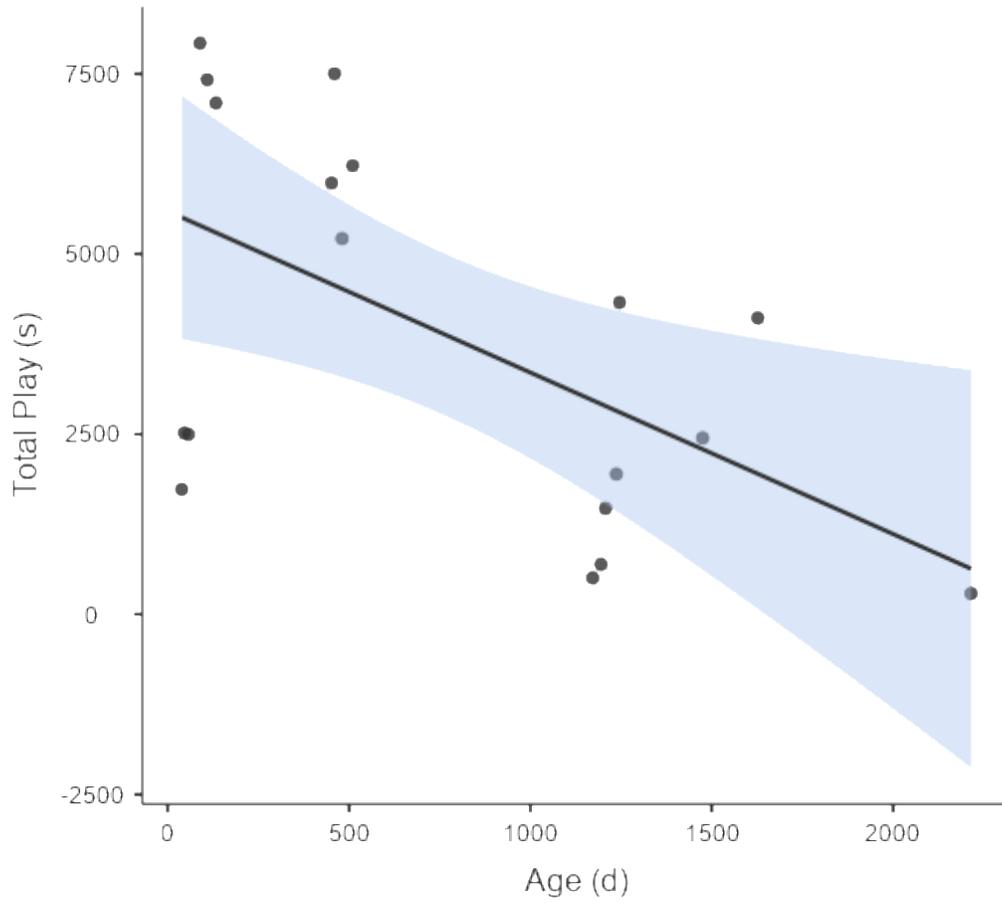
**Figure A1**

*2016 Negative Trend between Age and Play Frequency*



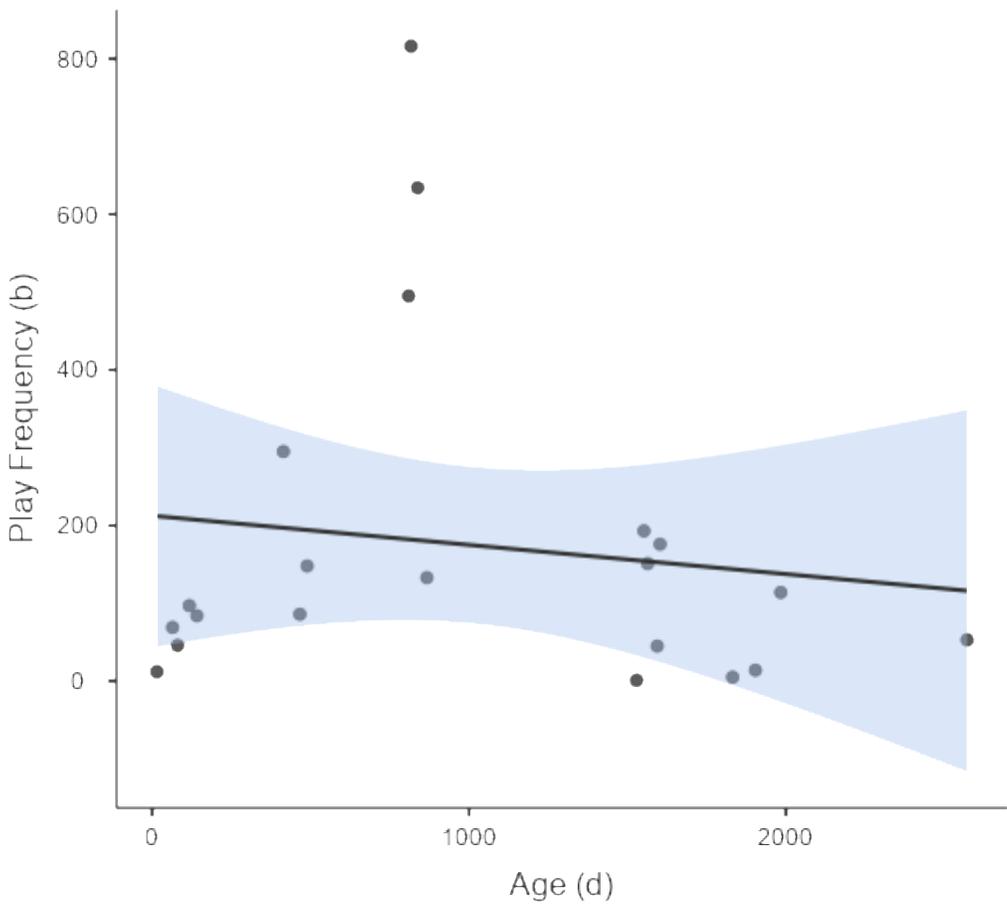
**Figure A2**

*2016 Negative Correlation between Age and Individual total Play Durations*



**Figure A3**

*2017 Negative Trend between Age and Play Frequency*



**Figure A4**

*2017 Negative Trend between Age and Individual total Play Durations*

