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Play in Immature Tibetan Macaques (*Macaca thibetana*): Location, Use of Play Signals, and Play Bout Termination at Mt. Huangshan, China

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PLAY IN IMMATURE TIBETAN MACAQUES (*MACACA THIBETANA*): LOCATION, USE OF PLAY SIGNALS, AND PLAY BOUT TERMINATION AT MT. HUANGSHAN, CHINA

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In Partial Fulfillment

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Primate Behavior

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by

Kaitlin R. Wright

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Graduate Studies

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ABSTRACT

PLAY IN IMMATURE TIBETAN MACAQUES (*MACACA THIBETANA*): LOCATION, USE OF PLAY SIGNALS, AND PLAY BOUT TERMINATION AT MT. HUANGSHAN, CHINA

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In this study, I examined the relationship between play behaviors, play location, the frequency of selected play signals, and play bout termination in Tibetan macaques (*Macaca thibetana*) during immature social play. I gathered video data at the Valley of the Wild Monkeys, Mt. Huangshan, China, and focused on 21 juvenile and infant macaques (zero to five years of age). I used an all occurrence sampling method to score play behaviors and play signals with an ethogram. I hypothesized that play groups would use play signals in functionally appropriate ways based on the location of the play bout, the number of audience members in proximity to the players, and play bout length. In the 283 playful interactions that I observed, immature macaques utilized multiple body and facial play signals in various constructs. These data show that immature Tibetan macaques use a versatile repertoire of play behaviors and play signals to sustain play in a tourism site.

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CHAPTER I

INTRODUCTION

Play may be among the most captivating behaviors in which animals engage. Although various forms of solitary and social play are observed in a wide range of species, play seems to be of particular importance to primates, with special relevance to young primates' cognitive and social development (Martin & Caro, 1985; Palagi et al., 2007). Many forms of social play involve complex body and facial signals. The use of play signals in a playful and social context is one of the most sophisticated types of communication (Fagan, 1981; Yanagi & Berman, 2014a). The function of play signals has been studied in many different animal taxa, although there have currently been no published studies of play signals in Tibetan macaques (*Macaca thibetana*).

Yanagi and Berman (2014a) found that seven play signals predicted the imminent occurrence of dyadic play in free-ranging juvenile rhesus macaques (*M. mulatta)* on Cayo Santiago, Puerto Rico. They later examined the function of these play signals in the same study area. The authors asked whether these different signals were associated with different (1) types of play, (2) intensities of play, (3) initiators of play, and (4) distances at which the signal is given (Yanagi & Berman, 2014b). The authors found that most signals were disproportionately associated with one or more aspects of play, and the candidate signals were used in a selective way by the juvenile rhesus macaques during the context of play. Yanagi and Berman hypothesized that this diverse use might aid the reinforcement, clarification, or emphasis of playful intention by the sender.

Yanagi and Berman (2014b) further hypothesized that visual signals during play may be particularly important in despotic societies that exhibit high levels of intense aggression. This is because play partners in despotic groups likely face higher risks associated with play compared to those that live in relaxed or tolerant groups. Rhesus macaques are considered to be highly despotic and are categorized as having a grade one dominance style (Thierry et al., 2000). Therefore, juvenile rhesus macaques may need to clarify more often that they are “only playing” to alleviate rising tension in the group. The authors argued that they would see the use of multiple play signals as a way to cope with intense aggression associated with social play in all despotic macaque species (Yanagi & Berman, 2014b).

Using Yanagi and Berman’s study as a model, the purpose of this research was to gain a better knowledge of the multiple play behaviors and interchangeable play signals Tibetan macaques utilize to maintain playful interactions in various contexts. I designed my study to expand the comprehension of the cognitive and communicative abilities of these macaques in the field of primatology. I hypothesized that play groups would use play signals in functionally appropriate ways based on the location of the play bout and the audience members in proximity to the players. To test this hypothesis, I have made the following predictions:

I. Play will occur more in locations outside of the provisioning area.

II. Third-party adult interference will end play more than other forms of play termination.

III. Following the findings of Yanagi & Berman (2014b), play bouts will begin more often with play behaviors rather than play signals.

IV. As the number of audience members in proximity to playing macaques increases, the number of play signals given by the players will also increase.

V. Play bout’s duration and rate of play signals will be positively correlated.

CHAPTER II

LITERATURE REVIEW

Defining Play

Defining play is difficult (Bekoff & Byers, 1981; Fagen 1981; Martin & Caro, 1985). Compared to better-understood behaviors, the boundary line between play behaviors and non-play behaviors is not always obvious. Therefore, the form and function of play behaviors remain poorly understood and controversial. Robert Fagan (1981) defined play as behavior that "functions to develop, practice, or maintain physical or cognitive abilities and social relationships, including both tactics and strategies, by varying, repeating, and/or recombining already functional subsequences of behavior outside their primary context" (p. 65). Although Fagan provided an operational definition of and criteria for play, he provided little information on what the behavior actually looks like making the definition difficult to apply. Play has been characterized as a functionless behavior or one that has no immediate purpose (Bekoff & Byers, 1981). However, it has also been suggested that play may serve to improve the cognitive and motor skills of young animals, preparing them for unexpected physical and social situations and providing them with tools to handle these situations with versatile emotional responses (Fagan, 1981; Burghardt, 2005; Spinka et al., 2001). Playing with juvenile conspecifics is typically the first non-mother activity to occur in juvenile animals (Poirer, 1970; Bekoff, 1972). By players performing behaviors similar in style, but in a different context, they may yield some payoff both in short and long-term success in foraging, hunting, or social abilities (Bekoff, Byers, & Allen, 1997).

Gordon Burghardt (1999) proposed a working method for identifying (rather than defining) play behaviors that considers five key criteria: (1) play has a limited immediate function, (2) play has an endogenous component, (3) play is structurally or temporally different than serious behaviors, (4) play behaviors must be repeated, and (5) play must occur in a relaxed field. These criteria allow for the recognition and clarification of play versus non-play behaviors in both young animals and adults. All five criteria must be met to label a behavior as playful in solitary or social contexts (Burghardt, 2005).

Play behaviors are generally categorized into locomotor-rotational and object play (both solitary) or social play (Bekoff & Byers, 1981; Fagen, 1981). Locomotor-rotational play, also known as activity or movement play, includes play behaviors with intense or sustained locomotor movements in a solitary context. Leaping, running, and prancing are examples of locomotor play. Object play, another form of solitary play, can be defined as behaviors where the player manipulates an object for no immediate benefit. Commonly seen in carnivores, object play may involve predatory movements such as shaking or grabbing without prey being present (Burghardt, 2005).

Social play is identified as interactive play occurring between two or more conspecifics that may influence each other's actions (Thompson, 1996). Social play is reciprocal (Fagan, 1981) and often includes quasi-aggressive behaviors, such as wrestling, biting, and chasing (Burghardt, 2005). Studying the aspects of social play that involve cooperation, communication, and learning may be critical to understand cognitive development in young individuals (Bekoff et al., 1997; Palagi et al., 2007).

Pellis and Pellis (1996) hypothesized that social play fighting in juvenile animals influences the development of dominance relationships later in life. Although gentle play fighting may be used to maintain affiliation, more intense rough-and-tumble play behavior may actually establish a dominance hierarchy in postpubertal juveniles, especially in male-male play bouts, through testing the play partner’s strength (Pellis & Pellis, 1996). In this way, an individual may use behaviors such as slap or chase to cultivate or stabilize a competitive edge in a play bout (van Leeuwen et al., 2011). The first individual to slap another player, based on the competitive fitness model, would have an advantage over the other player if the hitter then instigated a play chase. Van Leeuwen et al. (2011) found that in a captive group of juvenile gorillas, this slap and chase play fighting pattern was used frequently in competitive play bouts. Also, chases were frequently coupled with the occurrence of an open-mouth face by either the instigator or receiver, indicating a possible message to affirm playful intention. The authors’ findings suggest that gorillas may be sensitive to inequities during play fighting and capable of evaluating the level of roughness in a play bout that is appropriate to keep the interaction cooperative (van Leeuwen et al., 2011). By testing the competitive advantage one has over a peer in play, the partners are practicing aggressive retaliation that may be necessary later in life to defend or maintain resources.

Defining Play Signals

Some play researchers consider social play to involve one of the most sophisticated types of cognition and metacommunication, the use of play signals. Metacommunication can be defined as messages regarding contextually dependent communication (Bekoff, 1972; Cullen, 1972). For example, laughter and smiling are commonly used human forms of metacommunication (van Hooff, 1972). In dyadic play, play partners must transmit and perceive various messages from each other to qualify the subsequent behavior (Burghardt, 2005). The use of play signals, including various facial expressions, body movements, or gestures, are hypothesized to fill a crucial role in avoiding misunderstandings and maintaining a playful mood or context while performing potentially risky behaviors (Pellis & Pellis, 1996; Bekoff et al., 1997). These signals may help to avoid an escalation to aggression, especially for behaviors that may easily be misinterpreted such as play bite, play slap, or play fighting. Therefore, play signals can be defined as communicatory behaviors that function to promote, cultivate, and manage social play and demonstrate playful intentions (Bekoff, 1974; Fagan 1981; Yanagi & Berman, 2014a, 2014b). Having a diverse repertoire of play signals may be important for immature animals to be successful players, as it may be advantageous to use multiple body and facial signals to communicate in a bout. For example, Tomasello et al. (1989) observed the use of body signals, such as attention-getting hand gestures, in chimpanzee playgroups when the intended receiver did not see an individual’s play face. However, it is possible that factors such as an increase in play behavior intensity, play bout length, or the addition of players to a bout may break down the salient nature of the metacommunicative signal (Bekoff, 1972).

Palagi and colleagues (2007) observed the use of facial play signals in captive lowland gorillas (*Gorilla gorilla gorilla*). They evaluated the potential cognitive skills of juveniles in using play signals to adjust play behaviors during play bouts. The authors analyzed five predictions, but the most salient examined the frequency of play faces. The play face, also known as the open mouth play face, is a frequently reported play signal throughout primate play studies and is commonly associated with close-quarter contact, such as in play fighting (van Hooff, 1967; Pellis & Pellis, 1996). Pellis and Pellis (1996) argued that the play face signal might be used as a flexible, rather than static, message to indicate playful intention while the dynamics of a play bout quickly change. However, the play face may also function as a stimulus for the individual displaying the signal as a reward for playful engagement (Spijkerman et al., 1996). Palagi et al. (2007) predicted that the play face would occur more frequently when the risk of escalating into a conflict was elevated, such as when a play bout increased in vigor or when escape opportunities were limited. Overall, Palagi et al. (2007) found that juvenile gorillas were able to maintain a dyadic play session by appropriately using play signals. This therefore demonstrated the advanced cognitive ability of balancing both cooperation and competition during a play bout with a conspecific. In regards to their fifth prediction, the authors observed the selective use of play signals, such as the play face and the full play face, by males during play sessions with increased intensity. The play face is described as a signal where the mouth is opened with only the lower teeth exposed and the full play face is when both the lower and the upper teeth are exposed (Pellis & Pellis, 1996). The authors also found gorillas increased the amount of play signals used when escape possibilities were limited, such as when play bouts occurred in indoor enclosures. The authors' finding confirmed that juvenile gorillas are not only able to communicate with partners through facial play signals, such as the play face, but can also use play signals in flexibly and cognitively advanced ways depending on the social context (Palagi et al., 2007).

Similarly, frequent facial play signals have been observed and studied in Tonkean macaques (*Macaca tonkeana*). Pellis et al. (2011) examined the use of the bared-teeth display during play fighting in Tonkean macaques to assess the context in which facial gestures that are only relevant for signaling are used during play. The authors predicted that the commonly seen open-mouth, bared-teeth display would occur most frequently preceding contact during a play bout. The authors hypothesized that this display would be performed most often preceding bites that were directed at body parts visible to the recipient. They found that the open-mouth, bared-teeth display seemed to have multiple functions during play fighting because it occurred before play, during play, and when the sender withdrew from playful contact. So these signals may function to indicate "I want to play", "I want to remain playful", "I want you to remain playful", or “I want to stop playing.” However, the authors did not see strong evidence for play signals preceding visible bites, so they hypothesized that play signals may sometimes be emitted for the sender’s benefit and not to communicate with the play partner. Also, the authors argued that the play signals observed may function to alert third parties that they are “only playing”. If this is true, then the authors would expect that the signals would be performed more often in cases when a third party, such as an adult kin or a juvenile conspecific, is present and only in species in which participation by a third party is likely, by joining play or interfering with the bout to end play. However, the authors did not collect data on third parties for this study (Pellis et al., 2011).

Play signals may also play a critical role in prolonging play duration and maintaining a large number of players in a bout, compared to dyadic play. Short play bouts may be influenced by the misinterpretation of play signals and, similarly, long play bouts with highly aggressive behaviors, such as wrestle, may need to include a higher frequency of play signals (Spijkerman et al., 1996). Spijkerman et al. (1996) found that juvenile chimpanzees living in two different captive settings used various play signals to begin, maintain, and end playful interactions with different play peer group types and for different play bout lengths. Spijkerman et al. (1996) predicted that the play face would be observed when players interacted using aggressive behaviors, such as wrestle and gnaw. The authors found that wrestling bouts containing a play face lasted longer than wrestling bouts without a play face. In addition to this, Spijkerman et al. (1996) found a significant increase in players interacting with each other in bouts when a play face was used, indicating the importance of the play face to appeal to other juvenile conspecifics and encourage them to join the bout.

Although play has been studied in many different primate species, there are currently no published studies regarding play signals in Tibetan macaques. Furthermore, the large majority of play behavior and signal research has been conducted in a captive environment, due to the accessibly to multiple young primates in a confined area. These types of studies have rarely focused on play bouts with more than two players or investigated the location of the play bout in relation to human presence.

Tibetan Macaques

The genus *Macaca* consists of 23 species, widely distributed geographically throughout Africa and Asia (Thierry, 2011; Li et al., 2015). These species share similar patterns in social structure, such as constructing multi-male and multi-female groups, having overlapping home ranges, and philopatric females. Macaques are semiterrestrial and diurnal, capable of exploiting and living in a wide range of habitats, such as evergreen, deciduous, and coniferous forests, grasslands, swamps, and semideserts. They have cheek pouches and highly flexible and complex diets that allow them to exploit various niches and habitats (Thierry, 2011).

Tibetan macaques (*M. thibetana*), also known as Milne-Edwards' or Pere David's macaques, are the largest bodied of the *Macaca* genus and the most derived species of their particular lineage (Fooden, 1983; Thierry, 2011). Although they are most closely related genetically to Assamese macaques (*M. assamensis*), they resemble stump-tailed macaques (*M. arctoides*) in appearance and Barbary macaques (*M. sylvanus*) ecologically (Berman et al., 2004). Tibetan macaques have heavy bodies, short tails, and patterns of growth that are highly dependent on food intake (Thierry, 2011). They primarily eat leaves (Zhao, 1996), but also consume fruits and other plant parts, and prey on invertebrates, such as birds and snakes (Thierry et al., 2000; Thierry, 2011; Sheeran, 2013). Female macaques reach sexual maturity from two to five years of age, give their first birth generally between four and six years of age, and nurse infants for six to 12 months. In male macaques, puberty begins between three and four years of age, marked by an increase in agonistic behaviors, body weight, and testosterone levels. Tibetan macaques are seasonal breeders, and generally speaking, the number of offspring sired by a particular male is weakly correlated with the male's dominance ranking (Thierry, 2011; Xia et al., 2012b).

Tibetan macaque social organization consists of bisexual groups of 15-50 individuals that normally contain a sex ratio in favor of females (Thierry et al., 2000; Berman et al., 2004; Li et al., 2007; Sueur et al., 2011; Thierry, 2011; Sheeran, 2013). This organization is centered on dominance hierarchies and kin-bonded coalitions (Thierry, 2011). The dominance rank of females is based on matrilines, with a daughter obtaining her dominance rank right below her mother but above her older siblings (Zhao, 1997; Berman et al., 2004; Thierry, 2011). This influences intergroup competition among females and preferential bonds between kin (Thierry, 2011). Males disperse once they become adults and can transfer between groups during their lifespan, regardless of dominance rank (Zhao, 1996; Thierry, 2011). Although group males generally occupy the top ranks, females can occasionally outrank males (Berman et al., 2004). Adult social relationships strongly influence the socialization of immatures (Thierry, 2011), with the population in general showing a strong kin bias and strict linear hierarchies (Berman et al., 2004).

Macaque Dominance Style Grade Scale

Thierry et al. (2000) analyzed the social organization, including social and physical traits, of 16 species of macaques to determine the phylogeny of these traits. Due to the genus' wide geographic distribution and adaptive radiation, macaques show unique inter-specific variation in patterns of affiliation, reconciliation, dominance, aggression, nepotism, and temperament (Thierry, 1985, 1990; Thierry et al., 2000). From this variation, Thierry et al. (2000) proposed a continuous, 4-grade scale of dominance style with the first level being highly hierarchical and nepotistic and the fourth level being more tolerant or egalitarian. In his scale, Thierry and colleagues (2000) analyzed 22 different behavioral traits and referenced previously published data on the different behavioral qualities of the 16 species. Dominance style can be defined as the dominance relations, categorized by agonistic interactions, within dyads in a social group (Thierry et al., 2000). A difference in dominance style between primate taxa can be indicative of environmental variables, such as contest over food (Matsumura, 1999).

Grade one despotic species are generally marked by dominant individuals that show intense and highly asymmetrical patterns of aggression, little tolerance around resources, and infrequent reconciliation. Thierry et al. (2000) found that *Macaca mulatta*, *M. fuscata*, and *M. cyclopis* exhibit the highest degree of nepotism and therefore are included in grade one. Species with a grade four dominance style show the opposite tendencies, with low or moderate levels of kin bias in affiliation, tolerant and supportive interactions with group members, strong group cohesion, and maternal tolerance for infant handling by other group members. Macaque species with a grade four dominance style are *M. maura*, *M. nigra*, *M. ochreata*, and *M. tonkeana*, all endemic to Sulawesi (Thierry et al., 2000).

Although the species mentioned above fit easily into Thierry et al.'s (2000) scale, other macaque species are more difficult to categorize based on inconsistent patterns of the behavioral traits considered for the scale and a lack of relevant information available on a particular species. Thierry et al. (2000) classified species as a grade two if their behavioral traits were more similar to grade one than to grade four. Similarly, grade three macaques were classified based on their similarity to grade four rather than grade one. Tibetan macaques were placed on the third level of the scale, having more qualities associated with tolerant species rather than despotic species.

However, Thierry et al. (2000) lacked much of the relevant ecological data on wild populations of this species for the majority of the 22 behavioral traits they used to analyze their dominance style.

Berman et al. (2004) published a study that placed Tibetan macaques on the second level, moving them closer to the despotic end of the scale. Although Berman et al. originally speculated that the Tibetan macaque population studied would display a relaxed dominance style, they found that they were more despotic than previously thought. Berman et al. conducted research at Mt. Huangshan, China from 2000-2002, and from the collected data, constructed dominance hierarchies using the directions of all submissive interactions. The authors found that all three measures of bidirectional aggression (the percentage of total aggressive interactions, percentage of dyad aggression, and percentage of counter-aggression) occurred at rates similar to despotic macaque species with better-studied dominance styles. They also found that Tibetan macaque conciliatory tendencies were low compared to despotic macaques, especially for female-female interactions (Berman et al., 2004).

However, Berman et al. (2004) also found inconsistencies in the despotic dominance style of the Tibetan macaques studied. Female members of the group displayed a markedly high preference for female kin in proximity relationships and maternal tolerance for infant handling. Additionally, they found weak kin bias in tendencies to reconcile, commonly seen in tolerant species. Consequently, given the presence of both despotic and tolerant behavioral traits in this population, the dominance style of Tibetan macaques remains unclear.

Due to the despotic behavioral traits of Tibetan macaques, such as linear dominance hierarchies and low conciliatory tendencies, it is expected that their dominance style will impact immature play behavior. For example, in groups marked by a high level of aggression, play bouts may need to include a high rate of play signals to manage rising tension in the bout (Yanagi & Berman, 2014b). Furthermore, play bouts in proximity to dominant adult males and females may influence the structure and end of play, affecting the rate of play signals and the composition of players.

Effects of Provisioning

Provisioning a group of free-ranging non-human primates is a frequent part of habituation and tourism. Macaque tourism sites can be defined by free-ranging or semifree-ranging macaques living in a habitat that allows for humans to view and interact with the macaques (Fuentes et al., 2007). The idea behind macaque tourism is that it will uniquely provide economic encouragement for the local people at a tourist site to manage a prolific ecosystem. It may also provide protection to the primates that inhabit the area, by keeping part of the primates' range in a protected forest or park (Matheson et al., 2006). However, the impact of tourism on various primate taxa and their behavior, and its potential consequences is still largely unknown (Matheson et al., 2006; McCarthy et al., 2009). Specifically, tourism that involves provisioning may greatly increase the impact tourism can have on a species by altering group's size and ranging patterns (Berman et al., 2004). Furthermore, provisioning can increase intragroup aggression, infant mortality, and a species reliance on human food (Berman et al., 2004; Zhao and Deng, 1992).

Various tourism related studies have been conducted with Tibetan macaques at two sites in China, Mt. Emei and Mt. Huangshan (Berman et al., 2007). From the literature, it is apparent that visitor interactions have had a large impact on the aggressive behaviors in adult Tibetan macaques (Berman et al., 2004). Berman et al. (2008) collected observational data on infant mortality and stress indicators, and their relation to tourism with Tibetan macaques at Mt.

Huangshan. The authors found that tourism did not affect macaque birth rates, but it did increase macaque infant mortality. Additionally, Berman et al. (2008) found a high level of aggression directed by adult group members towards infants. Berman et al. (2008) speculated that infant mortality was directly linked to aggressive behaviors in the provisioning zone and high levels of tourists present. This high level of counter-aggression is characteristic of despotic species (Thierry et al., 2000).

Similarly, Matheson et al. (2006) examined the effect of tourism in Mt. Huangshan on threat and affiliative behaviors of two Tibetan macaque groups inhabiting the area. The authors found that the less habituated group spent less time within sight of the tourists and the more habituated group engaged in more affiliative behaviors, such as grooming, when within sight of the tourists (Matheson et al., 2006). In this way, the habituated group may be using affiliative behaviors and an increase of proximity to each other as coping mechanism to create a more stress-free and relaxed field. Furthermore, Matheson et al. (2006) found that threat patterns were generally between adult macaques and juvenile macaques and between juvenile macaques and humans. This evidence of intragroup redirectional aggression in both Berman et al.'s (2008) and Matheson et al.'s (2006) studies is consistent with Tibetan macaques' dominance style (Thierry et al., 2000; Berman et al., 2004).

Self et al. (2013) investigated the possible causes of the increase in infant mortality in the two groups of Tibetan macaques at Mt. Huangshan. The authors found a negative correlation between the amount of tourists present on the viewing platforms and infant-directed aggression, most frequently by dominant adult males towards the infants. Self et al. (2013) speculated that the infant-directed aggression was primarily caused by feeding competition in relation to the group being provisioned with corn. Furthermore, the authors found that infants would stay outside of the provisioning zones when corn was present. However, it is unclear if the infants avoided the provisioning zone at this time due to their lack of interest in corn or as a way to avoid the consequences of adult aggression (Self et al., 2013).

Recent studies have indicated that provisioning and human interaction may have a negative effect on the social play behaviors of young primates. de La Torre et al. (2000) examined the effects that varying levels of tourism pressure had on two groups of wild pygmy marmosets (*Cebuella pygmaea*) in Ecuador. The authors found a significant relationship between the number of tourists present and the amount of time the marmosets spent playing. The group exposed to a higher number of tourists spent less time playing than the group experiencing less human interaction. Furthermore, the group exposed to a higher number of tourists spent less time interacting with each other, including social play, in their preferred location, the lowest strata level of the forest. de La Torre et al. (2000) argued that this change in behavioral ecology was directly related to tourism with human pressure causing the marmoset group to use avoidance mechanisms to reduce the stress caused by human interaction.

Similarly, in a wild or captive setting, the occurrence of play may indicate positive welfare for a group affected by human interaction and provisioning. According to Burghardt's (1999) method for identifying play behaviors, play must occur in a relaxed field. This means that the animals must be free from stress before they can successfully engage in a playful interaction (Burghardt, 1999; Oliveira et al., 2010). However, it is possible that play may occur as a stress reducer and as a way for animals to create a relaxed field (Fagan and Fagan, 2004). Therefore, collecting data on the frequency of play behaviors for a provisioned group may provide valuable information on the effects of human interaction. Norscia and Palagi (2011) observed a captive family group of common marmosets (*Callithrix jacchus*) to gather data on changes in aggressive, play, and self-directed behaviors. The authors found a significant correlation between play behaviors and feeding times, with most play occurring directly before being fed. Norscia and Palagi (2001) concluded that this pre-feeding period was one marked with an increase in anxiety and therefore play was used by group members to alleviate the tension. This study suggests not only that provisioning may have a profound effect on play behaviors but also that data collection on immatures' playful interactions can provide insight into the environmental suitability a tourism site has for a species.

CHAPTER III

METHODS

Subjects and Study Site

I collected data for this study at the Valley of the Wild Monkeys in the Huangshan Scenic District, Anhui Province, China (Berman & Li, 2002; Li et al., 2007; McCarthy et al., 2009). My study subjects included 21 free-ranging immature Tibetan macaques (*M. thibetana*). The study subjects lived in one group, Yulingkeng A1 (YA1) and were between 1 month to 5 years of age. YA1 has been habituated to human presence since 1986 by Dr. Li Jin-Hua and colleagues for scientific research and since 1992 for tourism (Berman et al., 2004; McCarthy et al., 2009; Xia et al., 2012a; Xia et al., 2012b). The macaques at this site are provisioned with corn three to four times daily by the park staff and the feedings are visible to tourists (Berman & Li, 2002; Li et al., 2007; Xia et al., 2012a; Xia et al., 2012b). The monkeys are well-habituated to human presence and occasionally interact with people (McCarthy et al., 2009). In 1996, a fission event occurred due to group crowding, forming the Yulingken A2 troop (Li, Wang, & Han, 1996; Berman & Li, 2002).

The identities and kin relationships of all group members at this site are maintained by the researchers of Anhui University, and these data were available for this study (W. Xi, personal communication, 2015). I focused data collection on immatures between the ages of 1 month and 5 years, as adult-adult play is rare and may include a different frequency of play signals than occurs during immature play. The ages and dominance structure of group members were previously established on 25 July 2015, before the study period occurred. These data were available for my study and were used to determine identification and age/sex class of subjects (W. Xi, personal communication, 2015). I collected data at the study site from 3 August – 19

September 2015, 5-6 days per week for 6-8 hours daily, which resulted in approximately 400 hours of data collection in the field.

Procedures

At the study’s start, I collected preliminary data to test the modified ethogram and individual identification. Once I established reliability, I collected data using an all-occurrences sampling method (Altmann, 1974). I recorded play behaviors (Table 1; Appendix A) and play signals (Table 2; Appendix B) using a Canon HD Vixia camcorder. My observations occurred from various tourist-viewing platforms, near feeding sites, and near other locations that allowed for the visibility of and proximity to the immature macaques, but at a great enough distance (approximately 1.5 m) to prevent my inclusion in the play bout. Once players stopped engaging in play with each other, my observation continued until 10 seconds after the end of the bout to record the play bout in its entirety. I also recorded systematic notes on each player’s identity, their social attributes (sex, age, rank and kinship), proximity to other group members, and location of the play bout (Table 3; Figure 1). I estimated player’s proximity to group members in centimeters: within arm’s reach (<50 cm) or beyond arm’s reach (>50 cm). If a group member was in proximity of the play bout then they were considered to be part of the play bout’s audience. Each member of the play bout audience was counted to create an audience member tally. I noted ad libitum events that might potentially influence play (e.g. presence or absence of tourists, occurrence of provisioning, monkey “herding” by park staff).

Table 1.

Definition and Components of Play Behaviors

Type of Play	Behavior Component	Definition
Chasing	Leaping, running, walking	Locomotive actions, such as running, climbing and leaping towards or away from another individual, in which animals alternate the roles of chaser and chasee, without having body contact with each other.
Cuddling	Embracing, holding, hugging, touching	Slightly resembles wrestling, but in an extremely mild form, i.e., holding each other with very slight pushing of the body, but without any body displacement. Often resembles embracing.
Play biting	Biting, dragging, embracing, grabbing, hitting, leaping, lying, pinning, pulling, pushing, rolling, running, tackling, touching, walking	Play in which animals grapple and place their mouths on each other’s body. It typically involves similar behavior patterns to wrestling but occurs with biting. Biting and avoiding being bitten with body displacement are the central activity.
Slapping	Hitting with hands, touching, visual fixation	Two animals hit each other with their hands for a period of time without proceeding to a clearer form of play, nor terminating the play encounter.
Wrestling	Dragging, embracing, grabbing, hitting, leaping, lying, pinning, pulling, pushing, rolling, running, tackling, touching, walking	Also known as rough-and-tumble play. Includes play behaviors patterns in which two monkeys engage in mutual grasping, pushing, pulling and rolling, without attempts to bite on each other.

Yanagi & Berman (2014b), p. 1992.

Table 2.

Definition of Play Signals.

Play Signal	Definition
Crouch-and-stare	The animal's ventral surface is on/near the ground and its limbs are fixed, while maintaining the visual fixation on the partner (Symons, 1978a)
Dangle-and-stare	The animals stares at the partner while hanging from an object by the hind limbs, usually from a tree branch (Levy, 1979)
Gamboling	Bobbing, high stepping gait in which the forequarters and hindquarters are alternately raised (Symons, 1978a). Often accompanied by a rotation of head (Sade, 1973).
Hide-and-peek	The animal hides behind an object and then peeks at the partner, alternating the two behavior patterns.
Leg-peek	The animal stares at the partner through its legs with the top of its head against the ground (Symons, 1978a). The animal may hold its ankles or place forearms on the ground.
Look-back	The animal's body orients away from the partner in a fixed position on the four, while the head is turned toward the partner over the shoulder (Symons, 1978a; Levy, 1979).
Play face	Relaxed, open mouth face, typically observed during play bouts (Levy, 1979).
Roll-onto-back-and-stare	The animal rolls onto its back to lie on the back and stare at the partner (Levy, 1979).
Play Threat	The animal directs a lunge <2 body lengths towards another individual, ending the movement by hitting the ground, without facial expression.
Slap and Play Face	The animal hits another individual's body while simultaneously directing an open mouth face towards the individual.

Adapted from Yanagi & Berman (2014b), p. 1992.

Table 3.

List of Play Bout Locations at the Valley of the Wild Monkeys.

Location Name	Type of Location
Lower Waterfall	Provisioning Area
Platforms	Provisioning Area
Pool	Provisioning Area
Provisioning Ground	Provisioning Area
Stairs	Provisioning Area
Tea Tree Grove	Provisioning Area
Waterfall	Provisioning Area
Back Cliff	Non-provisioning Area
Bridge	Non-provisioning Area
Forest	Non-provisioning Area
Left Cliff	Non- provisioning Area
Right Cliff	Non- provisioning Area

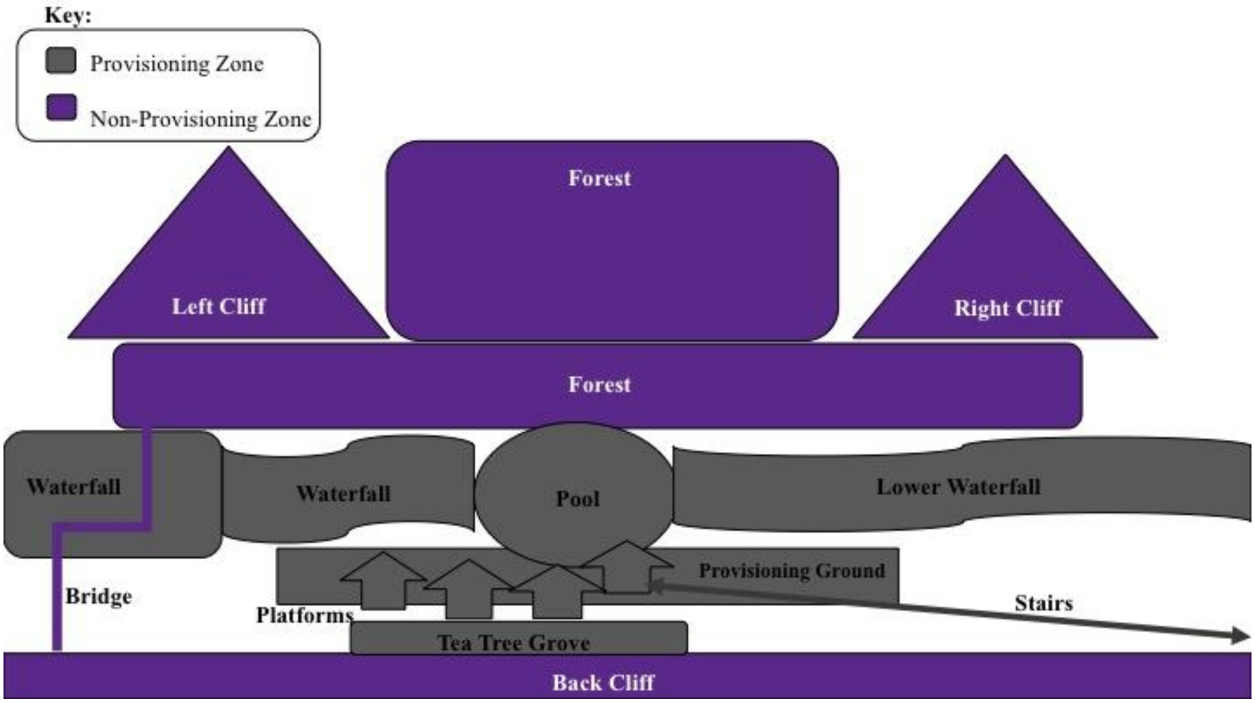

Figure 1. Map of play bout locations for YA1 at the Valley of the Wild Monkeys.

My data collection procedure resulted in 397 videos, ranging in duration of play and occurrences of play bouts. I categorized the videos into time blocks based on what time of day the play bout occurred: (1) 0800 to 1000 h, (2) 1001 to 1200 h, (3) 1201 to 1400 h, (4) 1401 to 1600 h, and (5) 1601 to 1800 h. Due to time and financial constraints, I used a randomized schedule and chose equally across all time blocks to code 50% (*N* = 198) of the videos collected for data analysis. From the video footage, I coded the timestamp, player identity, audience tally, and the play signals and behaviors of the participants (Appendix C). This resulted in 283 play bouts used for data analysis. The play signals and behaviors were scored using a modified ethogram from Yanagi and Berman (2014b). I added to the play signal ethogram previously unlisted behaviors, such as play threat and slap/play face. I also categorized the following locations where play bouts occurred: (1) non-provisioning area, where human interaction with macaques was minimal, and (2) provisioning area, where human interaction was frequent and corn was dispersed. Previous research conducted at the Valley of the Wild Monkeys divided the locations into quadrants, with the non-provisioning area categorized as Zones 4, 5, and 6 and the provisioning area as Zones 1, 2, and 3 (Matheson et al., 2006; Self et al., 2013). I considered play bouts successful when the start of the bout was marked by the exchange of physical contact, chasing, or other behaviors that fell within one or more of the play types or signals. I considered successful play bouts terminated when two players stopped interacting with each other, ceased looking at each other, started to engage in different activities, such as foraging or grooming, or began to interact with other individuals. The specific categories of play bout termination can be found in Table 4. I analyzed all play bouts that included ≥ 2 monkeys, which differs from the dyadic-specific nature of Yanagi and Berman's study (2014b). Using all playful interactions, regardless of player number, provided information on all possible dyads in a play bout and maximized the data available from a small sample size.

Table 4.

Definition of Play Bout Termination.

Play Bout Termination	Definition
Behaviors Not Play	Players begin to engage in any behavior/activity that is not considered under the category or criteria of play (Berman, Ionica, & Li, 2004, p. 1288).
Withdraw	Players move out of proximity from each other (out of arms reach) and no subsequent play behavior or signal is seen.
Adult Interference	Play bout is interrupted by an adult group member performing aggressive and non-aggressive behaviors towards any player (Berman, Ionica, & Li, 2004, p. 1288).

Reliability

I established reliability of individual identities and use of the ethograms during the preliminary study period before arriving at Mt. Huangshan using video footage from the site available through Central Washington University's Primate Behavior program. Once I arrived at the field location, another researcher familiar with the immature macaques assessed my ability to reliably identify the subjects. After data collection, I selected various video segments during which most of my ethogram behaviors (Table 1), signals (Table 2), play locations (Table 3), and play bout termination (Table 4) were exhibited, and I tested intra-observer reliability using 5% of videos from each time block subset. I scored the same video segments at the start and end of the study and compared the number of matches for each behavior, signal, location, and termination. I considered acceptable scores as ≥ 85% for ethogram behaviors, signals, locations, terminations, and animal identities.

Analysis

Using IBM SPSS Statistics (Volume 23) and VassarStats.net, I tested each prediction using various statistical methods, examining variables such as location, presence of tourists, audience number, and bout length. An alpha value (*p*) that equaled 0.05 was considered significant. I analyzed only successful bouts and the signals throughout a successful bout. All calculated values for chi-square goodness of fit tests were corrected for continuity.

Play Location. I used a chi-square goodness of fit test to test the prediction that play will occur outside of the provisioning area more frequently than inside the provisioning area. The null hypothesis was that play bouts should occur evenly inside and outside the provisioning area. I tested whether equal numbers occurred in the provisioning and in the non-provisioning areas of the total number of successful play bouts observed.

Play Bout Termination. I used two separate chi-square goodness of fit tests to test the prediction that third-party adult interference will end play more than other forms of play termination. The null hypothesis was that the three categories of play bout termination would be evenly distributed across all play bouts. First, I compared the total frequency of play bout terminations observed for (1) adult interference and (2) all other causes (combining the behaviors not play, and withdraw categories) (Table 4). Second, I compared the total frequency of play bout terminations observed in all termination categories.

To determine whether play bout termination was evenly distributed in relation to tourism, a chi-square goodness of fit test was used to compare the observed frequency of play bout termination type across tourist present and tourist absent categories.

Play Signals. I used a chi-square goodness of fit test to test the prediction that play bouts begin more with play behaviors than with play signals. The null hypothesis was that play bouts beginning with either a play signal or with a play behavior would be evenly distributed across all bouts. The total number of play bouts, where the beginning of play was observed, was compared for two categories: (1) play signal displayed and (2) no play signal displayed. In play bouts where no play signal was displayed, the play bout began with a play behavior.

I used a chi-square goodness of fit test to test the distribution of the total frequency of play signals across specific play bout audience numbers. I predicted that as the number of audience members increased, the frequency of play signals observed would also increase. The null hypothesis was that the observed frequency of play signals would be evenly distributed across all numbers of audience members. The total frequency of play signals (Table 2) observed were compared across the following categories: (1) zero audience members, (2) one audience member, (3) two audience members, (4) three audience members, (5) four audience members, and (6) five audience members.

To further test the prediction that as the number of audience members increases, the frequency of play signals observed will also increase, I used a Spearman correlation coefficient; testing the correlation between the frequency of observed play signals and audience member categories. The initial chi-square tests used to analyze the prediction would indicate that the distribution of play signals across audience member categories was not by chance. A Spearman correlation coefficient was used to find the rank order between two variables.

Furthermore, I used chi-square goodness of fit tests to analyze the significance of whether or not a play signal was observed directly after an audience member entered a play bout and directly after an audience member left a play bout. I predicted that during a play bout, as a new audience member is added to a bout, a play signal will be used by one of the players to clarify playful intention. The null hypothesis was that play signals will be evenly distributed with play behaviors when a new audience member enters a play bout. First, the total number of play bouts, where a new audience member entered the bout, was compared in two categories: (1) play signal given and (2) no play signal given. Second, the total number of play bouts, where an audience member left the bout, was compared in two categories: (1) play signal given and (2) no play signal given.

Lastly, I utilized two Spearman correlation coefficients to test the prediction that as the length of a play bout's duration increases, the number of play signals observed will also increase. The null hypothesis predicts that play signals would be evenly distributed across all play bout lengths. The length of play bouts were placed into the following categories, based on 60-second intervals: (1) a bout length of zero to 60 seconds, (2) bout length of 61 to 120 seconds, (3) bout length of 121 to 180 seconds, (4) bout length of 181 to 240 seconds, (5) bout length of 241 to 300 seconds, (6) bout length of 301 seconds or higher. First, the average number of observed play signals at each bout length category was compared to test the strength of the correlation between the variables. Second, the rate (calculated by the average number of play signals per 60 seconds) of observed play signals at each bout length category was compared to test the strength of the correlation.

CHAPTER IV

RESULTS

Over the course of 48 days, I observed the play behaviors and play signals of 21 immature Tibetan macaques at the Valley of the Wild Monkeys. I collected 397 videos of playful interactions involving immature macaques, including infant play. Using a randomized subset of data based on time blocks, I coded and used 174 videos for analysis. In total, 283 play bouts in this subset were observed, with 136 observations of the start of play, 183 observations of the end of play, and 94 observations of a complete play bout (where the start and end of play were clearly marked). Of the 283 play bouts coded, 216 occurrences of playful interactions in the non-provisioning area and 81 occurrences in the provisioning area occurred. In the 94 completed play bouts observed, the average length of a play bout was 64.7 seconds and the completed play bouts ranged in length from 1 second to 585 seconds. The number of players present in play bouts ranged from 1 player to 5 players. I recorded 415 play signals in all playful interactions coded. The average number of play signals seen in completed play bouts ($N = 94$) was 1.6 play signals per bout.

Reliability

To test intra-observer reliability, I scored the same video segments at the start and end of this study and compared the number of matches for each animal identity, behavior, signal, location, and termination type. The number of matches for the animal identities, behaviors, signals, locations, and termination type were then compared. Initial intra-reliability testing of animal identities was completed on 18 August 2015 at the field site, under the supervision of W. Xi. Animal identity matches were 86% reliable (13/15). Ethogram behaviors were 93% (133/142), signals were 87.5% (14/16), locations were 100% (162/162), and termination type were 100% (9/9) reliable. Furthermore the reliability of identification of actors and audience members present in video segments were scored and showed actor identifications were 87% (141/162) and audience identifications were 85.7% (138/161) reliable.

Play Location

Using a chi-square goodness of fit test, I tested the prediction that play will occur outside of the provisioning area more frequently than inside the provisioning area. I found a significant deviation from the expected values, with more play bouts observed in the non-provisioning area ($N = 217$) than in the provisioning area ($N = 82$), therefore supporting the prediction (Table 5; Figure 2; $\chi^2(1) = 60.06$, $p < 0.05$).

Table 5.

Statistical Output of Play Location Prediction.

Category	Observed Frequency	Expected Frequency	% Deviation
Non-Provisioning Area	217	149	+45.15
Provisioning Area	82	149	-45.15

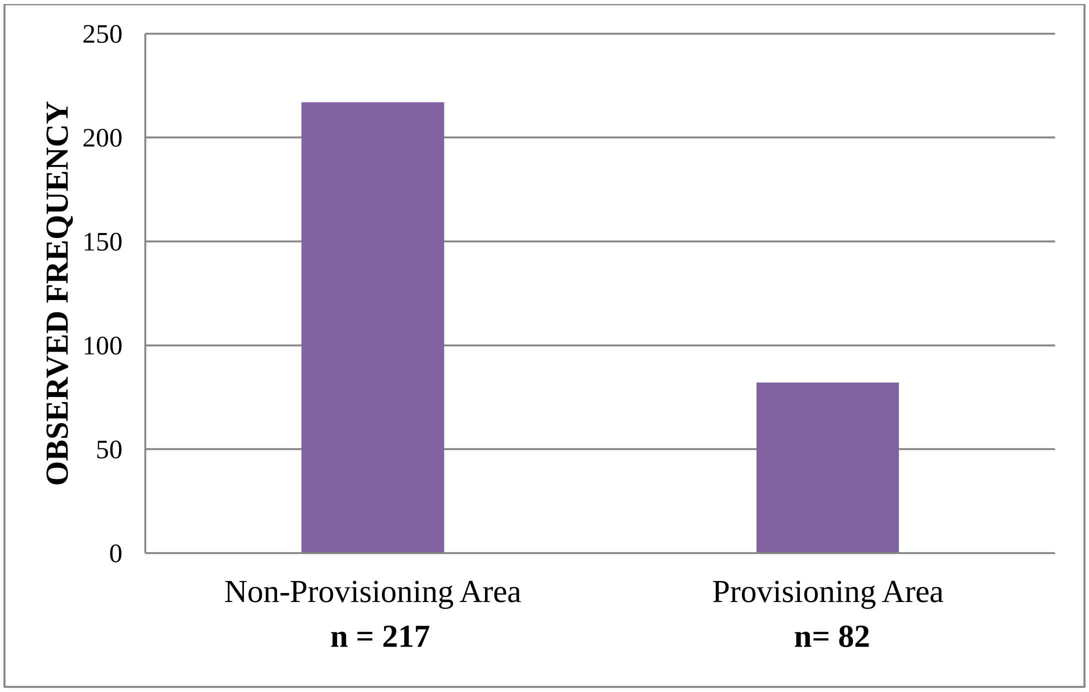

Figure 2. Bar graph of observed frequency of play bout location.

Play Bout Termination

To test the prediction that third-party adult interference will end play more than other forms of play termination, I first used a chi-square goodness of fit test to compare the two termination categories. The total frequencies of play bout termination observed were compared: adult interference (N = 16) and other causes (N = 167). The results showed a significant deviation from the expected values, however, the prediction was not supported as there was significantly less occurrences of adult interference compared to other causes ($\chi^2(1) = 122.96$, $p < 0.05$). I then used a chi-square goodness of fit test to compare all three termination categories. The total rates of play bout termination observed were compared for adult interference (N = 16), behaviors not play (N = 74), and withdraw (N = 94) categories (Table 6; Figure 3; $\chi^2(2) = 53.52$, $p < 0.05$). The results shows a significant deviation from the expected values, indicating that play bouts are ending more by behaviors not play and withdraw than any form of third party adult interference.

Table 6.

Statistical Output of Play Bout Termination.

Category	Observed Frequency	Expected Frequency	% Deviation	Standard Residual
Adult Interference	16	61.33	-73.91	-5.79
Behaviors Not Play	74	61.33	+20.66	+1.62
Withdraw	94	61.33	+53.27	+4.17

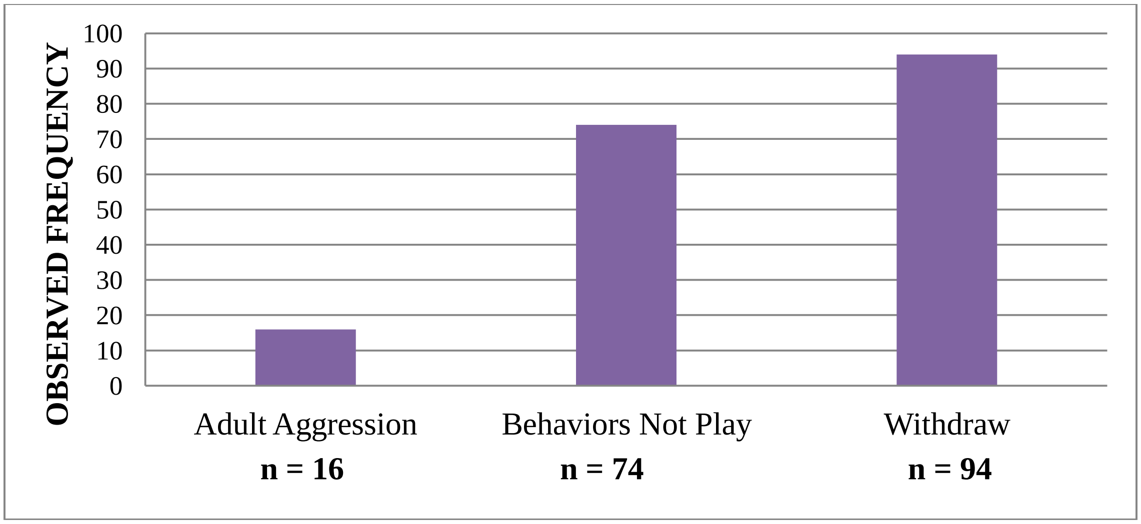

Figure 3. Bar graph of observed frequency of play bout termination.

I used a chi-square goodness of fit test to test whether play bout termination was evenly distributed in relation to tourism. I compared the observed frequency of play bouts that occurred in tourist present ($N = 71$) and tourist absent ($N = 65$) categories. The results showed no significant deviation from the expected values (Table 7; Figure 4; $\chi^2(1) = 0.6714$, $p = 0.18$).

Table 7.

Statistical Output of Tourist Impact on Play Bout Termination.

Category	Observed Frequency	Expected Frequency	% Deviation
Tourists Present	71	68	+4.41
Tourists Absent	65	68	-4.41

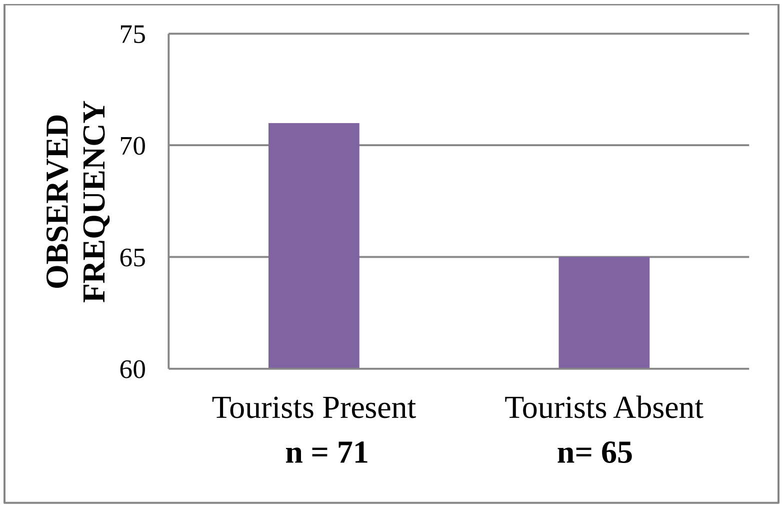

Figure 4. Bar graph of impact of tourist presence on play bout termination.

Play Signals

To test the prediction that play bouts begin more with play behaviors than with play signals, I used a chi-square goodness of fit test to compare the total frequency of play bouts, where the beginning of play was observed, in two categories: (1) play signal displayed (N = 28) and (2) no play signal displayed (N = 108). The results showed a significant deviation from the expected values and supported the prediction (Table 8; Figure 5; $\chi^2(1) = 45.88$, $p < 0.05$).

Table 8.

Statistical Output of Occurrences of Play Signals to Initiate Play Bouts.

Category	Observed Frequency	Expected Frequency	% Deviation
Play Signal Displayed	28	68	-58.82
No Play Signal Displayed	108	68	+58.82

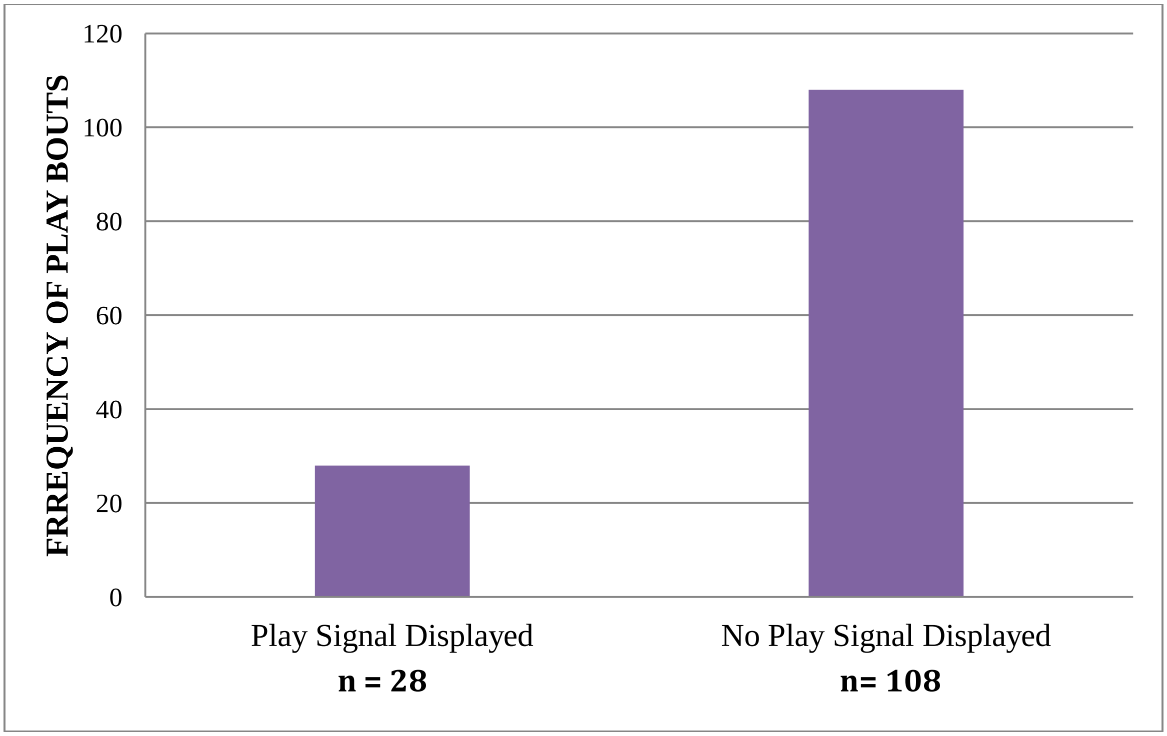

Figure 5. Bar graph of occurrences of play signals to initiate play bouts.

To further analyze the use of play signals in play bouts, I used a chi-square goodness of fit test to test the distribution of play signals across play bout audience number. I predicted that as the number of audience members increased, the frequency of play signals observed would also increase. I compared the frequency of play signals observed for zero audience members (N = 14), one audience member (N = 137), two audience members (N = 159), three audience members (N = 86), four audience members (N = 16), and five audience members (N = 3) categories. The results showed a significant deviation from the expected values and supported the prediction (Table 9; Figure 6; Figure 7; $\chi^2(5) = 335.46$, $p < 0.05$).

Table 9.

Statistical Output of Frequency of Play Signals for Various Audience Member Numbers.

Number of Audience Members	Observed Frequency	Expected Frequency	% Deviation	Standard Residual
0	14	69.17	-79.76	-6.63
1	137	69.17	+98.06	+8.16
2	159	69.17	+129.87	+10.8
3	86	69.17	+24.33	+2.02
4	16	69.17	- 76.87	-6.39
5	3	69.17	-95.66	-7.96

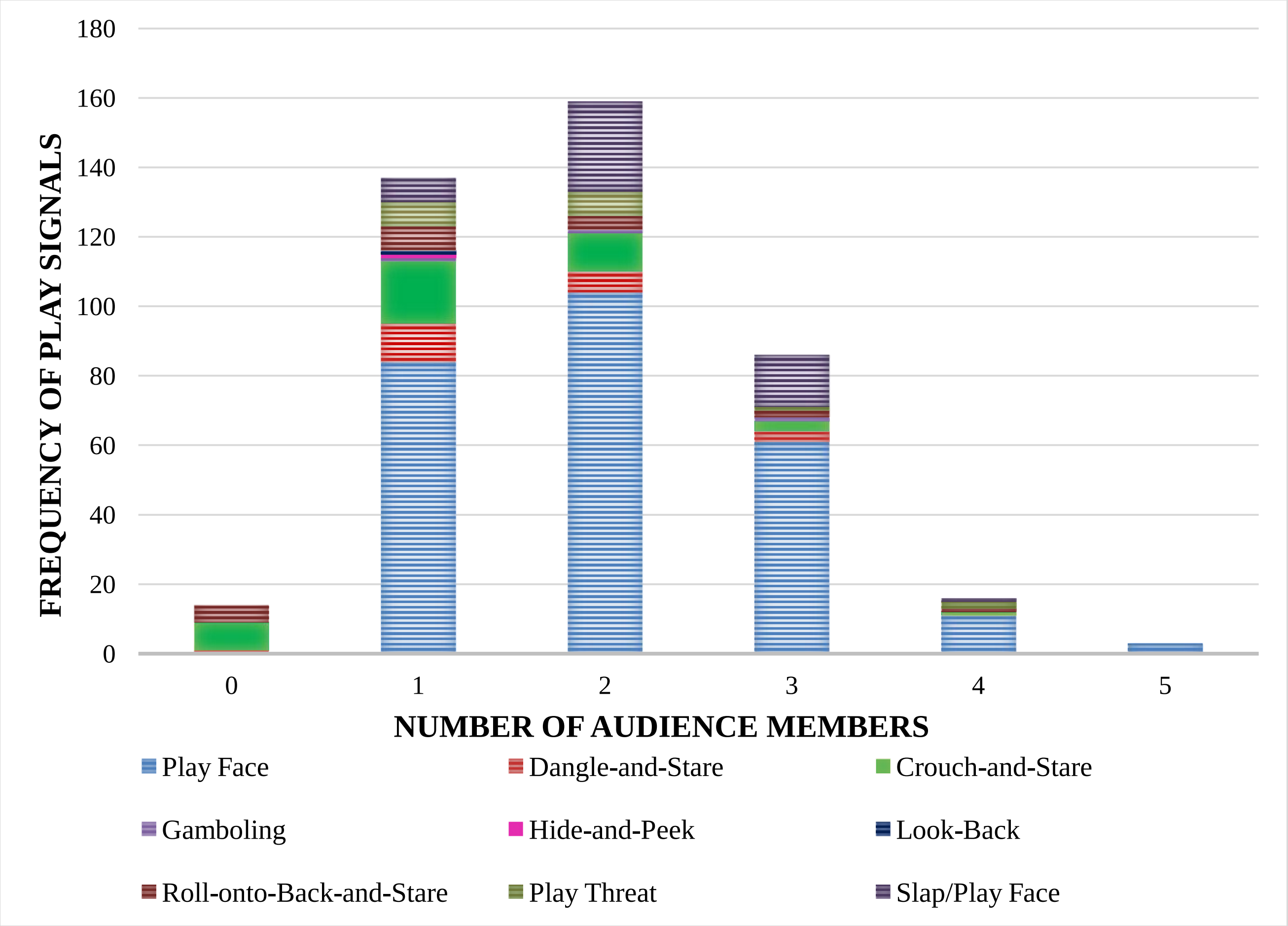

Figure 6. Bar graph of types of play signals with different audience members.

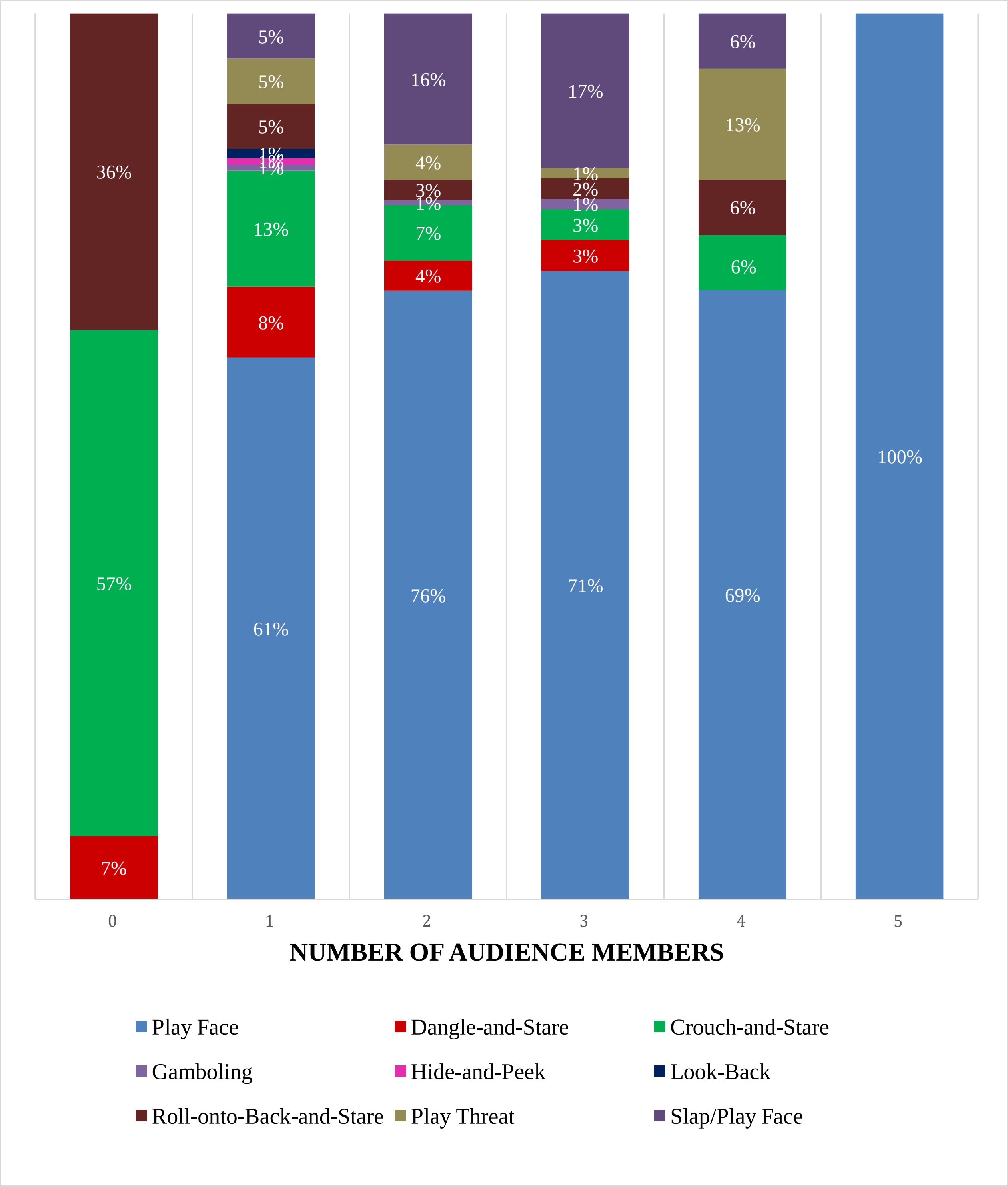

Figure 7. Bar graph of percentage of play signals with various audience members.

I used a Spearman correlation coefficient to further test the prediction that as the number of audience members increases, the frequency of play signals observed will also increase. A spearman correlation coefficient was used to test the correlation between the significantly different variables. The frequency of observed play signals for each audience category was calculated. The results showed a weak correlation that was not significant (r (4) = -0.371, p = > 0.05).

To test the prediction that during a play bout, as a new audience member is added to a bout, a play signal will be used by one of the players to clarify playful intention two chi-square goodness of fit tests was used. First, the total number of play bouts, where a new audience member entered the bout, were compared in two categories: (1) play signal given (N = 26) and (2) no play signal given (N = 230). The results showed a significant deviation from the expected values, however, the prediction was not supported (Table 10; Figure 8; $\chi^2(1) = 160.98$, $p < 0.05$). Second, the total number of play bouts, where an audience member left the bout, were compared in two categories: (1) play signal given (N = 24) and (2) no play signal given (N = 202). A significant deviation from the expected values were found (Table 11; Figure 9; $\chi^2(1) = 138.62$, $p < 0.05$).

Table 10.

Statistical Output of Play Signals with Audience Increase.

Category	Observed Frequency	Expected Frequency	% Deviation
Play Signal Given	26	128	-79.69
No Play Signal Given	230	128	+79.69

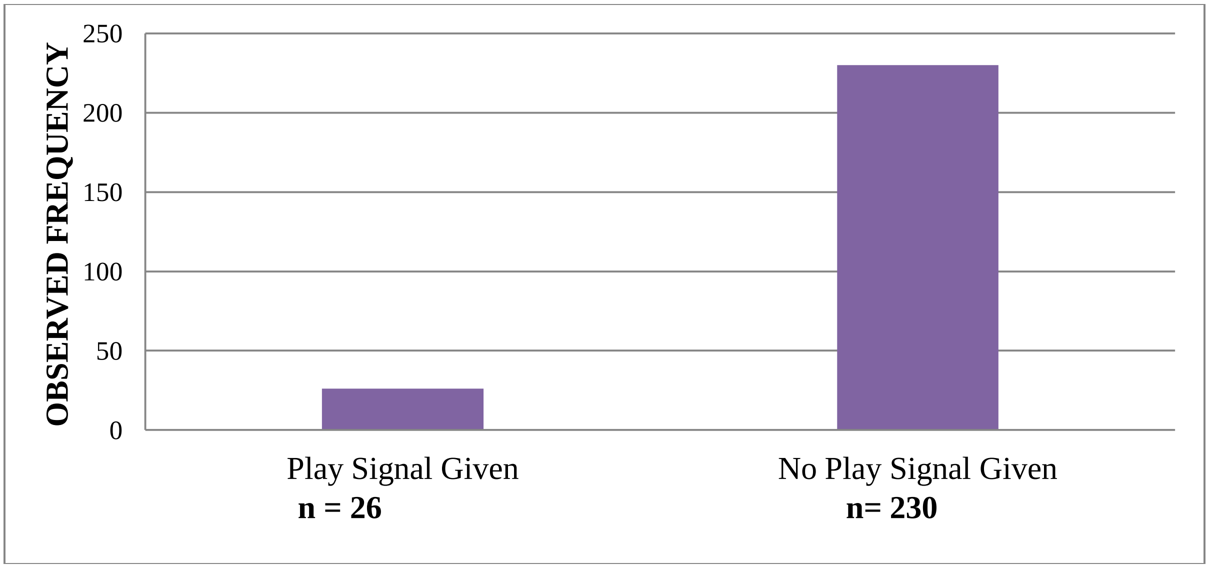

Figure 8. Bar graph of play signals with audience increase.

Table 11.

Statistical Output of Play Signals with Audience Decrease.

Category	Observed Frequency	Expected Frequency	% Deviation
Play Signal Given	24	113	-78.76
No Play Signal Given	202	113	+78.76

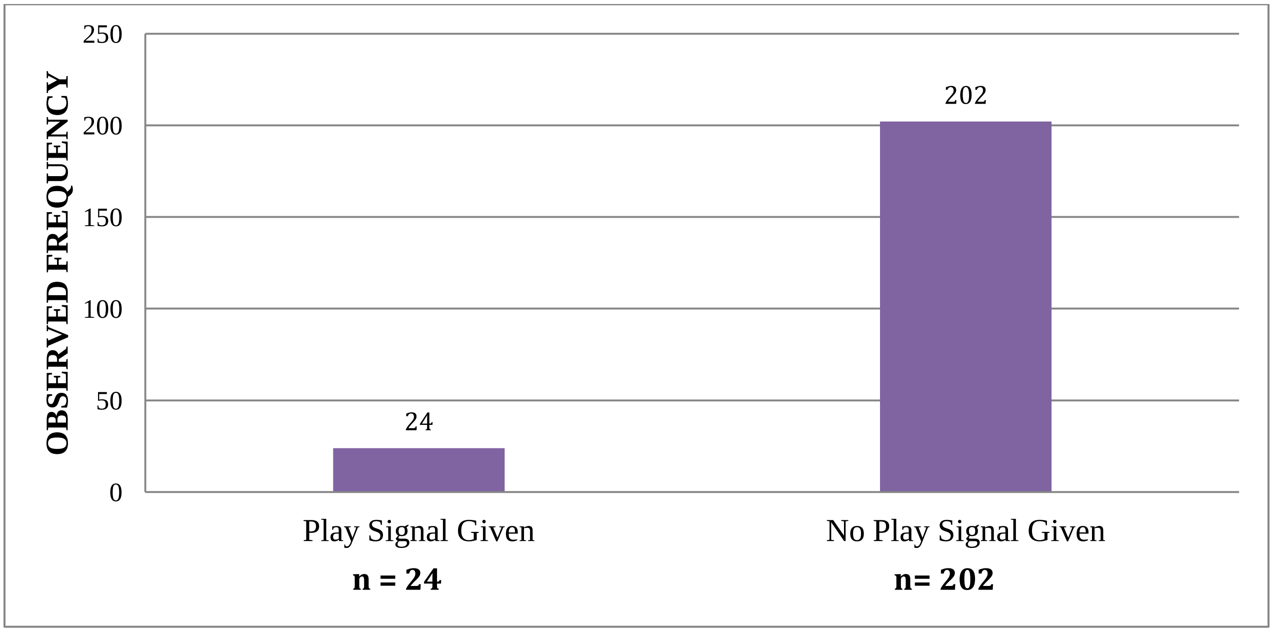

Figure 9. Bar graph of play signals with audience decrease.

I used two Spearman correlation coefficient tests to test the prediction that as the length of a play bout's duration increased, the number of play signals observed would also increase. First, the average number of observed play signals for each bout length category was analyzed to calculate the strength of the correlation between the variables. The results showed a strong correlation that was significant (r (5) = 0.964, p = < 0.05; Figure 10). Second, the rate of observed play signals for each bout length category was analyzed to determine the correlation between the variables. The results also showed a strong correlation that was significant (r (5) = 0.991, p = < 0.05; Figure 11).

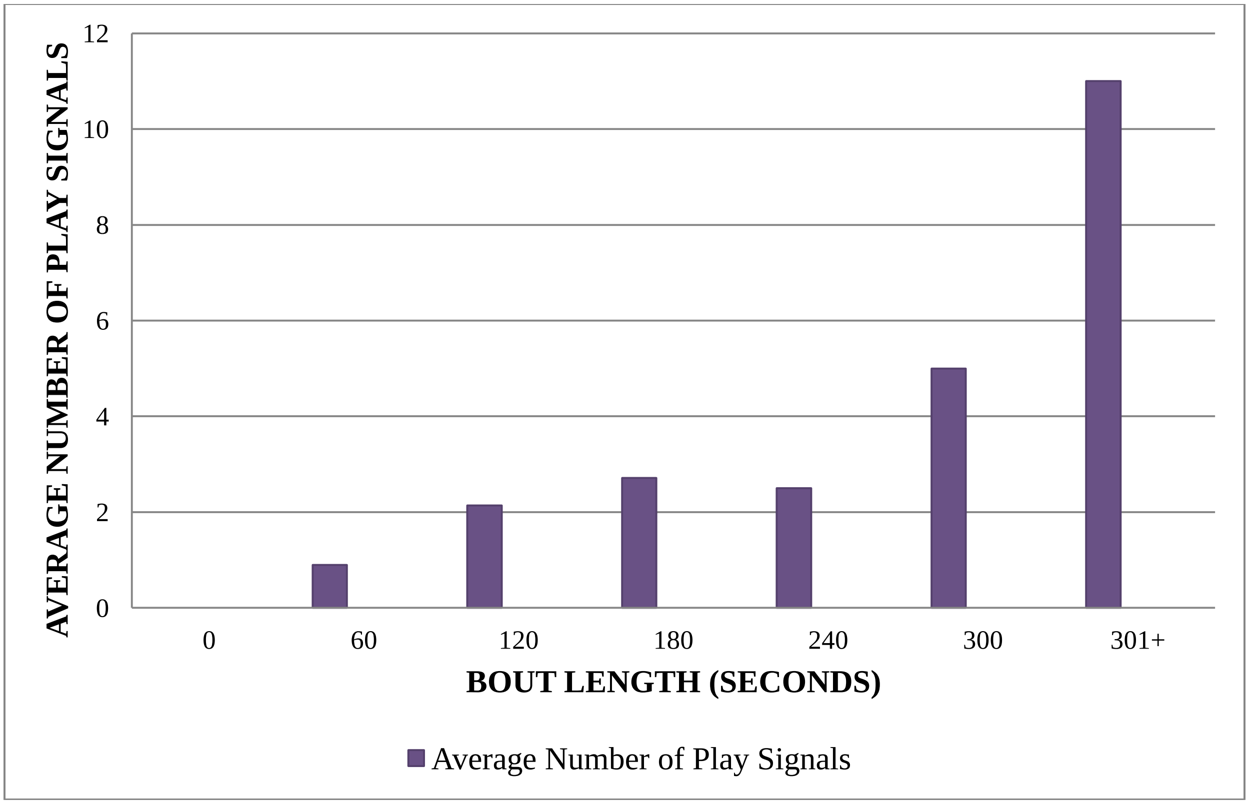

Figure 10. Bar graph of the average number of play signals per bout length.

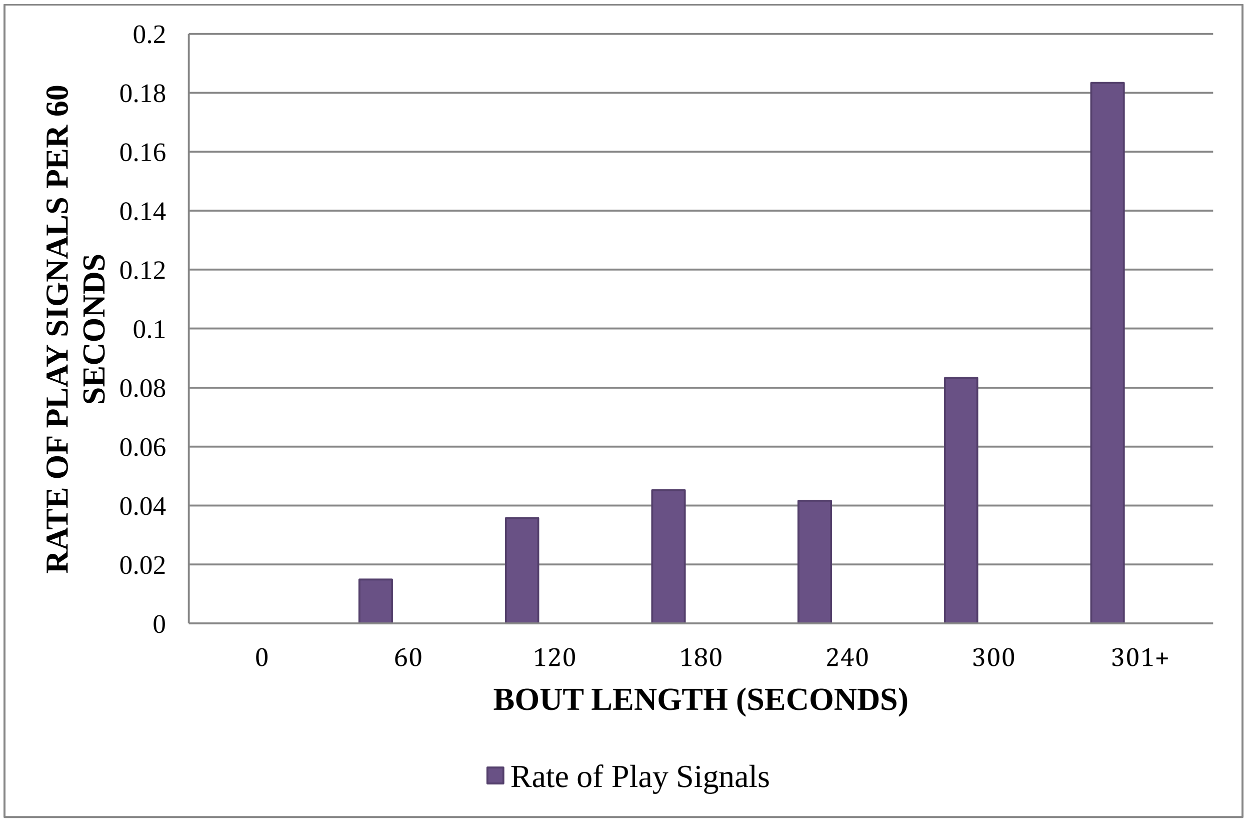

Figure 11. Bar graph of the rate of play signals per bout length.

CHAPTER V

DISCUSSION

Although play is easily recognizable, it is often difficult to concretely identify. Furthermore, the complexity and fluidity of playful interactions may be affected by the communicative abilities of the players, the location of the play bout, and how many players are in a bout. In this study, I aimed to explain how immature Tibetan macaques utilize multiple play signals in different locations based on various factors, such as tourist effect, audience members, and play bout duration. Previous research conducted by Yanagi and Berman (2014b) found the possibility of functionally referential signaling in juvenile rhesus macaque social play. They argued that the selection of play signals used by players was nonrandom, and the signals were necessary to reinforce and clarify playful intention. Furthermore, Yanagi and Berman (2012b) hypothesized that despotic macaques may need to use play signals more to emphasize the affiliative, rather than aggressive, nature of their behaviors. My study showed that immature Tibetan macaques play more in the non-provisioning area, with a play group of one to two audience members observed most frequently, and made use of various play signals to within these constraints. My results support to Yanagi and Berman's (2014b) prediction that macaque dominance style influences the structure of play.

Play Location

Using a chi-square goodness of fit test, I found that the prediction that play would occur more in the non-provisioning area than in the provisioning area was supported by a significant difference in the frequency of play bouts observed in each category. This finding is supported by previous research conducted at the Valley of the Wild Monkeys that found high rates of infant-directed aggression in the provisioning area, apparently as part of feeding competition (Self et al., 2013). Additionally, Self et al. (2013) argued that infants might actively avoid the provisioning area when corn is present to circumvent adult aggression. In this way, it is expected that play would occur more in the non-provisioning areas as a way to avoid adult aggression. Likewise, Yanagi and Berman (2014b) hypothesized that a macaque group marked by a despotic dominance style would play differently than a tolerant group. This hypothesis may further explain the uneven location distribution of Tibetan macaque play bouts in the non-provisioning area, away from the provisioning area that is characterized by increased redirectional aggression and counter-aggression from adult group members (Berman et al., 2004).

Palagi et al. (2007) found that a group of captive juvenile gorillas played in flexible way, with an increase of play signals observed when escape possibilities were limited and enclosure space was reduced. Palagi et al. (2007) argued that the increase in play signals seen indicated that play bouts in this area are perceived as riskier by the players. In this way, the immature macaques observed in the present study may, similarly to the juvenile gorillas, be able to perceive a location, such as the provisioning area, as riskier. Therefore, the immature macaques may play in a location where aggressive play behaviors are less risky to perform and where play bouts in general are easier in complexity to manage. However, it is possible that the immatures may play significantly less in the provisioning zone because of the presence of corn, and are therefore engaging in feeding rather than play.

Play Bout Termination

Although I found a significant deviation from the expected values, the prediction that third-party adult interference would end play more than other forms of play termination was not supported when analyzed with a chi-square goodness of fit test. Berman and colleagues hypothesized that due to their despotic nature (Berman et al., 2004), Tibetan macaque adults would interfere with play bouts that may be perceived by third parties as aggressive. The results showed that this is not the case. However, it is possible that immature macaques avoid the provisioning area as a way to directly manage the end of play themselves and avoid adult aggression. Furthermore, the results showed that Tibetan macaque play ends by players withdrawing from one another or players exhibiting behaviors outside of the context of play more significantly than adult aggression or any other form of adult behavioral interference. This finding further supports the argument that immatures may avoid the provisioning area and avoid adult interference to maintain play in a relaxed field.

I used a chi-square goodness of fit test to determine the distribution of play termination in relation to tourism. This test showed no significant deviation from the expected values. Therefore, tourists' presence or absence on the viewing platform at the Valley of the Wild Monkeys does not have a direct impact on the end of play. However, previous studies have shown that tourists do significantly affect Tibetan macaque adult behavior inside of the provisioning area (Berman et al., 2004; Matheson et al., 2007). Berman et al. (2004) found a higher level of counter-aggression in a group of Tibetan macaques that encountered humans more often. In this way, tourist presence may be threatening to the macaques (Matheson et al., 2007) and therefore create a stressful environment that is not conducive to playful interactions. This further indicates that immatures play more often in the non-provisioning area where adult aggression is lower and tourist presence is minimal.

Additionally, tourism may have other impacts on the occurrence of play. de La Torre et al. (2000) found a significant relationship between the number of tourists and the time spent playing in a preferred forest location in a group of pygmy marmosets. This change in behavioral ecology provides support to Burghardt's (1999) hypothesis that successful play bouts must occur in a relaxed field, where the individuals are free from stress (Oliveira et al, 2010). Therefore, it is expected that Tibetan macaque immatures would avoid playing in areas that they perceive as stressful. The results of this study supported this argument. However, it is possible that play behaviors may be used to create a relaxed field when tension is high (Fagen and Fagan, 2004). For example, Norscia and Palagi (2011) found an increase in play behaviors directly before feeding times in a captive group of common marmosets, and Palagi et al. (2006) found similar results in captive juvenile gorillas. It is possible that Tibetan macaques may use play as a way to dissipate tension building among the group. More research is needed to examine this possibility.

Play Signals

To test the prediction that more play bouts begin with play behaviors than with play signals, I used a chi-square goodness of fit test. The results supported the prediction and previous literature. Yanagi and Berman (2014b) found that play signals did not significantly mark the beginning of play in juvenile rhesus macaques. The authors argued that therefore play signals might function to clarify and reinforce playful intentions, rather than start a playful interaction.

Furthermore, using a chi-square goodness of fit test comparing the number of play signals for specific audience numbers, I found a significant deviation from the expected values. Several conclusions can be drawn from these results. First, it appears that subjects use play face the most compared to all other play signals, regardless of audience number. This may indicate the salient nature of the play face signal when there is a receiver present (van Hooff, 1967; Pellis and Pellis, 1996) or when an aggressive play behavior escalating to a conflict is possible (Palagi et al., 2007). This conclusion is further supported by the lack of observation of play face in the zero audience member category. In this way, play face may be an important communicative tool when a player is in close proximity to the sender (van Hooff, 1967; Pellis and Pellis, 1996).

Additionally, play face may function as a flexible, rather than static, signal that can be used in a variety of contexts (Pellis and Pellis, 1996). For example, play face may be important in the clarification of play when the dynamics of the bout changes, such as the addition of a player, an increase in vigor, or a change in location. However, the frequent occurrence of play face may be an involuntary artifact of the sender’s enjoyment of the bout rather than a message for players (Spijkerman et al., 1996).

Second, within the zero audience member category, only three play signals were observed: (1) crouch-and-stare, (2) dangle-and-stare, and (3) roll-onto-back-and-stare. This may indicate the need to use a complex body and facial signals to attract players to begin a bout, rather than a facial only signal, such as play face. Tomasello et al. (1989) observed the use of attention-getting gestures in juvenile chimpanzees when the signal receiver did not see an individual’s play face. In this way, a play signal that involves a combination of two or more signals may be necessary to reinforce the sender’s message. The present study supported this speculation, by Tibetan macaque immatures choosing multiple play signals from their diverse repertoire to indicate their willingness to play.

Third, I observed the combination of slap (a play behavior) and play face (a play signal) significantly when compared to other play signals, in relation to audience members. It is possible that the playful intention of a slap behavior may need to be clarified as play because of its aggressive nature (Burghardt, 1999; Pellis and Pellis, 1996). In this way, the slap behavior and the play face signal would negate each other. Additionally, this combination may be a way for players to maintain their competitive advantage in a play bout while still continuing to successfully play with another individual (van Leeuwen et al., 2011). According to the competitive fitness model, this type of play may be beneficial in the long-term for juveniles to practice aggressive behaviors before dominance hierarchies are established in adulthood (van Leeuwen et al., 2011). In future studies, it may be expected to see this combination of behavior and signal in immature males because of its aggressive nature.

I used a Spearman correlation coefficient to further test the prediction that as the number of audience members increases, the number of play signals observed will also. The results showed a weak correlation that was not significant and indicate a possible threshold for the salient disposition of play signals past a certain audience member number. Although it was expected that more play signals would be necessary in a larger playgroup (Spijkerman et al., 1996), this was clearly not true for my study. The results may indicate that two audience members (three players total) is the most common playgroup, with the message of play signals used in this type of bout holding much more weight compared to play signals used in large playgroups. One conclusion that can be drawn from these results is that play bouts with more players increase the complexity of the bout, making them harder to manage (Bekoff, 1972). This breakdown of communication may be more readily seen in despotic macaques due to the increase in aggression and therefore higher level of risky play bouts. Another apparent conclusion from these results is that smaller play bouts may reinforce affiliation between group members, whereas larger playgroups may be used to test individuals' strengths (Pellis and Pellis, 1996). Therefore, signaling may be crucial in a small playgroup to reaffirm affiliation rather than aggression.

Due to the deviation from the expected outcome of the relationship between play signals and audience members, I conducted two chi-square goodness of fit tests. I predicted that during a play bout, as new audience members are added to a bout, play signals will be used by one of the players to clarify and reiterate playful intention. The results showed that when new audience members are added to a bout, no play signal is significantly displayed. Furthermore, when a player leaves a play bout, no play signal is significantly displayed. This may indicate that play signals have multiple functions, as they are observed before play, during play, and when players withdraw from one another (Pellis et al., 2011).

Lastly, I examined the length of play bouts in relation to the number of play signals used. I predicted that as the length of a play bout increased, the number of play signals observed would also increase. The Spearman correlation coefficient showed a strong correlation that was significant, supporting the prediction. This may indicate the importance of play signals to sustain the length of play bouts. Previous literature has shown that short play bouts are often marked by a misinterpretation of signals, whereas long play bouts are marked by an increase in play intensity (Spijkerman et al., 1996). Spijkerman et al. (1996) found in a group of captive gorillas play face was used most often in long play bouts involving wrestle and gnaw behaviors. Furthermore, Spijkerman et al. (1996) observed an increase in third parties joining the play bout when the play face signal was used. The present study showed that play signals may function in a similar way to play signals used by gorillas, with the longest play bout containing the most play signals observed.

Conclusion and Future Recommendations

In conclusion, the immature Tibetan macaques at the Valley of the Wild Monkeys were able to appropriately maintain playful interactions in different locations through the use of multiple play signals. Within all audience member numbers, play face was the most frequently observed signal, possibly indicating its salient and flexible nature. Tibetan macaque immatures significantly played more in the non-provisioning area, possibly affected by increase adult aggression, the despotic dominance style of the group, and effects of provisioning. However, Tibetan macaques managed play through the utilization of a diverse repertoire of play signals, which combine body and facial gestures, to begin play, encourage the continuation of play, and end play. Furthermore, although tourism did not have a direct impact on the playful interactions observed for the present study, provisioning might have an effect on play. More research is needed on the difference in behavioral ecology in the non-provisioning and provisioning areas for this group before additional questions regarding play can be answered. However, the present study may begin to provide valuable insight on tourism and the environmental stability of a provisioned group, using play as an indicator of a stress free field.

Recommendations for Future Research

For future research, I recommend increasing the amount of data analyzed. Yanagi and Berman (2014b) observed 1304 successful play bouts, compared to my study that had 283 successful play bouts. However, both Yanagi and Berman’s (2014b) study and my own had a comparable number of study subjects. In this way, it would be beneficial for future research to extend the time spent collecting data at the Valley of the Wild Monkeys to increase the number of observed play bouts. Additionally, to test the possibility of play signals representing functionally referential communication between immatures, I recommend recording play intensity in relation to play signaling.

Lastly, it would be highly beneficial to compare my results with studies focused on other despotic macaque species to determine the effect dominance style may have on play. Likewise, comparing the present study of a provisioned group of Tibetan macaques to a non-provisioned and unhabituated group may shed lights on the effects tourism can have on play.

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APPENDIX A

Photos of Play Behaviors

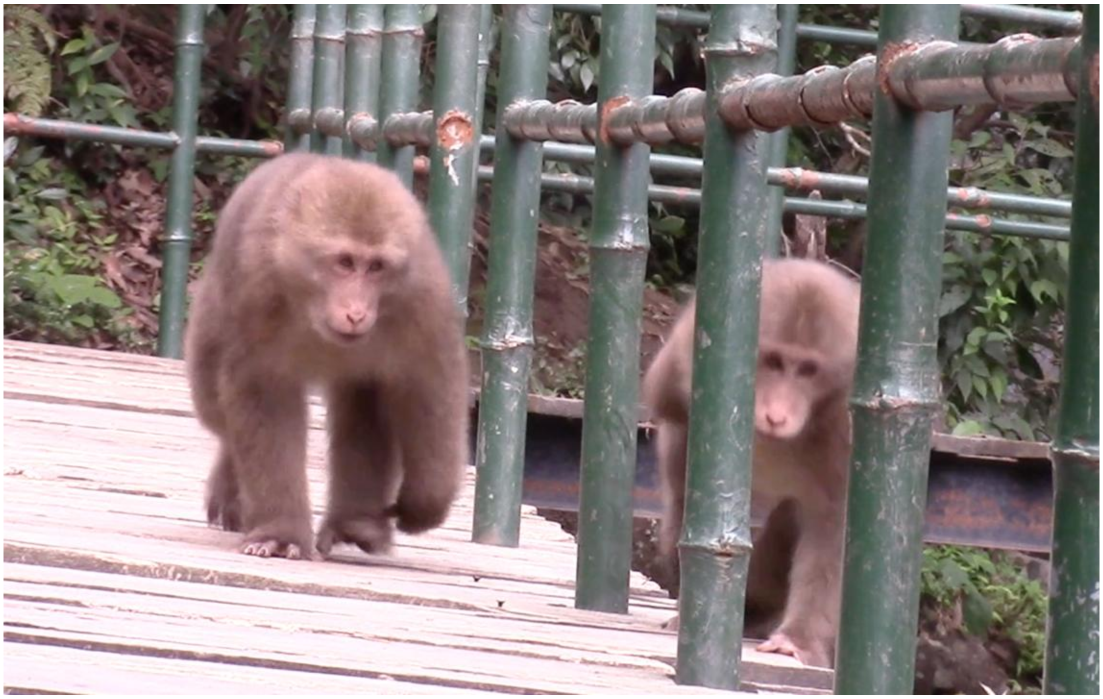


Figure 1A. Chasing behavior

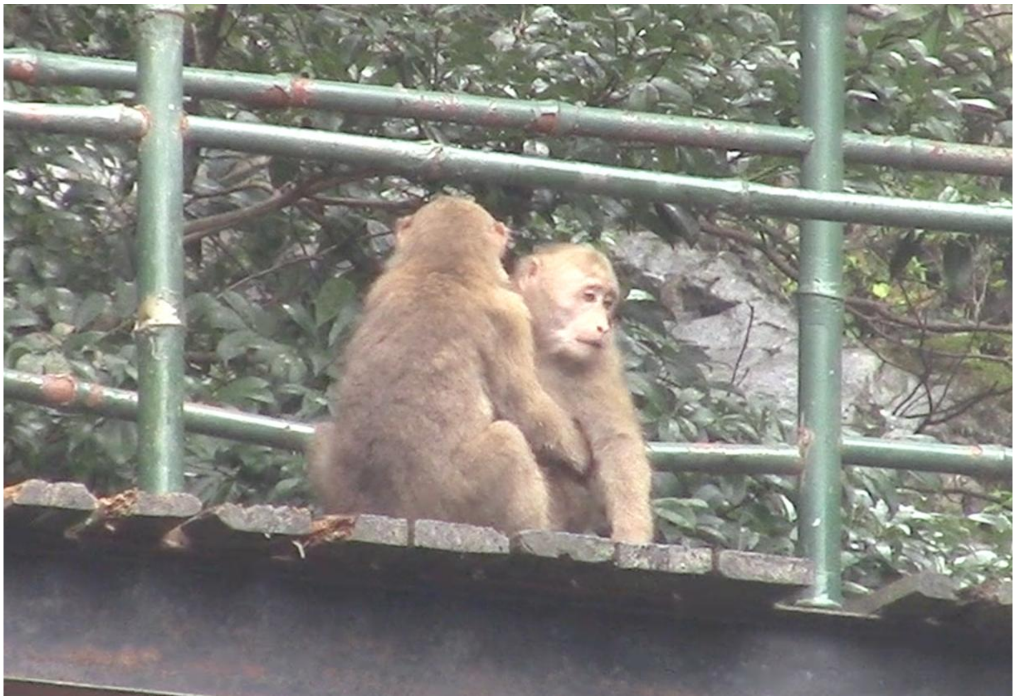


Figure 2A. Cuddling behavior

Figure 3A. Play biting behavior

Figure 4A. Slapping behavior

Figure 5A. Wrestling behavior

APPENDIX B

Photos of Play Signals

Figure 1B. Crouch-and-stare signal

Figure 2B. Dangle-and-stare signal

Figure 3B. Gamboling signal

Figure 4B. Hide-and-peek signal

Figure 5B. Look-back signal

Figure 6B. Play face signal

Figure 7B. Roll-onto-back-and-stare signal

Figure 8B. Play threat signal – Juvenile

Figure 9B. Play threat signal – Infant

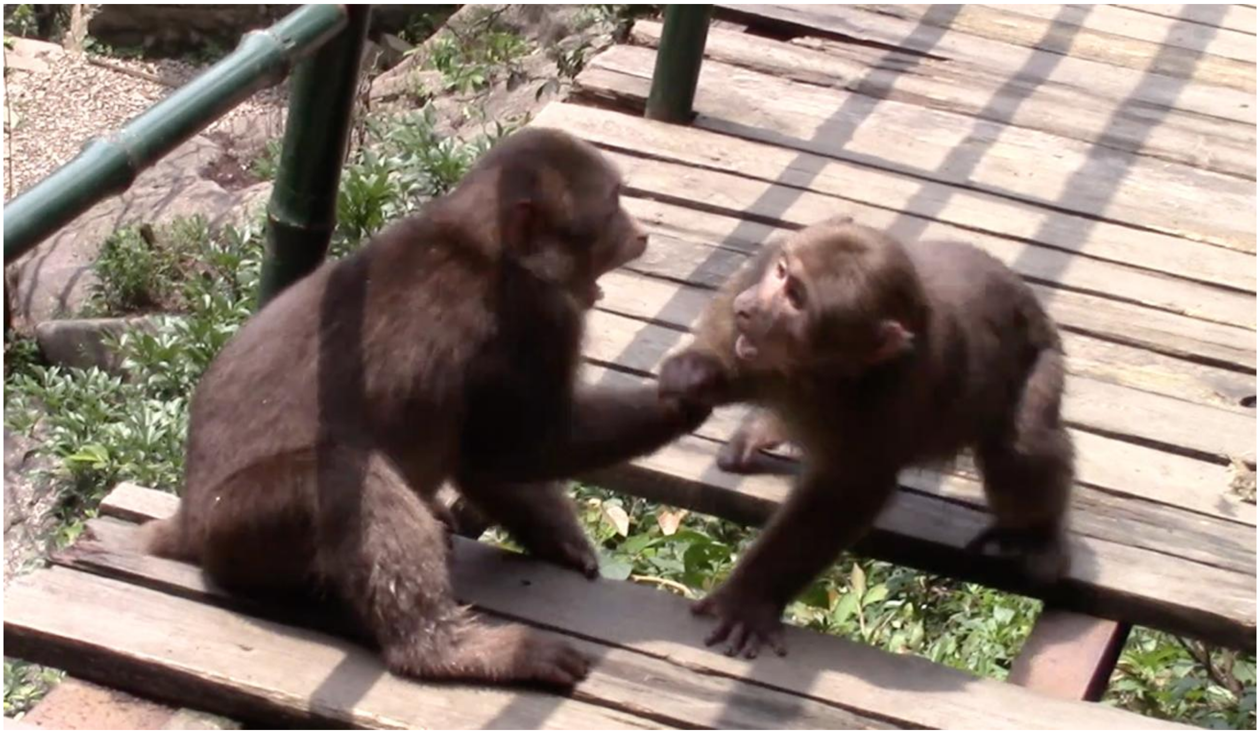
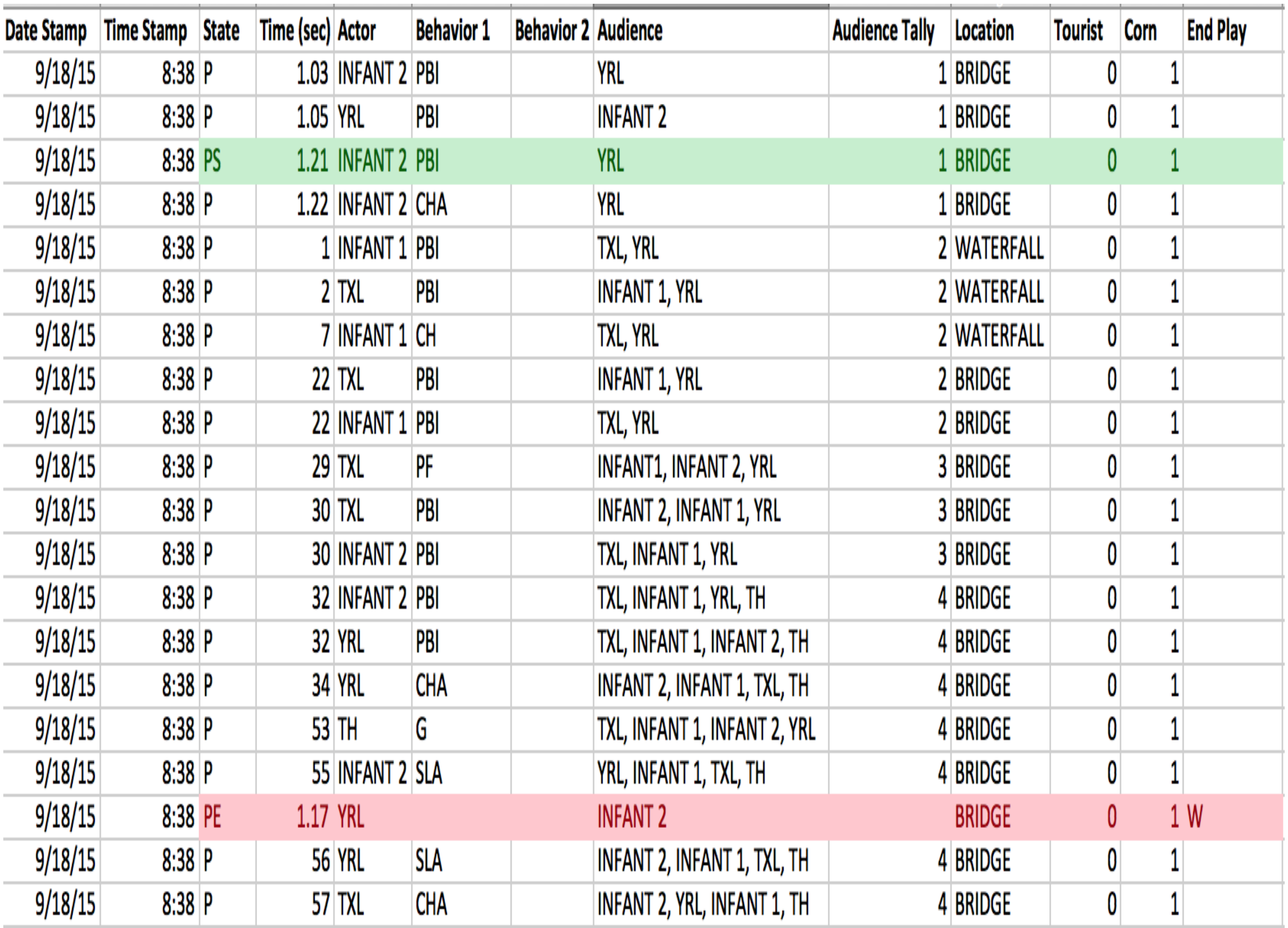


Figure 10B. Slap behavior and play face signal

APPENDIX C

Sample Data Sheet



Date Stamp	Time Stamp	State	Time (sec)	Actor	Behavior 1	Behavior 2	Audience	Audience Tally	Location	Tourist	Corn	End Play
9/18/15	8:38	P	1.03	INFANT 2	PBI		YRL	1	BRIDGE	0	1	
9/18/15	8:38	P	1.05	YRL	PBI		INFANT 2	1	BRIDGE	0	1	
9/18/15	8:38	PS	1.21	INFANT 2	PBI		YRL	1	BRIDGE	0	1	
9/18/15	8:38	P	1.22	INFANT 2	CHA		YRL	1	BRIDGE	0	1	
9/18/15	8:38	P	1	INFANT 1	PBI		TXL, YRL	2	WATERFALL	0	1	
9/18/15	8:38	P	2	TXL	PBI		INFANT 1, YRL	2	WATERFALL	0	1	
9/18/15	8:38	P	7	INFANT 1	CH		TXL, YRL	2	WATERFALL	0	1	
9/18/15	8:38	P	22	TXL	PBI		INFANT 1, YRL	2	BRIDGE	0	1	
9/18/15	8:38	P	22	INFANT 1	PBI		TXL, YRL	2	BRIDGE	0	1	
9/18/15	8:38	P	29	TXL	PF		INFANT1, INFANT 2, YRL	3	BRIDGE	0	1	
9/18/15	8:38	P	30	TXL	PBI		INFANT 2, INFANT 1, YRL	3	BRIDGE	0	1	
9/18/15	8:38	P	30	INFANT 2	PBI		TXL, INFANT 1, YRL	3	BRIDGE	0	1	
9/18/15	8:38	P	32	INFANT 2	PBI		TXL, INFANT 1, YRL, TH	4	BRIDGE	0	1	
9/18/15	8:38	P	32	YRL	PBI		TXL, INFANT 1, INFANT 2, TH	4	BRIDGE	0	1	
9/18/15	8:38	P	34	YRL	CHA		INFANT 2, INFANT 1, TXL, TH	4	BRIDGE	0	1	
9/18/15	8:38	P	53	TH	G		TXL, INFANT 1, INFANT 2, YRL	4	BRIDGE	0	1	
9/18/15	8:38	P	55	INFANT 2	SLA		YRL, INFANT 1, TXL, TH	4	BRIDGE	0	1	
9/18/15	8:38	PE	1.17	YRL			INFANT 2		BRIDGE	0	1	W
9/18/15	8:38	P	56	YRL	SLA		INFANT 2, INFANT 1, TXL, TH	4	BRIDGE	0	1	
9/18/15	8:38	P	57	TXL	CHA		INFANT 2, YRL, INFANT 1, TH	4	BRIDGE	0	1	

Note: Green line indicates the observed start of a play bout; the red line indicated the observed end of a play bout.