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Good Cop/Bad Cop: A comparative analysis of affiliative and aggressive behaviors by adult female and male olive baboons with infants at Randilen Wildlife Management Area, Tanzania

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SIT Study Abroad

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Definitions

Affiliative behaviors: well-intentioned behaviors that have been correlated to positive relationship building in previous studies (Bardi et al., 2004)

Aggressive behaviors: ill-intentioned behaviors that have been correlated to punishment, stress, or antagonization in previous studies (Bardi et al., 2004)

Estrus: a periovulatory state characterized by visible perineal swelling known as a "sexual swelling" (Higham et al., 2009; Weyher et al., 2014)

Lactation: a period of infant nursing characterized by active suckling or enlarged nipples (Higham et al., 2009)

Wildlife Management Area (WMA): An area for community-based wildlife conservation (The United Republic of Tanzania Board of Resource Management and Tourism, 2013)

Table 1: Behavior descriptions and categorization (Bardi et al., 2004; Moscovice et al., 2009; Silk et al., 2016**)*

Behavior	**Description**	**Categorization**
Carrying	Transporting an infant with the infant sitting or clinging on the adult's back	Affiliative behaviors
Grooming	The cleaning or maintenance of an infant's fur and skin	Affiliative behaviors
Ventral clinging	An infant clinging to its mothers ventrum (underside; abdomen)	Affiliative behaviors
Lip-smacking	Rapid and repetitive opening and closing of lips directed at an infant	Affiliative behaviors
Huddling	Embracing an infant closely with both arms	Affiliative behaviors
Manipulation	Using hands or feet to explore infant	Affiliative behaviors
Grunting upon approach**	Grunting when approaching an infant or another adult carrying an infant	Affiliative behaviors
Proximity	Sitting within arm's reach of an infant	Affiliative behaviors
Brow wipe	Rapid movement of hand across an infant's brow	Aggressive behaviors
Muzzle wipe	Rapid movement of hand across an infant's muzzle	Aggressive behaviors
Startling	Rapid jerking motion of the infant's body	Aggressive behaviors
Growling and snarling	Loud vocalizations and bearing of teeth intended to intimidate	Aggressive behaviors
Chasing*	Running in pursuit of an infant	Aggressive behaviors
Head bob and ground slaps*	Nodding of the head while slapping the ground to intimidate an infant	Aggressive behaviors
Lunging*	Attacking an infant suddenly	Aggressive behaviors
Biting*	Biting an infant; causing harm to an infant with one's teeth	Aggressive behaviors

Abstract

This study investigated the infant-directed behaviors of adult male and female olive baboons in Randilen Wildlife Management Area in April of 2022. The objectives were 1) To determine the difference between olive baboon males and females in frequency and duration of listed behaviors towards infants; 2) To classify the interactions of adult male and adult female olive baboons with infants as either primarily affiliative or primarily aggressive; 3) To determine the frequency of selected behaviors at different reproductive phases (lactation, estrus, neutral, indeterminant) amongst female olive baboons towards infants. A single baboon troop in Randilen Wildlife Management Area was observed over 8 days using continuous focal sampling.

It was found that females had a significantly greater quantity of affiliative interactions with infants than males (Degrees of Freedom=1, N=2, Fisher's Exact Test, $p=0.0004$). Females also spent significantly more time performing the behaviors ventral cling (Mann-Whitney U Test, $p<0.0001$), huddle (Man-Whitney U Test, $p<0.0001$), groom (Man-Whitney U Test, $p=0.017$), and carry (Man-Whitney U Test, $p=0.017$), with infants than males with infants. There was not a statistically significant difference in the durations males and females spent in proximity to infants (Man-Whitney U Test, $p= 0.498$). Both females and males had primarily affiliative relationships with infants (male-to-infant behaviors= 86.27% affiliative; female-to-infant behaviors= 100% affiliative). There was a significant difference in affiliative behaviors of females at different reproductive phases (Degrees of Freedom=1, N=2, Chi-squared Test, $p<0.05$). Females in estrus had proportionally more "Contact" behaviors versus "No Contact" behaviors than neutral females (Degrees of Freedom=1, N=2, Fisher's Exact Test, $p=0.047$) and lactating females did not have significantly different affiliative behaviors compared to neutral females. Lactating females performed the most affiliative behaviors on average (average number of affiliative behaviors: Lactating= 8.75, Estrus= 2, Neutral= 1.94).

Recommendations for future research include repeating this study with a greater sample size and longer observation period. This study could also be performed with infants as the focal subjects. Rather than observing and recording observations of a focal adult interacting with infants, more meaningful data might be drawn from recording how a focal infant interacts with male and female adults. More data could potentially be collected and fewer interactions between infants and adults would be overlooked.

Chapter 1: Introduction

1.1 Background Information

Primates are incredibly intelligent and social creatures (Opie et al., 2012). They live in complex societies where several social variables have contributed to the evolution of certain behaviors (Kappeler & Van Schaik, 2002; Opie et al., 2012). Such societies are organized in five different forms: monogamy, polygyny, polyandry, polygynandry, and solitary individuals (Kappeler & Van Schaik, 2002; Smuts et al., 1987). These forms describe the mating system of a population- a mated pair-bond, a single male with multiple females, a single female with multiple males, multiple females with multiple males, and a lone individual, respectively (Kappeler & Van Schaik, 2002). Depending on the mating system of a population, the behaviors employed to enhance one's reproductive success, and therefore their fitness, vary greatly. For example, in monogamous pair-bonded callitrichids, obligate paternal care includes infant-carrying which requires a high level of investment and is crucial to male fitness (Dunbar, 1995; Kappeler & Van Schaik, 2002). Conversely, in a polygynous society where a male mates with multiple females, males will likely invest in their offspring less because they have access to multiple other reproductive opportunities (Dubuc et al., 2014; Kappeler & Van Schaik, 2002). Rather than spending energy on ensuring the survival of one infant, a male can instead optimize his reproductive success by producing many infants and investing little in the care of each (Dubuc et al., 2014; Kappeler & Van Schaik, 2002). The mating system of a primate population thus informs how an adult will interact with and invest in their offspring.

Olive baboons live in polygynandrous societies which entail multiple females mating with multiple males (Smuts et al., 1987). Their behaviors reflect what is advantageous to their fitness in such a system and various behaviors have evolved based in simple questions of costs versus

benefits. If a male in a polygynandrous mating system is investing time and energy into infant caretaking, he is ensuring the safety of his offspring but at the cost of losing other potential mating opportunities (Kappeler & Van Schaik, 2002). Trade offs of costs and benefits also exist in female behaviors, for example regarding infant carrying. In a polygynandrous society where males tend to invest less, females carry infants more frequently (Altmann & Samuels, 2018; Darling et al., 1998). If a female baboon decides to carry her growing infant as her troop is travelling, she ensures the infant will not get left behind. This is at the cost of additional energy expenditure bearing the weight of the infant (Altmann & Samuels, 2018; Darling et al., 1998). If the female chooses not to carry her offspring, however, the additional energy expenditure of producing more milk for an active infant will also be a significant cost (Altmann & Samuels, 2018). The female's decision to carry her infant will be dependent on her offspring's age, size, locomotor independence, nutritional independence, the level of paternal investment, and other variables (Altmann & Samuels, 2018). The polygynandrous mating system in olive baboon troops therefore shapes how males and females interact with their infants and what behaviors will be advantageous to their own fitness.

Specific factors that influence adult interactions with infants are reproductive phase in females and paternal certainty in males. In females, hormone levels that fluctuate at different stages in their reproductive cycles greatly affect infant directed behaviors (Bardi et al., 2004). Quality and quantity of affiliative behaviors- those that are conducive to positive relationship building- were found to be unequivocally associated with changes in sex steroid and cortisol levels (Bardi et al., 2004). Additionally, stress-related or aggressive behaviors and reduced infant contact is also associated with cortisol levels (Bardi et al., 2004). Hormone levels, and therefore stage in a female's reproductive cycle, have major influence on adult female-to-infant interactions. As hormone levels fluctuate, the number of affiliative or aggressive behaviors may fluctuate.

An adult male olive baboon will decide his level of involvement and his behavior towards an infant primarily based on how certain he is that he has sired that infant (Busse & Hamilton, 2017; Langos et al., 2013). Paternal certainty is predicted based on the timing of previous copulations and based on potential mate guarding efficacy (Langos et al., 2013). Another mechanism that contributes to paternal certainty is the formation of relationships with females by secondary males- males other than an infant's father- also called "friendships" (Städele et al., 2019). A study of friendships in *Papio anubis* found that a mother's two closest associates during lactation following a previous birth included the sire of the next offspring 77% of the time (Städele et al., 2019). Such friendships influence a male's behavior towards females and their infants and are characterized by high levels of proximity, grooming, and support, with low rates of aggression (Moscovice et al., 2009; Städele et al., 2019). Thus, understanding the effects of paternal certainty in a polygynandrous society is necessary to interpreting how males interact with females and with infants.

1.2 Problem Statement

Throughout the animal kingdom, varying organizations of sociality govern how different species interact within their communities. Amongst all animal classes, 'core units' describe cohesive groups of closely associated individuals where primary social interactions occur (Grueter et al., 2020). In mammals especially, the compositions of core social units in different species are incredibly diverse (Grueter et al., 2020). For example, in African elephants and sperm whales, core units include closely associated breeding females and their calves; in Hamadryas baboons, core units consist of single-male, multi-female harems; in reticulated giraffes, core unit composition is variable throughout the species (Grueter et al., 2020). These varying organizations dictate how animals and their closest associates behave with regards to spatial distribution, feeding competition, mating competition, and all other elements of conspecific interaction (Grueter et al., 2020).

Amongst primate species, diversity of social organization further intensifies. The three primary recognized social organizations in primates include pair-living, neighborhood and solitary-living, and group-living species (Kappeler & Van Schaik, 2002; Smuts et al., 1987). This high level of diversity allows for variation in distribution patterns, grouping and mating systems, and type and quality of social relationships (Kappeler & Van Schaik, 2002). Within these social organizations exist five primary mating systems which influence the behaviors that will optimize an individual's fitness (Kappeler & Van Schaik, 2002). The intricacies of conspecific primate behavior therefore are affected by a myriad of multilevel social variables that are not yet fully understood in existing research.

On the individual level, the cumulative result of these social complexities is manifested in each behavior. Analyzing different behaviors has implications for understanding the sociality of a species and for the evolution of sociality broadly (Grueter et al., 2020; Opie et al., 2012). Specific interactions that require further investigation include that between adults and infants as they have particular importance to understanding reproductive success in different mating systems. Research on adult and infant interactions in olive baboons is lacking and previous research calls for a more in-depth analysis of the nature of adult male-to-infant relationships specifically (Städele et al., 2019). The behaviors of adult males with infants in the presence of females at different ovulatory phases also requires further research (Higham et al., 2009). Additionally, insufficient research has been done comparing male and female infant-directed behaviors and how those behaviors change throughout a female's reproductive cycle. This research sought to fill this gap by analyzing the nature of adult-to-infant interactions in both sexes and amongst females at different reproductive phases.

1.3 Significance

Understanding the behaviors of primates offers insight to the evolution of hominin sociality (Grueter et al., 2020; Opie et al., 2012; Städele et al., 2019). Monogamy is theorized to have evolved from a polygynandrous ancestral species (Opie et al., 2012) and this study contributes to the academic discussion of human and non-human sociality by analyzing interactions within a polygynandrous mating system. Not only will understanding social interactions of polygynandrous species offer insight to the evolution of early hominin sociality, but it will also supplement our interpretation of modern human social interactions. This research therefore contributes to a multidisciplinary discussion with implications in fields of anthropology, biology, psychology, and sociology.

1.4 Justification

Adult male-to-infant interactions in olive baboons have been studied insufficiently (Busse & Hamilton, 2017; Städele et al., 2019). Much research exists on maternal behavior in primates including in olive baboons (Altmann & Samuels, 2018; Bardi et al., 2004; Frank & Silk, 2009), but comprehensive analyses comparing the sexes are scarce. Investigating the nature of relationships between adult males and infants was necessary to understand the benefits and/or detriments a male's presence may have to an infant's development. This, as well as a comparison of the sexes, were necessary to having a more complete knowledge of olive baboon sociality and troop dynamics. Previous research also called for further study of intra-specific male behavior relative to a female's reproductive state (Higham et al., 2009). This study supplements existing knowledge on maternal relationships, discusses the implications of the female reproductive cycle on such interactions, provides new insight to adult male and infant relations, and provides novel analyses comparing how the sexes behave with infants.

1.5 Scope

This study was concerned with the behavior between adults and infants of the species *Papio anubis*. The behaviors recorded were limited to a predetermined list (Table 1) and there was an equal number of affiliative and aggressive behaviors being evaluated. Nursing by mothers was not counted because it is solely a female behavior. Each individual was attempted to be observed for a 15-minute focal period, however, many focal periods were interrupted if the individual moved out of sight. The observations were limited to adult females with infants and adult males with infants, hence excluding interactions involving sub-adults and juveniles. This study was isolated to a single baboon troop in Randilen WMA. The subjects were known to be a resident troop that had a consistent presence in the area. Observation only occurred during the morning approximately 6:30 AM until 10 AM, and evening approximately 4 PM until 8 PM. Observing where the baboons retired for the night and beginning observation as they woke helped track the troop and ensure the same troop was analyzed throughout the study. This study did not include any behaviors occurring at peak temperatures in the afternoon or after the troop has ascended for the night

1.6 General Objective

i. To better understand the interactions of male and female adult olive baboons with infants at Randilen Wildlife Management Area

1.7 Specific Objectives

i. To determine the difference between olive baboon males and females in frequency and duration of listed behaviors towards infants (Table 1)

ii. To classify the interactions of adult male and adult female olive baboons with infants as either primarily affiliative or primarily aggressive

iii. To determine the frequency of selected behaviors at different reproductive phases (lactation, estrus, neutral, indeterminant) amongst female olive baboons towards infants

1.8 Hypotheses

i. Infant-directed behaviors will be significantly different between adult males and females with male interactions being primarily aggressive and female interactions being primarily affiliative. This is because maternity is certain, and a mother will be inclined to promote the health of her infant; whereas paternal uncertainty will incline males to harass infants they believe to be sired by other males.

ii. Females will exhibit significantly more affiliative behaviors during lactation than during estrus or neutral phases of the reproductive cycle. This is because sex hormone levels change dramatically during this period and estrogen levels are correlated to increased affiliative maternal behaviors (Bardi et al., 2004).

Chapter 2: Literature Review

2.1 Adult Female and Infant Interactions

Much research has been conducted regarding maternal investment. Altmann and Samuels (2018) investigated the maternal costs of infant carrying and assert that infant carrying is the costliest form of parental care after lactation. They described how mothers carry neonates continuously and rarely carry infants over the age of eight months (Altmann & Samuels, 2018). Their study on maternal costs of infant carrying found that the proportion of time that an infant is carried steadily declines as they age (Altmann & Samuels, 2018). Also, the likelihood of a mother carrying her infant does not change significantly with time of day nor season and the likelihood of a non-mother carrying an infant is low (Altmann & Samuels, 2018). Previous research has also indicated that adult females are more likely to groom mothers with an infant than non-mothers (Frank & Silk, 2009). Similarly, adult females are fourteen times more likely to grunt upon approaching other females that are carrying infants compared to those without infants (Silk et al., 2016). Silk et al. (2016) observed that grunting upon approach of a mother with an infant also increased the likelihood of the approaching female handling that infant by forty-eight times and was correlated to a lower likelihood of aggression.

Other studies of female behavior investigate a range of adult female-to-infant interactions and their correlation to hormone levels (Bardi et al., 2004; Wittig et al., 2008). In their study, Bardi et. al. (2004) found that adult female-to-infant grooming interaction is common. Grooming is the cleaning of the skin and fur of an individual and is a maintenance behavior found to be highly correlated to affiliative relationship building (Bardi et al., 2004; Wittig et al., 2008). Grooming is highly kin biased, meaning relatives are more likely to groom each other than nonrelatives, and grooming is more commonly directed at females (Wittig et al., 2008). Grooming is also correlated to glucocorticoid levels, an indicator of stress (Wittig et al., 2008). During periods of social

instability, glucocorticoid levels increase and females reduce the diversity of their grooming to a smaller group of preferred partners (Wittig et al., 2008). Grooming then contributes to alleviating social stress and decreasing glucocorticoid levels (Wittig et al., 2008). Other behaviors such as brow wipe, muzzle wipe, and startle have been linked to the acting mother's increasing stress and anxiety levels (Bardi et al., 2004). These behaviors, amongst many others, were found to be correlated to the involved female's cortisol and sex steroid hormone levels which fluctuate at different phases of their reproductive cycles (Bardi et al., 2004). It was therefore necessary for this research to note any indications of intense social stress in the troop and the interacting female's ovulatory state (lactation, estrus, neutral, or indeterminant) as it has contributed to interpreting behavioral data results.

2.2 Adult Male and Infant Interactions

The interactions of male olive baboons and infants lack substantial, specific research. A study by Städele et al. (2019) researched a prominent method of parental investment in male olive baboon in the form of "friendships" with an infant's mother- relationships between a mother and a non-father. In friendships, males spend more time in proximity to the mother and infant providing protection against feticide and infanticide (Cheney et al., 2015; Moscovice et al., 2009). Such relationships are also characterized by increased frequency of grooming and decreased aggression (Städele et al., 2019). Males in friendships with a female engage in affiliative infant-directed behaviors more frequently, including infant-carrying (Moscovice et al., 2009). Another primary form of paternal care that exists associated with friendships and with a male's own kin is intervention and support in aggressive disputes (Moscovice et al., 2009).

Males spend much less time carrying infants than females (Altmann & Samuels, 2018). Male carrying is observed in savanna baboon species, but is poorly understood (Busse & Hamilton,

2017). Primary hypotheses suggest male infant carrying is a mechanism used by adults to prevent attacks by other males, or that it is a protective behavior performed by males on infants they have likely sired (Busse & Hamilton, 2017). A study on wild chacma baboons analyzed the relationship between paternity and male infant carrying and found that males tended to carry their probable offspring (Busse & Hamilton, 2017). This supported the hypothesis that male carrying effort is a protective behavior, not and exploitative behavior (Busse & Hamilton, 2017). This study called for further research of male infant carrying in olive baboons (Busse & Hamilton, 2017).

A publication on male-driven grooming in baboons noted that adult male grooming behaviors are predominantly directed towards adult females as a mating effort (Weyher et al., 2014); however, Städele et al. (2019) found that grooming, and other affiliative efforts within friendships during non-receptive periods are a parenting effort, not a mating effort. Weyher et al. (2014) found that male-driven grooming is not significantly correlated to the time of day nor the reproductive state of the involved female (Weyher et al., 2014). Male-driven grooming also does not increase with the presence of an infant (Weyher et al., 2014).

Aggressive behaviors of males towards females and infants include agonistic buffering, infanticide, growling or snarling, chasing, and other forms of harassment (Moscovice et al., 2009). Agonistic buffering is the use of an infant to avoid conflict- a subordinate male will hold an infant above his head or carry an infant when approaching a dominant male as to ensure he is not attacked (Busse & Hamilton, 2017). Other aggressive behaviors are directed at non-kin and in severe, rare, cases, include infanticide (Zipple et al., 2017). Zipple et al. (2017) cites the prevailing theory that infanticide benefits a male's fitness by accelerating a female's ovulatory cycle and returning a lactating female to a sexually receptive state. This would then provide the infanticidal male with

an additional mating opportunity. The risk of infanticide is greatest when a mother is lactating (Moscovice et al., 2009).

2.3 Implications for This Study

Past research provided insight as to how this study my be impactful to understanding the evolution of human sociality. A previous study of olive baboons revealed that a relationship between a mother and the sire of her offspring that persists through the period when she is not sexually receptive increases the male's chances of siring her next offspring (Städele et al., 2021). This implies that a male who maintains a relationship with a female during non-receptive periods may have greater reproductive opportunities and therefore will have increased fitness. This could indicate the emergence of long-term breeding bonds from a polygynandrous mating system. Therefore, the theory that monogamy evolved from a polygynandrous ancestral species must be further investigated and understanding the relationships between males, females, and infants is crucial to that investigation.

Review of previous research also revealed potential pitfalls in data collection methods that this study prepared for and attempted to avoid. Research that employed broad, troop-wide, continuous observation reported inconsistency in their ability to record all behaviors, especially if interactions occurred simultaneously amongst multiple individuals. For this reason, focal sampling techniques that have been successful in other research (Fedurek & Lehmann, 2017; Frank & Silk, 2009; Moscovice et al., 2009; Rose, 2000) were employed. These previous studies, amongst other publications, were critical to informing what gap exists for this study to fill, what techniques were most suitable for data collection, and what background information was necessary to further investigate the relationships between male and female baboons with infants.

Chapter 3: Methodologies

3.1 Study Area: Randilen Wildlife Management Area

Randilen WMA is located in the Monduli district of the Arusha region in northern Tanzania, Figure 1(Tanzania Tourist Board, n.d.). The area is governed by eight Maasai villages that interact with the wildlife in the form of anti-poaching measures, herd grazing, and human-wildlife conflict mitigation techniques that prevent wildlife from invading village crops. Mitigation techniques that directly affect wildlife include the use of chili bombs, flashlights, throwing stones, and thorned fencing; however, the villagers cited elephants and some ungulates as the primary intruders, not baboons (Personal communication, February 2022). This information was collected during interviews conducted in February of 2022 with a Maasai tribe living in Randilen WMA. Other anthropogenic activity includes tourist camping, tourist game drives, sightseeing walks, and six tourist lodging complexes (Tanzania Tourist Board, n.d.).

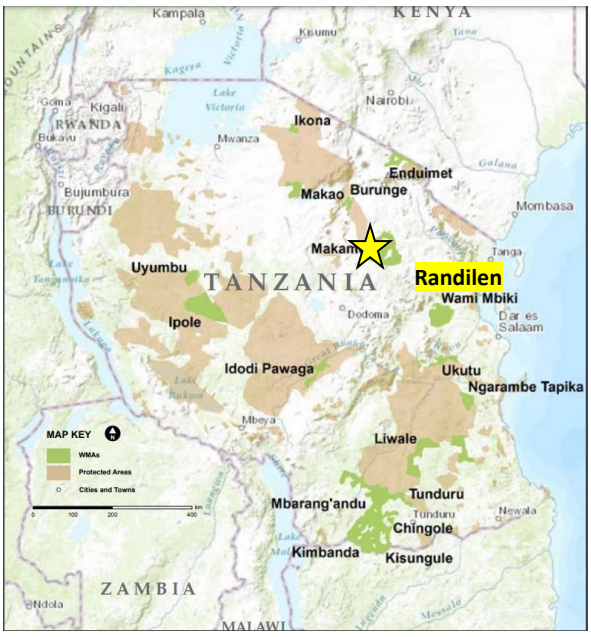

Figure 1: WMAs in Tanzania

Randilen WMA occupies 31,200.68 hectares of land in a woodland savanna type ecosystem (Tanzania Tourist Board, n.d.). Mammal species personally documented in Randilen WMA include olive baboons, zebras, vervet monkeys, impalas, warthogs, giraffes, wildebeests, buffalos, dik-diks, gazelles, jackals, mongooses, and elephants. During data collection all these species, except vervet monkeys, were observed as well as bush bucks, water bucks, and

hyrax. The bush bucks, water bucks, warthogs, and hyrax were observed near the baboon troop and occasionally interacting with the baboons during data collection.

There were two primary locations where the baboons were observed- a large, dried riverbed (Figure 2) and a rocky hill called "Sunset Hill" (Figure 3). At Sunset hill it is notable that the area was surrounded by tall grass that hosted a high density of ticks. It is also notable that at Sunset Hill, many focal periods were interrupted as baboons went out of view. Rocks and trees in the area made this made data collection more difficult, however much data was still recorded.

Figure 2: Riverbed Location

Figure 3: Baboons sitting on Sunset Hill

The wet season in the Monduli district occurs between November and May, which included the study period in early to mid-April (*April Weather in Moduli, Tanzania*, n.d.). In April, the probability of precipitation ranges from 36-44% and the average monthly rainfall is 105mm (*April Weather in Moduli, Tanzania*, n.d.). During the time of data collection, the average high temperature was 26ºC and the average low temperature was 16ºC; the peak temperatures occurred between 2 PM and 7 PM (*April Weather in Moduli, Tanzania*, n.d.). Data collection was impacted by heavy rain during one observation period on day 6 of data collection.

Randilen WMA was chosen to be the study area because it fits the following criteria: the area is known to have a consistent presence of a large resident troop of baboons, the baboons have minimal human contact, they are free-range and not enclosed in any way, and they have little

contact with man-made items or structures. Other sites that were considered, such as outside of the gates at Ngorongoro National Park or Lake Manyara National Park, were disqualified from consideration because the baboons travel down paved roads interacting with cars and people and spend time in human populated areas. For this study, baboon behavior was intended to be studied with as little anthropogenic interference as possible.

3.2 Study Design

This was an observational study that was both quantitative and qualitative in nature. Behavior frequency and duration will be the basis of quantitative analysis and contextual observations will be the basis of qualitative analysis. Throughout the data collection period, a single baboon troop will be tracked. To ensure a single troop remained the focus of this study, observation stopped when the troop nested and began as they woke up. An understanding of the baboon troop's home range assisted in assuring the same troop was studied each day. Identifying the troop was made easy after the first observation period because there was a male and female with partial albinism. They were conspicuous and helpful in identifying the study troop.

Individuals were observed at different times of the day- morning and night. The baboons were not observed in the afternoon because this troop was known to hide in shaded areas during the hottest hours of the day. This was found to be accurate during this study. The same number of females and males were be observed, and a predetermined list of behaviors (Table 1) as well as contextual observations were recorded. This was a case study that reflects behaviors and trends associated with polygynandrous social structures in many species.

3.3 Sample Size

An accurate count of the entire baboon troop was not established. The troop often had some individuals in plain view and some individuals out of view in tall grass or trees. During a seemingly spontaneous stampede through the riverbed on day 3 of data collection, 168 individuals were

counted. This is an underestimate of the total population size because several individuals were likely missed, however it can safely be reported that the troop was at least 168 individuals. What provoked the stampede was not confirmed.

An equal number of adult females and males were observed- 33 females, 33 males, 66 total adults. This study intended to observe each subject for a 15-minute focal period, but as expected many subjects moved out of view during their observation. Only 38.8% of focal subjects completed a 15-minute focal period uninterrupted.

3.4 Sampling Techniques

Random focal sampling was employed for data collection. Observation focused on a single individual for a continuous 15-minute observation period and only the interactions involving that individual was recorded. To ensure each focal subject was selected randomly, a random number generator was used, and adults were counted from left to right until that number was reached (e.g., if the number generator read "46", adults were counted from the left-most individual until the 46th individual was reached and that would be the randomly selected focal subject). Only behaviors described on the predetermined list (Table 1), ovulatory phase in females, and relevant contextual observations were recorded. Focal observation was conducted on an equal number of adult females and males.

Observation began early in the morning (approximately 6 AM), a break occurred in the afternoon during peak temperatures, observation resumed in the evening (approximately 4 PM) and ended when the baboons return to trees to nest, or it became too dark. To ensure one troop of baboons was the focus of this study, it was documented when they woke up, when they went to sleep, and where they went to sleep. This study troop also included two baboons with partial albinism that aided in the identification of the troop. Observation occurred over the span of 8 days.

During observation, the observer used a voice recorder and written notes to efficiently collect data and record all observations in real time. Along with recording behavior frequency, sex involved, duration, and contextual observations, the stage the involved female was at in her reproductive cycle was be classified (lactation, estrus, neutral, or indeterminant) because previous studies demonstrate hormone levels during these periods have a significant impact on adult female-to-infant behavior (Bardi et al., 2004). Reproductive phase was classified based on observing active nursing of an infant or enlarged nipples (lactation stage), the presence of a sexual swelling (estrus stage), or neither of these physiological indicators (neutral stage). If the reproductive stage could not be determined (indeterminant), observations as to why a classification could not be made were recorded.

3.5 Methods

The method of data collection was continuous focal observation of a randomly selected individual. A randomly generated number was used to select the first focal subject. The focal subject was observed for a 15-minute period and all behaviors listed in Table 1 were recorded. Focal sampling was selected for this study because previous primate research has found it to be an efficient technique in measuring individual activity budgets (Gilby et al., 2011). Scan sampling is also a common technique employed in behavioral studies, but it is best used when analyzing a particular behavior throughout a group rather than multiple behaviors of an individual (Gilby et al., 2011). During the 15-minute observation periods, continuous focal sampling was employed rather than interval focal sampling. This implies that observations were recorded throughout the focal period rather than recording only what was happening instantaneously upon an interval of time (e.g., recording behaviors every five minutes). Although interval focal sampling has been found to be more time efficient, it risks missing brief behaviors that could occur between observation intervals (Rose, 2000). It was important to this study that brief interactions were not

overlooked because agonistic behaviors are often of very short duration (Fedurek & Lehmann, 2017); however, previous research has found both continuous and interval focal sampling to yield similar estimates of primate activity budgets (Rose, 2000).

3.6 Data Collection Instruments

A voice recording device (Olympus VN-541 PC) was used to ensure all observations were recorded in real time. It proved to be very helpful in ensuring continuous observation was not interrupted to write information down. A notebook was used to record observations after a focal period ended and to compile data from the voice recorder. Binoculars (Nikon Trailblazer) and a camera (Nikon Coolpix B500) assisted with visibility and allowed documented behaviors to be captured and further analyzed after data collection. Park Ranger Lobulu assisted with his knowledge of the park geography and of the movements of the target study troop. A four-wheel-drive vehicle (Daihatsu Terios 2006) was used for transportation within the park both on paths and off-road. The vehicle used during the study period proved to be ill-equipped for the road and off-road conditions which interfered with data collection on day 6 and 7.

3.7 Data Analysis

The three sets of data that were analyzed include the duration of male-to-infant behaviors compared to female-to-infant behaviors, the quantity of those interactions, and the quantity of infant-directed behaviors comparing females in categories “estrus”, “lactation”, or “neutral”. Pearson’s Chi-squared Test, Fisher’s Exact Test, and the Mann-Whitney U Test, a nonparametric t-test, were employed. In the Chi-squared test (Equation 1), O represents the observed values and E represents the expected values. In Fisher’s Exact Test (Equation 2), letters a, b, c, and d represent values from a contingency table and n represents the total frequency. ‘p’ is the P-value.

Equation 1: Chi-Squared Test

$$\chi^2 = \sum \frac{(O_i - E_i)^2}{E_i}$$

Equation 2: Fisher's Exact Test

$$p = \frac{(a+b)!\,(c+d)!\,(a+c)!\,(d+b)!}{a!\,b!\,c!\,d!\,n!}$$

Limitations to using the Chi-squared Test included that at least 80% of calculated expected values had to be greater than 5, the test could not apply to averages, and it could not be applied to continuous variables, such as time. The Fisher's Exact Test was useful in analyzing smaller data sets. It also could not be applied to averages or continuous variables, but it could be applied to small data sets where the Chi-square Test was ineffective. The Mann-Whitney U Test could be applied to continuous variables with sample sizes greater than 5. These tests were helpful in determining if the difference between multiple data sets was due to sampling or if it was likely due to some other acting variable. The Chi-Squared Test and Fisher's Exact Test were applied to the quantities of infant-directed behaviors by males and females and of females at different reproductive stages. The Mann-Whitney U Test was applied to the durations of each behavior.

When comparing the quantities of affiliative behaviors performed by males or females, two approaches were taken to interpret data. Some of the affiliative behaviors (Table 1) had too little data to be properly analyzed. To interpret the data, a Chi-Squared test was applied to only the behaviors that had sufficient sample sizes- ventral cling, huddle, and proximity- excluding the other affiliative behaviors. It is important to note that "lip-smack" was excluded from all calculations because it was not performed by either sex during data collection. In attempt to include the data of all other affiliative behaviors, a second approach was grouping behaviors into "Contact Behaviors" (huddle, ventral cling, carry, groom, and manipulate) and "No Contact Behaviors"

(proximity and grunt upon approach). Chi-squared analysis was performed comparing behavior quantities of males and females with respect to these two groups.

When comparing the quantity of affiliative behaviors amongst females in estrus, lactating females, and neutral females, both statistical tests were used. First, Chi-squared Test was applied to compare all three groups with respect to Contact and No Contact behaviors. Then, Fisher's Exact Test was applied to neutral females versus females in estrus with respect to Contact and No Contact behaviors, and in another test, with respect to all behaviors that had sufficient data (carry, huddle, groom, ventral cling, and proximity). These two tests were also done comparing the infant-directed behaviors of neutral females to lactating females.

The Mann-Whitney U Test was employed to analyze how the durations of each infant-directed behavior differed comparing females and males. The test was applied to each behavior that had sufficient data including huddle, proximity, ventral cling, groom, and carry. The other affiliative behaviors and the aggressive behaviors did not have large enough sample sizes to use this test.

3.8 Ethical Considerations

Considerations of baboon disturbance and environmental disturbance were of primary concern. To minimize baboon disturbance, there was no direct interaction with the baboon troop and noise was kept to a minimum. Observations were made from a reasonable distance as to reduce disturbance of the troop while still being positioned for effective data collection. Walking was preferred over driving as to reduce carbon emissions and auditory disturbance. The Sunset Hill location the baboons often resided at was within walking distance of the ranger's post. Off-road driving was necessary, however established paths were utilized when available as to reduce damage to the vegetation. The "leave no trace" rules were employed while camping during the data collection period on location- all trash brought in was carried out, human waste disposal was

contained to existing lavatories, and general efforts to minimize the environmental impact of camping were enacted.

Chapter 4: Results

4.1 General data

The total active observation time was 636.71 minutes. 33 males and 33 females were observed. Of the 66 focal periods, 38.81% lasted their full duration of 15 minutes uninterrupted. The focal periods cut short were primarily stopped due to the focal subjects moving out of view (e.g., moving behind rocks or trees). 25 of the 66 focal subjects (37.31%) had no infant interactions for the duration of their focal period. Of the females, 18% were in estrus, 12% were lactating, 55% were classified as neutral, and 15% could not be classified (Figure 4).

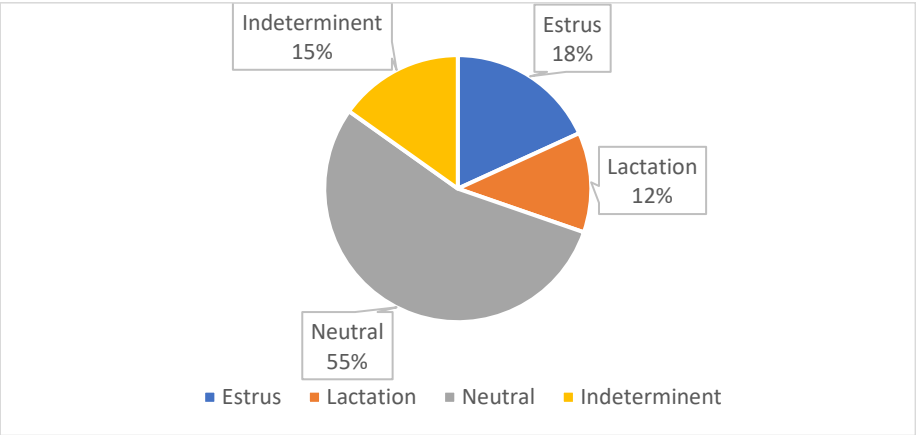

Figure 2: Distribution of Reproductive Phases Amongst Observed Females

4.2 Objective #1: To determine the difference between olive baboon males and females in frequency and duration of listed behaviors towards infants (Table 1).

Adult female and male olive baboons were determined to engage in affiliative and aggressive behaviors with infants in different proportions. 100 affiliative behaviors and 0 aggressive behaviors were recorded for females. 44 affiliative and 7 aggressive behaviors were recorded for

males. These data reflect significant difference not due to chance or random sampling (degrees of freedom=1, N=2, Fisher's Exact Test, p= 0.0004).

Males versus Females- Behavior Quantities

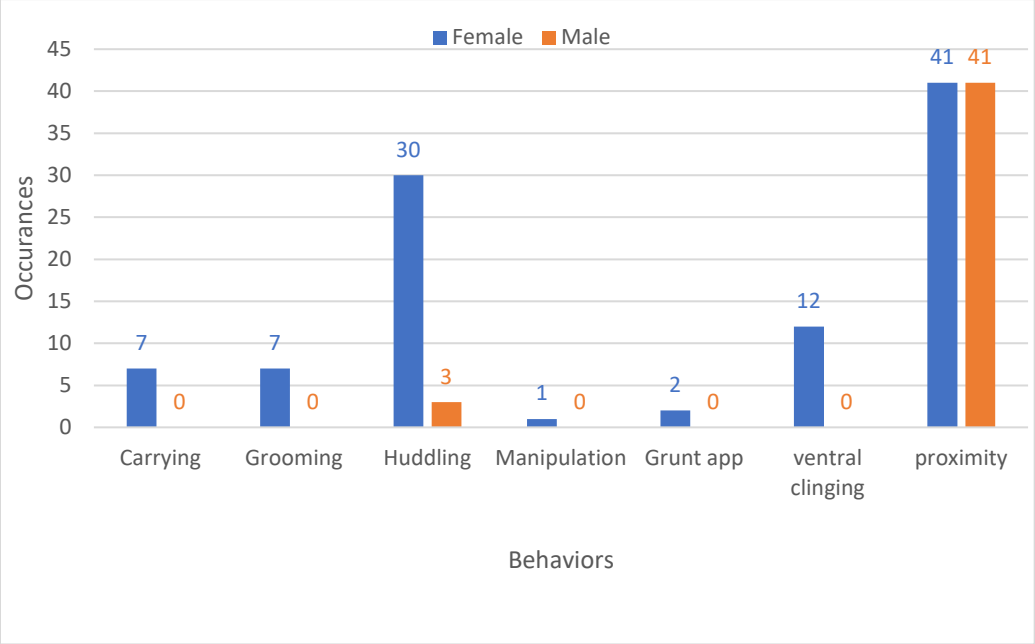

Figure 3: Quantities of Each Affiliative Behavior

Females had proportionally more affiliative behaviors than males. When analyzing the occurrences of specific affiliative behaviors, only the categories "Huddle", "Cling", and "Proximity" (Figure 5) had sufficient data to apply a Chi-squared Test.

This test determined that there was a significant difference in the quantity of these behaviors not due to chance (degrees of freedom=2, N=3, Chi-squared Test, $p<0.001$). There was found to be a significant difference between males and females in the quantities of Contact and No Contact behaviors (degrees of freedom=1, N=2, Chi-squared Test, $p<0.001$). There was insufficient data to analyze aggressive behaviors; 0 aggressive behaviors were recorded for females and 7 aggressive behaviors were recorded for males.

Males versus Females- Behavior Durations

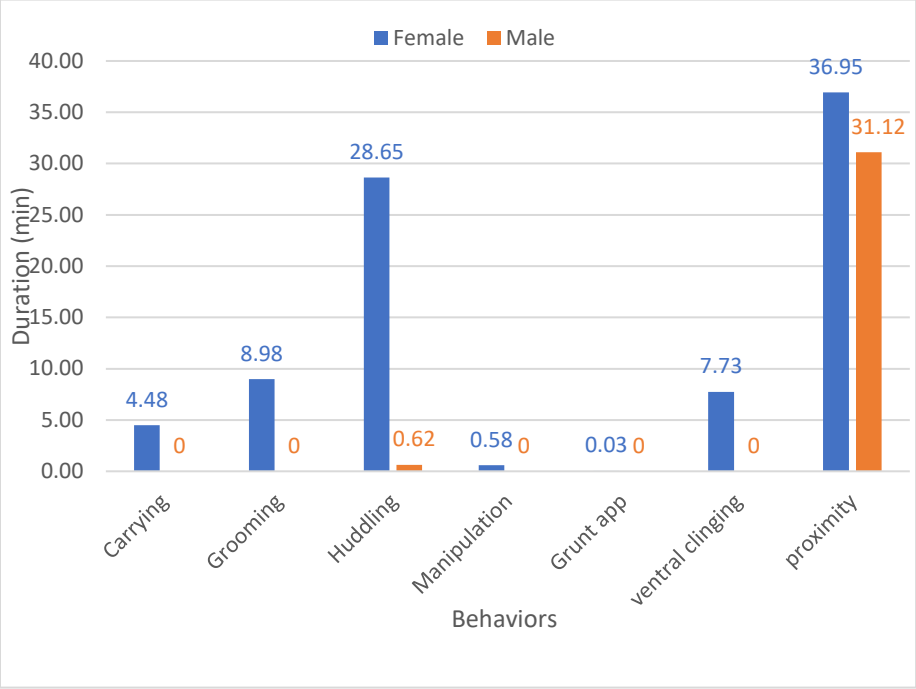

Figure 4: Total Durations of Each Affiliative Behavior (min)

Difference was also noted in male and female time budgeting regarding infant interaction. Adult females spent 87.38 minutes performing affiliative behaviors, 180.79 minutes not interacting with infants, and no time performing aggressive behaviors out of their total 268.17 minutes of observation (Figure 10). Males spent 31.73 minutes engaged in affiliative interactions, 0.283 minutes engaged in aggressive interactions, and 337.50 minutes not interacting with infants out of their total 368.51 minutes of observation (Figure 11). To compare, females spent 32.59% of their time performing affiliative infant-directed behaviors whereas males spent 8.61% of their time. Females spent 0% of their time performing aggressive behaviors and males spent 0.077% of their time. Females also spent more time on average performing each affiliative behavior (Figure 7) and had a greater diversity of affiliative behaviors (Figure 8; Figure 9).

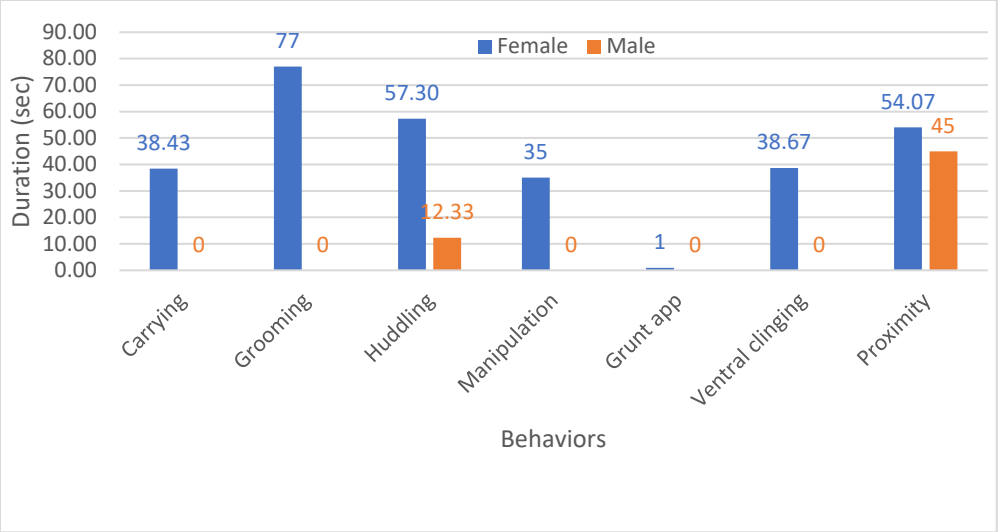

Figure 5: Average Duration of Each Affiliative Behavior (sec)

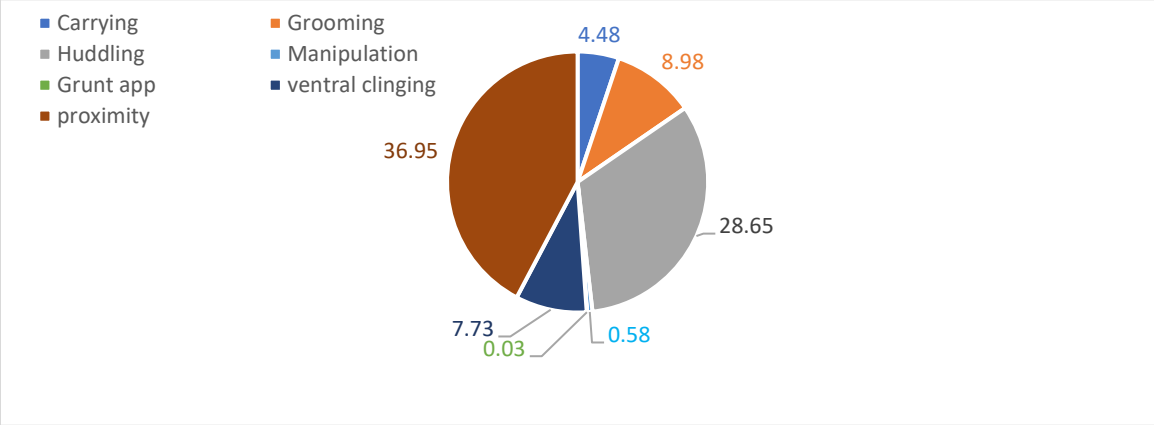

Figure 6: Time of Female Affiliative Behaviors (min)

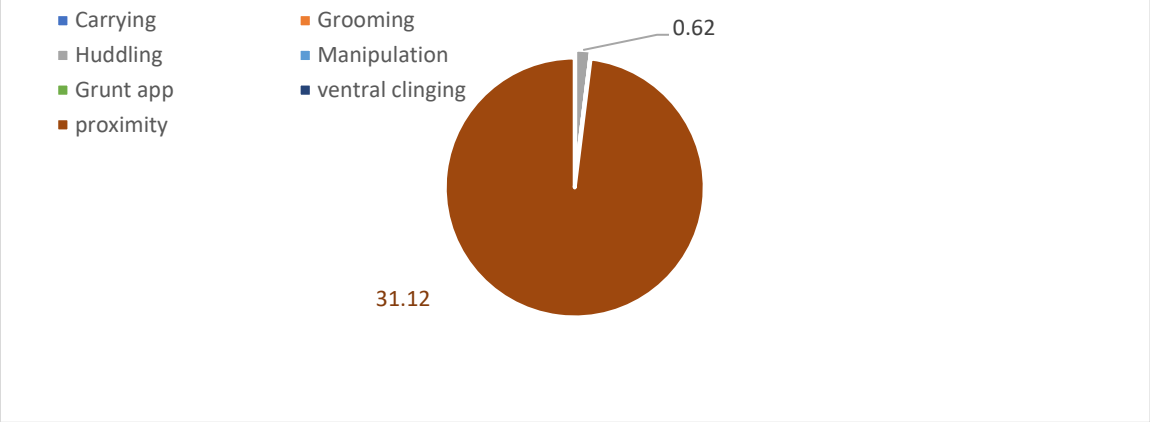

Figure 7: Time of Male Affiliative Behaviors (min)

When comparing the amount of time males and females spent engaged in each affiliative behavior with infants, the Mann-Whitney U Test yielded significant results. Females engaged in infant carrying (Mann-Whitney U Test, $p=0.017$), grooming (Mann-Whitney U Test, $p=0.017$), huddling (Mann-Whitney U Test, $p<0.0001$), and ventral clinging (Mann-Whitney U Test, $p<0.0001$), significantly more than males with infants. Males and females, however, were in proximity to infants for similar total durations (Mann-Whitney U Test, $p=0.498$).

4.3 Objective 2: To classify the interactions of adult male and adult female olive baboons with infants as either primarily affiliative or primarily aggressive.

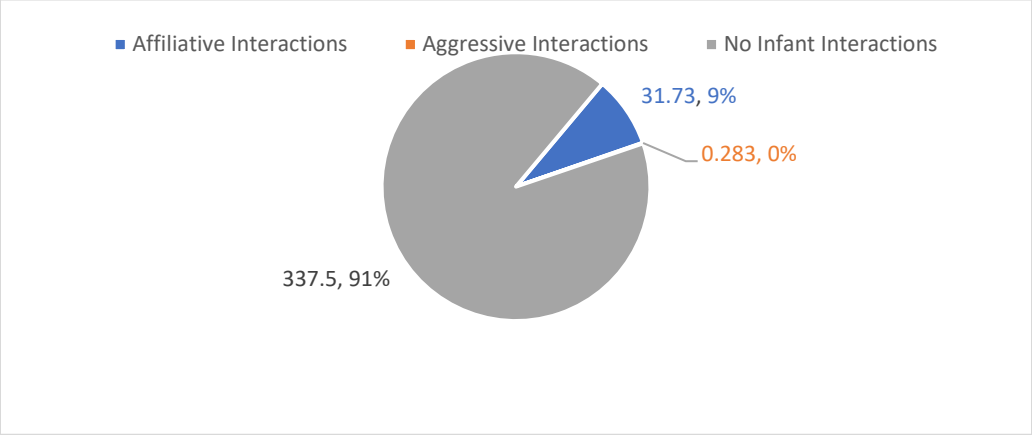

Figure 8: Total Male Observation Time (min)

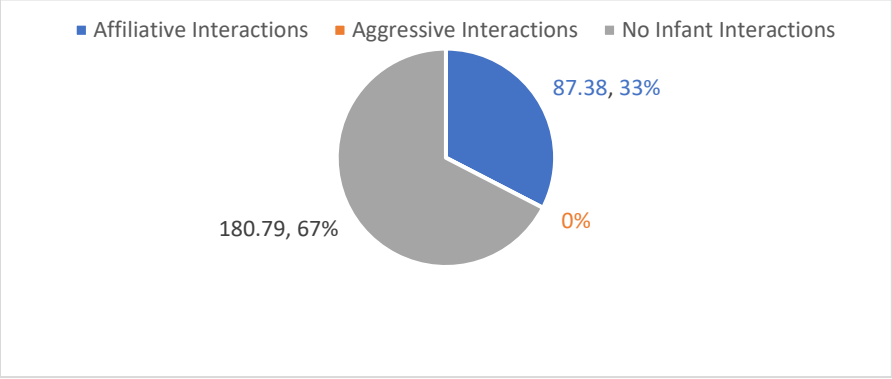

Figure 9: Total Female Observation Time (min)

A larger percentage of the total female observation time included affiliative behaviors (32.59%) compared to males (8.61%) and a larger percentage of the total male observation time included no infant interaction (91.31%) compared to that of the females (67.41%) (Figure 10; Figure 11). Of the time females were interacting with infants, 100% of the time and 100% of the interactions were affiliative behaviors (Figure 12). During the time males were interacting with infants, 99.1% of the time and 86.27% of the interactions were affiliative behaviors (Figure 13). 13.73% of the time males were interacting with infants was aggressive behaviors.

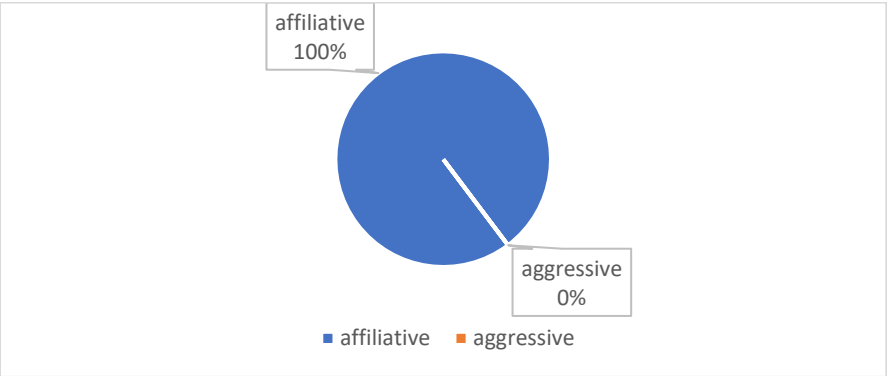

Figure 10: Proportion of Affiliative and Aggressive Behavior Quantities (female)

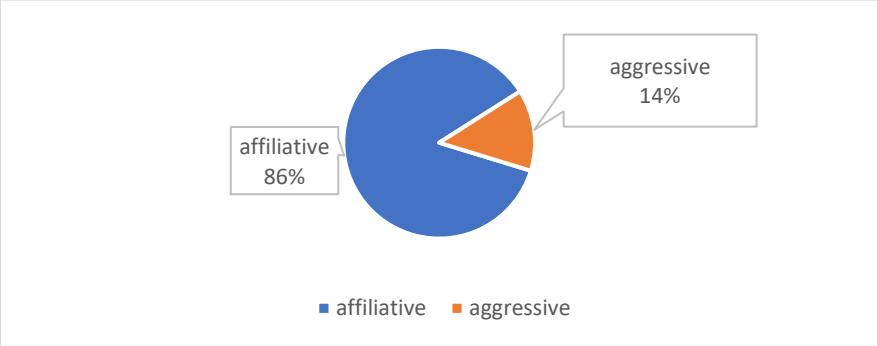

Figure 11: Proportion of Affiliative and Aggressive Behavior Quantities (male)

4.4 Objective 3: To compare the frequency of selected behaviors at different reproductive phases (lactation, estrus, neutral, indeterminant) amongst female olive baboons towards infants

There was a statistically significant difference in the number of affiliative behaviors towards infants by females in the categories “Neutral”, “Lactation”, and “Estrus” (Figure 12). When comparing the quantity of Contact and No Contact behaviors between the three groups of females, a Chi-squared analysis suggested there was a statistically significant deviation in the observed data from what would have been expected if the reproductive phase had no influence on female behavior (Degrees of Freedom= 1, N=2, Chi-squared Test, $p<0.05$).

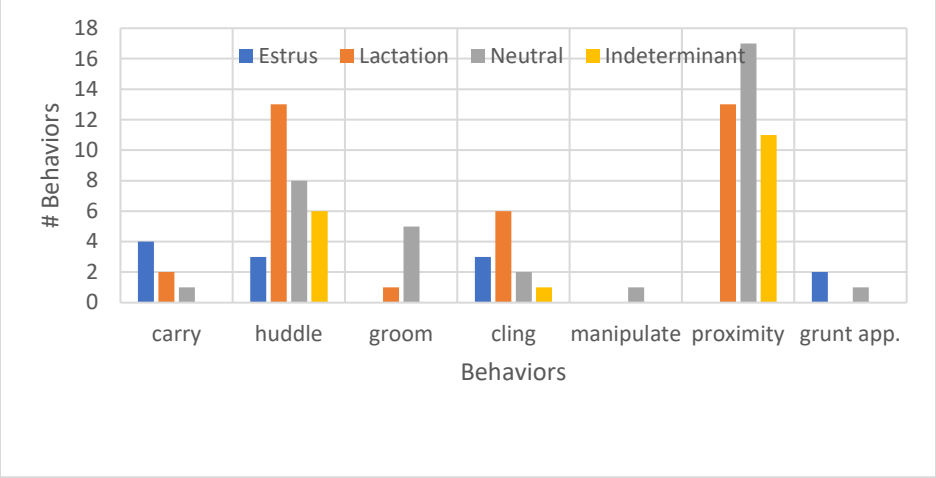

Figure 12: Female Affiliative Behaviors at Different Reproductive Phases

A significant difference was found between neutral females and females in estrus when comparing the quantity of Contact and No Contact behaviors (Degrees of Freedom= 1, N=2, Fisher’s Exact Test, p=0.0467). The proportion of Contact behaviors was higher for females in estrus than neutral females. Fisher’s Exact Test was also used to compare the five behaviors with sufficient data (carry, huddle, groom, ventral cling, and proximity) performed by females in estrus and neutral females. The result supported that there was significant difference (Degrees of Freedom= 4, N=5, Fisher’s Exact Test, p=0.00018). The Contact and No Contact behaviors of lactating females and neutral females was found to not be significantly different (Degrees of Freedom= 1, N=2, Fisher’s Exact Test, p =0.336). When applying Fisher’s Exact Test to neutral

and lactating females comparing the specific, ungrouped, behaviors with sufficient data (carry, huddle, groom, ventral cling, and proximity) the results supported the previous conclusion- no significant difference (Degrees of Freedom= 4, N=5, Fisher's Exact Test, p-value=0.149). It is notable that on average, lactating females performed more affiliative behaviors (Figure 14), and on average performed the three most common behaviors more than females in estrus or neutral females (Figure 13).

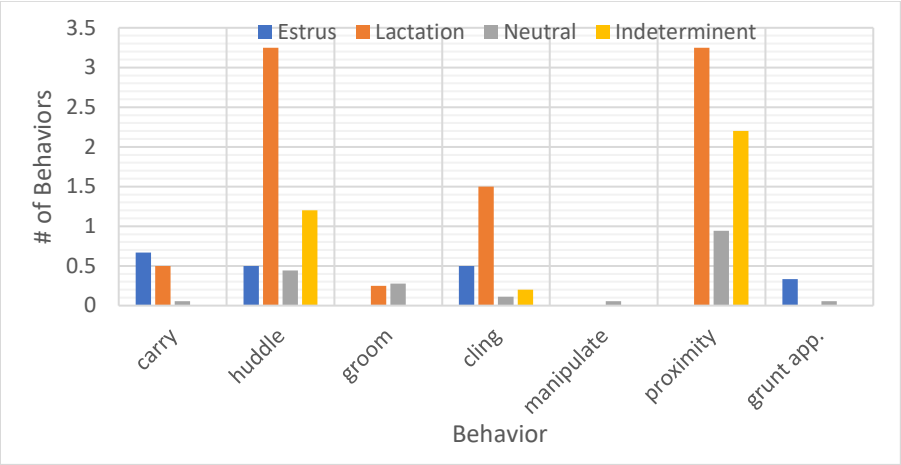

Figure 13:Average Number of Each Behavior per Individual at Each Reproductive Phase

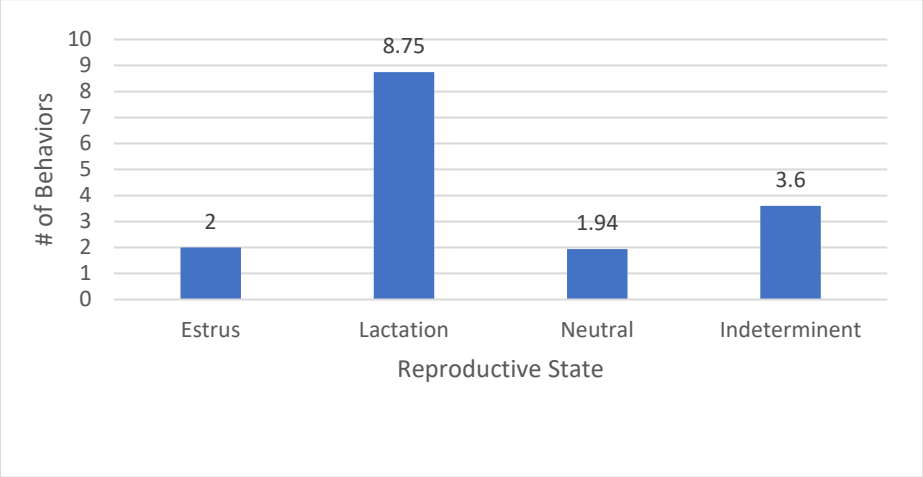

Figure 14: Average Total Number of Affiliative Behaviors per Each Reproductive Phase

Chapter 5: Discussion, Conclusion, and Recommendations

5.1 Discussion

Specific Objective #1

Females spent significantly more time than males interacting with infants in positive ways that were supportive of the infant's health or safety. Grooming behaviors, for example, are directly correlated to an individual's health (Akinyi et al., 2013). As such, the high density of ticks at Randilen WMA, particularly at the Sunset Hill site (Figure 3), and the increased amount of female grooming behaviors support that female are inclined to perform behaviors that benefit their offspring's health. A study by Akinyi et al. (2013) analyzed the correlation between the amount of grooming in baboons, an individual's tick load, and their packed red-cell volume- an indicator for anemia. They found that individuals that were groomed more had lower tick loads and higher packed red-cell volume, signifying a lower likelihood of anemia (Akinyi et al., 2013). The results indicating that females engaged in infant grooming for significantly longer durations than males could support the hypothesis that in a polygynandrous mating system, females are more inclined to invest in an infant's health. This is likely related to the fact that maternity is certain; because a female can be certain they are investing in their own offspring or the offspring of related kin, there is a certain benefit to their own fitness by promoting the related infant's health. Males, who in a polygynandrous system may not have complete paternal certainty, could be less inclined to promote the health of an infant that they may or may not have sired. This would support the observed results of greater duration of infant grooming by females.

Similarly, behaviors that promoted infant safety, including ventral clinging, carrying, and huddling, tended to be more frequently performed by females. During data collection, it was observed that females engaged in these behaviors a greater number of times for longer durations

than males. Ventral clinging and carrying are important locomotor behaviors that also serve a protective, safety related purpose (Nakamichi & Yamada, 2009). It logically follows that females engaged in these behaviors more than males because females are more inclined to promote the safety of their infant due to maternal certainty. In olive baboons, neonates and infants are usually carried by females ventrally until they reach 2 months of age and then are carried dorsally until 8 months of age (Nakamichi & Yamada, 2009). It has been observed, however, that olive baboon infants up to a year old might be carried in instances of troop raids or alarms (Nakamichi & Yamada, 2009). This suggests that both modes of carrying, ventrally and dorsally, are important to ensuring neonate and infant safety. The observed data aligns with this suggestion. Females engaged in infant clinging and carrying behaviors more frequently and for longer durations than males; in fact, males were not observed engaging in these behaviors at all. This may be because these behaviors are energetically expensive, and males may not be inclined to invest so heavily in an infant they have not certainly sired. Females would be inclined to protect their infants because due to gestation, lactation, and the rearing of a neonate, each infant is a substantial energetic investment for a female and ensuring the safety of each infant is crucial to their reproductive success, whereas males can more easily access multiple mating opportunities with less infant investment.

Interestingly, time spent in proximity to infants was not significantly different between males and females and proximity behavior quantities were equal. Maintaining proximity to infants is an important behavior to infant safety as it provides protection from general antagonization and infanticide (Minge et al., 2016; Rosenbaum et al., 2016). In gorillas, a species with highly variable group compositions, it was found that in groups with a single male and multiple females there were strong male-to-infant relationships with high levels of proximal association; conversely, groups

with multiple males exhibited weaker male-to-infant associations (Rosenbaum et al., 2016). This is in-line with other studies that analyzed the relationship between paternal certainty and the strength of bonds between adult males and infants (Rosenbaum et al., 2016). This previous research contradicts what was exhibited in the focal baboon troop. In a polygynandrous mating system with low paternal certainty, it would be expected that male-to-infant associations would be significantly weaker than female-to-infant associations. Other research on cercopithecine species specifically, however, has found increased associations and affiliative interactions between males and infants despite polygynandrous mating systems (Minge et al., 2016). It was found in Assamese macaques, and similarly in Rhesus macaques and Chacma baboons, that in multi-male mating systems where paternity is not certain, the level of predicted paternal certainty was related to the strength of bonds between males and immature individuals (Minge et al., 2016). Males had strong bonds with infants despite not having absolute paternal certainty (Minge et al., 2016). Therefore, although the observed data contradicts what is commonly found in polygynous and polygynandrous societies, similar observations have been made in other cercopithecine species (Minge et al., 2016). Further research is required to clarify male-to-infant associations in a polygynandrous species.

Aggressive behaviors towards infants in this study did not occur enough to draw meaningful discussion comparing those performed by males or females. It can be noted, however, that some baboon species are known to exhibit a distinctive culture of low aggression (Sapolsky, 2006), but patterns of overt, intragroup aggression vary based on species (Honess & Marin, 2006). It is commonly believed that male primates are more aggressive than females, but this is not true in some species where rates of aggression are low and variation exists based on the individual irrespective of sex, such as in Rhesus macaques (Honess & Marin, 2006). The fact that few

instances of aggressive infant-directed behaviors were observed does agree with previous research that claims olive baboons in general are not very aggressive (Sapolsky, 2006), however, little discussion comparing the males' and females' levels of aggression towards infants can come from the collected data with such a low sample size.

Specific Objective #2

It was found that both female and male relationships with infants were primarily affiliative. This is supported by the aforementioned research that found generally low rates of aggression in some baboon species (Sapolsky, 2006). It is notable that male baboons were observed spending less time interacting with infants in any manner than females with infants. This could be a consequence of paternal uncertainty in a polygynandrous species. Due to uncertain paternity, males may interact with infants less and focus their time and energy on maximizing reproductive opportunities. During observation, copulation attempts by the 33 male focal subjects were observed on 5 occasions. Many more instances were observed amongst non-focal males throughout the observation period as well. Frequent engagement in reproductive behavior and infrequent engagement with infants reflects what is commonly reported in males of polygynandrous species (Rosenbaum et al., 2016). Reduced infant investment and the maximization of reproductive events aims to optimize male reproductive success in a polygynandrous system and is supported by this study's data.

Specific Objective #3

This study found significant difference in infant-directed behaviors amongst females at different phases of their reproductive cycle. The result that females in estrus had significantly more "Contact" behaviors than neutral females and lactating females did not is supported by previous research on maternal behavior and hormone levels. The hormone oxytocin is known to be involved in a female's reproductive cycle and to be associated with maternal behaviors (Moscovice &

Ziegler, 2012). In a past study, it was found that females in estrus have significantly higher levels of oxytocin than females at other phases of their reproductive cycle (Moscovice & Ziegler, 2012). This is likely triggered by an influx of estrogen during ovulation and is also observed in humans (Moscovice & Ziegler, 2012). Increased oxytocin and estrogen levels likely contributed to the increased maternal behaviors observed amongst females in estrus, compared to lactating females or neutral females in this study.

5.2 Conclusion and Recommendations

In conclusion, this study found that adult female and male olive baboons interact with infants differently. As hypothesized, females were found to perform more affiliative behaviors for longer durations than males. Contrary to the initial hypothesis, females in estrus were found to perform affiliative behaviors in greater proportions than lactating or neutral females. Also contrary to initial predictions, both males and females were found to have primarily affiliative relationships with infants. These findings have important implications for understanding polygynandrous species broadly, and for investigating the evolution of human sociality from a polygynandrous ancestral species. How adults of each sex prioritize infant investment reflects what reproductive strategies are advantageous to their individual fitness. If paternal investment in a polygynandrous species were to increase, relationships with a mother may be maintained through nonreceptive periods of her reproductive cycle and could give way to long-term pair bonds. This study did not have sufficient data to model the interactions of a potential ancestral polygynandrous species that gave way to human sociality, but it did yield results regarding maternal behavior during estrus that are also observed in humans (Moscovice & Ziegler, 2012).

Future research should repeat this study with a larger sample size. Although significant results were deduced, a larger sample size would provide a better understanding of each selected

behavior. A larger sample size and longer observation period would also allow for greater data collection of aggressive behaviors which remain under-studied in existing literature. Also, this study could be performed with infants as the focal subjects. If this study was performed observing how infants interacted with adults rather than how adults interact with infants, more data could potentially be collected. A large number of the focal adults had no infant interactions so focusing on infants may allow for a greater number of infant interactions to be observed. Additional research should also investigate the relationships between adults and juveniles and adults with subadults.

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