VARIATION IN PATTERNS OF ALLOCARE IN CAPTIVE HAMADRYAS BABOONS (*PAPIO HAMADRYAS*): THE POTENTIAL EFFECTS OF ENVIRONMENT AND KINSHIP IN THE DEVELOPMENT OF NOVEL BEHAVIOR

by

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ABSTRACT

AMANDA RAE CARTER. Variation in patterns of allocare in captive hamadryas baboons (*Papio hamadryas*): the potential effects of environment and kinship in the development of novel behavior. (Under the direction of DR. DIANE K. BROCKMAN)

The goal of the this research was to examine the social dynamics among extended matrilines of Hamadryas baboons (*Papio hamadryas*) housed at the North Carolina Zoo (NCZ) in Asheboro, North Carolina, including the putative existence of allocare, defined as care provided to an infant by a conspecific other than the mother. This behavior does not typically occur in wild populations in which females disperse from their natal groups. Previous research at the NC Zoo has suggested the presence of allocare behaviors in this population (Gastil, 2014). I tested the hypothesis that allocare is strongly dependent upon the existence of extended female kin-groups in captivity. I predicted that allocare would occur in extended kin groups of mother-infant pairs and be absent in extended non-kin groups of mother-infant pairs. My hypothesis was weakly supported. Tinka was observed receiving allocare more frequently than the other focal subjects, and an affect of matriline was observed on the frequency of approach and agonistic behaviors as well.

DEDICATION

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INTRODUCTION

The goal of the this research was to examine the social dynamics among extended matrilines of Hamadryas baboons (*Papio hamadryas*) housed at the North Carolina Zoo (NCZ) in Asheboro, North Carolina, including the putative existence of allocare, defined as care provided to an infant by a conspecific other than the mother. This behavior does not typically occur in wild populations in which females disperse from their natal groups. Previous research at the NC Zoo has suggested the presence of allocare behaviors in this population (Gastil, 2014). I tested the hypothesis that allocare is strongly dependent upon the existence of extended female kin-groups in captivity. I predicted that allocare would occur in extended kin groups of mother-infant pairs and be absent in extended non-kin groups of mother-infant pairs. The results of this study will contribute toward an evaluation of currently proposed hypotheses for the evolution of allocare and provide potential insights into the impact of environment on the development of this behavior in a captive population. The appropriateness of this species for this research resides in the fact that females at the NCZ are forming matrilines within kin groups over time, which is predicted to provide opportunities for maturing females to engage in allocare of their related siblings, thereby providing new insights into the role captivity plays in the development of atypical behaviors—i.e., allocare.

The frequency with which allocare occurs among primates is quite variable and appears to be tightly linked to social living and the availability of caretakers, the vast majority of allocare consequently having been observed to occur in social-living anthropoid primates (Tecot et al. 2013). Previous comparative research on anthropoid primates suggests that allocare may be a reproductive strategy that allows mothers to increase their reproductive rates via early weaning of dependent young and shortened interbirth intervals. However, this strategy is predicted to be strongly influenced by the cost incurred by infants in the presence of female-female competition within groups (Ross and MacLarnon, 2000).

Previous studies of wild Hamadryas baboons indicate that this species exhibits a harem social system wherein females transfer from their natal groups to neighboring harem groups and establish their rank within the female dominance hierarchy (Sigg et al., 1982; Swedell, 2002). The objective of this research was to investigate patterns of variation in allocare in extended female kin-groups of captive Hamadryas baboons in which females remain in their natal groups and consequently establish strong social bonds with related kin, the latter providing opportunities for the expression of allocare. The importance of this research resides in the new insights that may be gained into the conditions under which allocare may be observed in an environment of decreased competition among group-living, hierarchical captive primate populations and how female-female relationships and competition play a role in the presence of allocare.

The theoretical foundation for this research is situated in parental investment theory. Parental investment theory is concerned with explaining the evolution of sex differences in parental care (Wade and Shuster, 2002). Trivers (1972) defines parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving.” According to this theory, sex differences in parental care should be expected (Trivers, 1972; Bateman 1948). Females are expected to invest more in their offspring than males as their reproductive success is limited by their egg production. In contrast, male reproductive success is limited by the number of inseminations males acquire (Bateman, 1948). As a result of their increased level of investment, females are expected to be choosy when selecting a mate and should choose mates that confer maximum fitness benefits (Trivers, 1972; Zeveloff and Boyce, 1980). Males would only be expected to invest in offspring if the benefits of such an investment outweighed the costs.

The work of Trivers (1972) and Bateman (1946) contributed to the formation of this theory which has become the foundation for most of the current research being done on sexual selection and mating systems, but there are those who are in fundamental disagreement with them. For example, Wade and Shuster (2002) argue that the differences in the energetic investment exhibited by both sexes in their gametes do not influence sex differences in mating strategies or parental care as has been asserted previously by Trivers (1972) and Bateman (1946). They claim that contrasting parental care with offspring desertion "violates the necessary relationship between mean male and female fitness" (Wade and Shuster, 2002, pg. 285). Wade and Shuster (2002) posit that male parental care evolves whenever half of the magnitude of the indirect effect of paternal care on offspring viability exceeds the direct effect of additional mating success gained by desertion and that the evolution of parental care is independent of maternal care.

There are energetic costs of maternal care associated with lactation and infant transport, which in some species can be mediated by the presence of conspecifics that can provide support to the mother through allocare (Tariff, 1997). The greater these costs are, the more difficult it is for the female to be the sole caretaker. As a result, mothers may allow other conspecifics to assist in providing care for her offspring. This is what is known as allocare.

ALLOCARE: TERMS AND EVOLUTIONARY CONTEXT

Allocare is defined as care that is provided by other group members and includes allomaternal care (i.e., care provided by group members other than the mother of the infant) and alloparental care (i.e., care provided by group members other than by the parents of the infant) (Gursky, 2007). Allocare-taking includes several different behaviors such as provisioning, carrying, huddling or communal nesting, babysitting, and predator protection or within group resource defense as behaviors that are exhibited by allocare givers (Isler and van Shaik, 2012). Fathers, related females and males (Wang and Novak, 1992), and unrelated male (Paul et al., 1996) and female (Small, 1990) conspecifics have all been documented providing allocare in various species.

While allocare is argued to provide substantial benefits to the mothers as well as costs to the allocare givers, there are actually costs and benefits to both mothers and allocare givers. The benefits of allocare for mothers include reduced energy expenditure associated with infant carrying (Clutton-Brock, 1991; Isler and van Schaik, 2012) and increased fertility and infant survivorship (See Isler and van Schaik, 2012 and Crittenden and Marlowe, 2008; Ross and MacLarnon, 2000). The cost to mothers comes from the potential risks group members pose to a mother’s infant. In a species with high levels of female-female competition, there is a risk of an infant being abused or injured (Silk, 1980) and also the possibility of an infant being “aunted to death” by a young, nulliparous female conspecific (Hrdy, 1976; Paul and Thommen, 1984).

The benefit to related conspecifics providing allocare is an increase in their inclusive fitness. Previous research shows that allocare providers are often relatives, which suggests that kin selection may play a strong role in the development of allocare

(Ross and MacLarnon, 2005). By caring for the infant of a relative, the caregiver promotes infant survival and increases the lifetime reproductive success of their relative, which increases their indirect fitness. The costs of allocare to the caregiver include energetic costs associated with infant transport, reduced foraging time occasioned from infant transport, and increased predation risk (Tardif, 1997).

While the costs of allocare to non-kin may be similar to those of kin, the benefits to unrelated individuals providing allocare are less clear. While the evolution of allomaternal care is readily explained among related individuals as a form of kin selection, that provided by non-kin is more difficult to explain as its existence appears to be contrary to what would be expected based on parental investment theory. Previous studies suggest that allocare provided by non-kin may provide direct fitness benefits to the caregivers specifically as it relates to learning crucial parenting skills (O'Brien and Robinson, 1991; Hamilton, 1964).

Four major hypotheses have been advanced to explain the evolution of allocare: kin selection, mutualism, reciprocity, and benefits of philopatry. *Kin selection* predicts that relatives should preferentially receive aid over nonrelatives and that closer relatives should receive more aid than more distant relatives (Hamilton, 1964). Caring for related, but non-descendent offspring, can lead to an increase in overall fitness and has been observed a variety of vertebrates (see Wasser, 2012), including wedged-capped capuchin monkeys (*Cebus olivaceus*). The results of O'Brien's and Robinson's (1991) research suggested that relatedness between the allocare-taker and the infant was the most important determinant of the presence of allocare and that female siblings were four times more likely to participate in allocare than non-sibling females.

Mutualism occurs when a relationship between two conspecifics is beneficial to both participants as demonstrated in the learning-to-mother hypothesis. The learning-to-mother hypothesis posits that young nulliparous females gain maternal skills while aiding in the care of young conspecifics, thereby potentially increasing the caregiver's future reproductive success as well as the survivorship of her infants (Gursky, 2007). Golden lion tamarins provide excellent support for the learning-to-mother hypothesis. Previous research on golden lion tamarins (*Leontopithecus rosalia*) revealed that females who had the opportunity to provide allocare to an infant before producing offspring themselves had higher rates of infant survival than females who were inexperienced (Hoage, 1978; Baker and Woods, 1992).

Reciprocity has also been proposed as a mechanism for the evolution of allocare. Reciprocity is defined as an exchange of benefits, which can be the same fitness units or different types of units (i.e., food resources, mating opportunities, etc.). The exchanged fitness units must be costly to the donor and beneficial to the recipient, but the average cost of the donor should be less than the average benefit to the recipient (Trivers, 1972; de Waal and Bronsan, 2006). The exchange of benefits may not occur immediately and may involve time-delays such as that predicted in the mating effort hypothesis, which posits that male primates may use an exchange of fitness units in order to increase their chances of mating with a female. Adult baboons (*Papio spp*.) were found to have higher than expected mating success with the infant's mother after establishing close friendships/caregiving relationships with the infant (Smuts, 1986).

The "*benefit of philopatry*" is the fourth proposed mechanism for the evolution of allocare. Philopatry refers to the tendency of organisms to stay in (or return to) their home territory. The “benefits of philopatry” hypothesis posits that nonbreeding helpers remain at home only when there is a net fitness benefit in doing so (Stacey and Ligon, 1991). The quality of territories can vary greatly and organisms are expected to remain in territories that increase their chance of survival and reproductive success. According to Komdeur (2006):

> “Traditionally the evolution of alloparental care is viewed as a two-step process: the decision to delay dispersal and independent breeding, usually as a consequence of the existence of constraints on independent breeding, and the decision to behave as alloparents by which individuals that have delayed dispersal gain a net fitness benefit.” (2006, pg. 729)

Callitrichids provide support for this hypothesis. Marmosets and tamarins exhibit frequent twinning and accelerated infant development as well as a high level of paternal care. In addition to the care provided by the father of these offspring, the older siblings also remain in their natal territory and help raise the new infants (Goldizen, 1990). The lack of available, open territories for offspring to disperse to and begin their reproductive careers also reduces potential predation risks associated with dispersal into a new territory. Remaining in their natal territory allows the older siblings to retain access to the resources of their home range and increase their indirect fitness through caring for their younger siblings (Bales et al., 1999).

MAMMALIAN CONTEXT OF ALLOCARE

Mammals exhibit a wide variety of social systems, reproductive strategies and degrees of parental involvement in caring for immatures. Among group-living (i.e., multimale/multifemale social groups) and pair-bonded species, mothers are most often the primary care givers, but males and other females in the group have also been observed providing assistance in caring for immatures (Tecot et al., 2013). Reproductive strategies associated with socially living species include two categories of breeders: singular breeders and plural breeders.

A singular breeding species is characterized by the monopolization of reproduction by a dominant individual/pair (high reproductive skew) (Jameison, 1997) and the communal care of young (Hayes, 2000). Singular breeding can be seen in a variety of mammal species (e.g., the dwarf mongoose (*Helogale parvula*): Rood, 1980; prairie voles (*Microtus ochrogaster*): Wang and Novak, 1994, Hayes, 2000; various canids, including Artic foxes (*Alopes lagopus*), golden jackels (*Canis aureus*), silver-backed jackels (*Canis mesomelas*), and coyotes (*Canis latrans*): Moelhman and Hofer, 1997; marmosets/tamarins (Callitrichidae *spp.*): French, 1997). For example, meerkats (*Suricata suricatta*) live in groups composed of 3-25 members where a dominant male and dominant female are responsible for the majority of the offspring born into the group (Clutton-Brock et al., 1998). Before the young reach three weeks of age, they remain in a breeding burrow that is guarded by helpers of both sexes who are sexually mature but have not yet bred (Clutton-Brock et al., 1998) and are usually closely related to the young (Clutton-Brock et al., 2001).

A plural breeding species is characterized by an even distribution of mating and reproduction among all adults in the social species (low reproductive skew) (Jameison, 1997) and little or no cooperative care of young conspecifics (Hayes, 2000). Groups are typically composed of multiple breeding females, the majority of which are philopatric and remain in their natal groups. Those females that do emigrate from their natal group do so with other female members of the social group (Lukas and Clutton-Brock, 2011). Examples of plural breeding mammals include, but are not limited to, spotted hyenas (*Crocuta crocuta*) (Frank, 1986a), capuchin monkeys (*Cebus spp.*) (Burkart et al., 2009), and degus (*Octodon degus*) (Hayes et al., 2009). In particular, spotted hyenas reside in large clans consisting of adult males, adult females, and juveniles of both sexes (Frank, 1986a). Multiple females in the group breed simultaneously although only higher-ranking females experience greater reproductive success (Frank, 1986b; Szykman et al., 2001). As is the case with spotted hyenas, cooperative care/raising of young is typically not found in plural breeding species and each female is independently responsible for the care of her offspring.

ALLOCARE IN PRIMATES

Prosimians (e.g., lemurs, lorises, galagoes, tarsiers) and anthropoid primates (e.g., monkeys, apes, humans) exhibit highly variable social systems and reproductive strategies that lead to a wide range of adult-immature social interactions. With few exceptions (i.e., tamarins, marmosets, night monkeys), the vast majority of primate species are plural breeding species with groups containing multiple breeding females (Lukas and Clutton-Brock, 2011). As plural breeding mammals, cooperative care of young should not be expected, but several primate species do, in fact, display allocare-taking behavior (see below).

Primates are born altricial and require an extended period of care, which is consistent with K-selected patterns of life history. The development and maintenance of strong social bonds are essential for the infant to develop appropriately physically, cognitively, and socially (MacKinnon, 2007). Allocare presents an opportunity for the infant to form these strong social bonds with multiple conspecifics.

Prosimians exhibit tight seasonality in reproduction, which means that they can only breed during certain times of the year every year (Brockman and van Schaik, 2005). Lemurs typically produce smaller neonates than anthropoid primates (Young et al., 1990), and the presence of allomaternal care does not translate into more rapid infant development, nor does it yield reduced interbirth intervals in lemurs as it does in anthropoid primates (Tecot et al., 2013). Furthermore, prosimian primates exhibit a variety of social grouping patterns including noyau (mouse lemurs (*Microcebus spp.),* lorises (*Loris spp.*; *Nycticebus spp.*)), pair-bonded (indris (*Indri indri*)), and multimale/multifemale social groups (e.g., ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi*), brown lemurs (*Eulemur fulvus*)) (see Strier, 2007).

Previous research had indicated that allocare was absent in all lemur species (Ross, 2000), but recent research indicates otherwise (Tecot et al., 2013; Bastain and Brockman, 2007). In fact, there is evidence that allocare is found in species that park their infants as well as in species that constantly carry them (Gursky, 2007). For example, fat-tailed dwarf lemur (*Cheirogaleus medius*) fathers have been observed babysitting offspring immediately after birth (Fietz, 1999), and infant carrying has been observed in a variety of species (Tecot et al., 2013). Adult males, juvenile males, and siblings have been observed carrying infants in blue-eyed black lemurs (*Eulemur flavifrons*) (Andrews, 1998), and infant carrying by fathers and siblings has been observed in gray baboon lemurs (*Hapalemur griseus*) (Grassi, 2001). Allomaternal nursing has also been observed in a several lemur species including mouse lemurs (Eberle and Kappeler, 2006); red ruffed lemurs (*Varecia rubra*) (Vasey, 2007); and black and white ruffed lemurs (*Varecia variegata*)(Baden, 2011).

Gursky (2007) observed subadult spectral tarsiers (*Tarsius tarsier*) participating in infant transport, food sharing, playing, and grooming, but caretaking by adult males was rarely observed. In addition, alarm calls were found to be given more frequently by subadult spectral tarsiers when infants were present, which suggests that subadults may spend more time scanning for potential predators when infants are present than when they are absent (Gursky, 2007). It has been suggested that the watchfulness over infants by group members other than the mother improves both the mother's foraging efficiency and increases the likelihood of infant survival (Gursky, 2007; Morland, 1990).

Among anthropoid primates allocare has been reported to occur at relatively high frequencies (see Tecot et al., 2013; Lewis and Pusey, 1997). Allocare has been observed in several species of New World monkeys including capuchin monkeys (*Cebus spp.)* (Burkart, et al., 2009), golden lion tamarins (*Leontopithecus rosalia*) (Rapaport, 2011), and spider monkeys (*Ateles geoffroyi*) (Watt, 1994). Callitrichids (marmosets and tamarins) are typically described as pair-bonded, monogamous species although some callitrichids display degrees of polyandry and polygamy (Dunbar, 1995; Goldizen, 1990). In both wild and captive populations, males and other non-breeding group members are principally responsible for most of the carrying of the infants and also exhibit grooming and protective behaviors (Dunbar, 1995). Callitrichid young are routinely provisioned until well after weaning by both parents and allocare-givers which is in contrast to what is known about typical juvenile primates (Bolter and Zihlman 2007; Rapaport, 2011). Such a high level of paternal care has been assumed to have evolved as a result of the high level of twinning present in callitrichids and associated cost carrying infants (Wright, 1984; Wright 1990). The offspring are born already weighing a significant proportion of the mother's weight [approximately 23.6% in pygmy marmosets (*Cebuella pygmaea*), 21.4% in common marmosets (*Callithrix jacchus*), 18.9% in golden lion tamarins (*Leontopithecus rosalia*), and 14.7% in cotton-top tamarins (*Saguinus oedipus*)] (Leutenegerr, 1980). This high level of paternal investment has also been hypothesized to be the consequence of high level of assumed paternal certainty resulting from their pair-bonded social structure. Titi monkeys (*Callicebus spp.)* and owl monkeys (*Aotus spp*.) are also pair-bonded species that are characterized by extensive obligate paternal carrying (Tecot et al., 2013).

Old World monkeys (i.e., ceropithecines and colobines) also exhibit allocare, including vervet monkeys (*Ceropithecus aethiops sabaeus*) (Fairbanks, 1990), patas monkeys (*Erythrocebus patas*) (Muroyama, 1994), and Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) (Xi et al., 2008). For example, Barbary macaques are characterized by a promiscuous mating system (Small, 1990) in which females mate with multiple males, which leads to paternal uncertainty, yet males still show a high level of interest in young conspecifics (Paul et al., 1996). Paul et al. (1996) determined that males appear to use relationships with infants to buffer their conflicts with other males (see also Ménard et al., 2001), and Small (1990) found that Barbary macaque infants are the focus of attention for all troop members. She posited that interest by all troop members in infants promotes infant socialization and aids in establishing and maintaining social contacts.

While pongids and hylobatids have generally been thought to be less inclined to exhibit allocare (Silk et al., 2005; Burkart et al., 2009), studies of wild chimpanzees (*Pan troglodytes*) in Tanzania revealed that smaller infants were handled by individuals other than the mother, with nulliparous subadult females being the most earnest caretakers (Nishida, 1983). Food sharing has been observed in bonobos (*Pan paniscus*) in both related and non-related individuals (Hohmann et al., 1999), but there is some question as to whether it should be considered allocare-taking or simply tolerated theft (Burkart et al., 2009). The allocare-taking behaviors exhibited by the great apes are thought to be more affiliative rather than true allocare as they are assumed to not be motivated by other-regarding preferences (Silk et al., 2005). Allocare has been observed in Hylobates (gibbons, siamangs) wherein siamang (*Symphylangus syndactylus*) males provide support in the form of infant carrying, which appears to shorten the mother's interbirth interval (Lappan, 2008).

Humans (*Homo sapiens*) exhibit allocare as well. A variety of mating systems have been observed in humans, the particular culturally-mediated system being dependent upon cultural and religious values and norms (see Kramer, 2010). The mating systems of foraging societies are of great interest because they are believed to be the most similar to that of early human populations. Marlowe (2003a) found that, generally, foraging societies with higher levels of male contribution to subsistence are generally more monogamous than those with lower levels of male contribution to subsistence. Among monogamous societies, humans are pair-bonded, so theoretically, high paternal investment would be expected, but fathers are not the only group members who provide allocare.

Crittenden and Marlowe (2008) report that among the Hazda, children receive care from a wide range of helpers, with fathers as well as grandmothers engaging in a considerable amount of the caretaking (see also Marlowe, 1999). Their results showed that, not unexpectedly, related individuals spend more time holding and caring for an infant than nonrelated individuals. These results lend further support to the idea advanced by Ross and MacLarnon (2000) that kin selection likely plays a strong role in the development of allocare behavior. Allomothering by grandmothers has been hypothesized to increase mothers' fertility by shortening inter-birth intervals (Isler and van Schaik, 2012; Crittenden and Marlowe, 2008) and decreasing maternal energy expenditure (Meehan et al., 2013; Marlowe, 2003b) as well as providing an opportunity for the related allomothers to increase inclusive fitness (Gibson and Mace, 2005).

It’s important to note that while research has shown that allocare is present among these human groups, there are multiple ways for nonmaternal caregivers in foraging societies to lighten the work load of the mother (Marlowe, 2003a; Marlowe, 1999; Meehan et al., 2013). The benefits of nonmaternal caregiving is evident in the Aka foragers of central Africa wherein grandmothers have been reported to significantly reduce a mother’s energy expenditure by as much as 216kcal across a 9-hour observation period (Meehan et al., 2013). Among the Hadza, women normally have the greatest foraging returns, but when mothers experience decreased foraging rates, male provisioning substantially supplements the foraging rates of mothers, and this critical reliance on male provisioning is thought to favor pair bonding (Marlowe, 2003b)

ALLOCARE IN CONTEXT: BABOONS (*PAPIO SPP.*)

Baboons (*Papio spp.)* can be found across the African savannah and the Arabian Peninsula, and they generally have very similar social structures. All baboon species, except for Hamadryas baboons, are characterized by female philopatry and matriline-based hierarchies where offspring inherit the rank of their mothers (Bergman et al., 2003). Allocare has been recorded for multiple species of baboons, but they do not all exhibit the same patterns of allocare.

Female chacma baboons (*Papio cynocephalus ursinus*) have been observed using their infants to solicit grooming from conspecifics (Henzi & Barret, 2002). Grooming for infant access was initiated by potential handlers and was likely to not be reciprocated. Higher ranking females required longer grooming times before allowing their infants to be handled than lower ranking females. Olive baboons (*Papio anubis*) have been observed providing allocare consistent with the mating effort hypothesis (Smuts, 1986). Previous research has shown that males will form relationships with lactating females and their offspring as a strategy for improving the probability of acquiring mating with the mother in the future (Lemasson et al., 2008). These friendship dyads were characterized by higher rates of allogrooming and infant handling.

Female yellow baboons (*Papio cynocephalus cynocephalus*) have been observed handling and carrying infants belonging to other females (Silk et al., 2003), young infants being most attractive to conspecifics. Mothers of young infants were approach by other adult females on average once every 6 minutes, and other females attempted to handle their infants approximately once every 9 minutes (Silk et al., 2003). Generally, females related to infants were more readily able to gain access to those infants.

BACKGROUND: HAMADRYAS BABOONS (*PAPIO HAMADRYAS*)

❖ Geographic Range

Hamadryas baboons, also referred to as desert baboons or sacred baboons, are the northernmost species of baboon and are widely regarded to be the most divergent and specialized subspecies of *Papio* (Swedell et al., 2008). They range throughout the semi-arid regions of the Horn of Africa, including parts of Ethiopia, Sudan, Somalia, Djibout and Eritrea, as well as the southwestern tip of the Arabian Peninsula (Swedell, 2002). While they once may have been considered sacred in Egypt, they are now extinct within the region (Gippoliti & Ehardt, 2008; Rowe, 1996).

Hamadryas baboons are classified as a species of least concern by the International Union of Conservation of Nature in 2008 (Gippoliti & Ehardt, 2008), and that classification has not been changed within the last 7 years. This species is known to be quite abundant and is not experiencing major, widespread threats. In fact, the current population is listed as increasing (Gippoliti & Ehardt, 2008), although there may be local pressures affecting populations related to major agricultural expansion (Gippoliti & Ehardt, 2008).

❖ Sexual Dimorphism

Hamadryas baboons (*Papio hamadryas*) exhibit extreme sexual dimorphism in body size. Adult males weigh between 20-30 kg with females weighing only half as much (Rowe, 1996). Sex differences in this species can also be observed in their coat color. Both males and females have long, dense fur, but males have a silver-grey coat and a mantle while females have a brown coat and lack a mantle (Rowe, 1996). Young Hamadryas baboons are born black and turn olive-brown as they mature.

- Reproduction

Male Hamadryas baboons mature between 4.8 and 6.8 years of age when their testicles descend, and females experience menarche between 4 and 5 years of age with a mean of 4.3 years (Sigg et al., 1982). On average, males sire their first infant between 9.5 and 13 years old. The age of a male when he sires his first offspring depends strongly on his place in the social hierarchy, which can be influenced by the composition of the social group and group dynamics. Females give birth to their first infant, on average, at the age of 6.1 years. Following the birth of a surviving infant, females experience a mean of 14 months anovulatory with an average interbirth interval (IBI) of 24 months (Sigg et al., 1982).

- Diet

Like other baboons, Hamadryas baboons appear to be omnivores (Gippoliti & Ehardt, 2008; Swedell et al., 2008). However, there is some speculation that the lower species richness and diversity of their habitats compared to those of other baboon species (*Papio spp.*) suggests that they may subsist on fewer plant species than other baboons, but this has never been confirmed quantitatively. In fact, there had not been any systematic assessment of Hamadryas diets in any part of their range until 2008 when Swedell et al. (2008) published the first year-round quantitative data on dietary composition and seasonality in wild Hamadryas baboons at the Filoha field site in central lowland Ethiopia. The results of this research revealed a seasonal pattern in the number of plant species contributing to the monthly diet, which decreased gradually from the long rains of July and August to the peak dry months of May and June (Swedell et al., 2008). These investigators also found that the two species of plants (*H. thebaica* and *A.*

senegal) that comprised the majority of the species' annual feeding time were also the only two plant species that were consumed during every month of the year. Baboons in this study were also observed preying on guinea fowl (*Numida*), dik diks (*Madoqua*), and hares (*Lepus*), although the authors reported these events as being rare (Swedell et al., 2008)

- Social Organization

The social organization of Hamadryas baboons is variable and is composed of three hierarchical levels, the first of which is one-male units (OMUs) called harems which contain two to five females, most of which are adults, and their dependent offspring (Altmann, 1990). Several one-male units coalesce into larger groups called bands (Swedell, 2002). In these bands, the cohesion of one-male units is maintained by aggressive herding behavior of the leader males from each of the one-male units. The third and final level of this hierarchical social organization is the troop. Troops are formed by an even greater number of one-male units, and, in contrast to bands, troops do not function as cohesive social groups, but individuals only appear to assemble together at sleeping sites (Swedell 2002), and group composition can change from day-to-day (Altmann, 1990).

Hamadryas baboons have traditionally been characterized as a non-female bonded (sensu Wranghum, 1980), male-dominate species wherein females migrate out of their natal groups and join neighboring harems (Kummer, 1968). The strongest social bonds are those between a leader male and his females with female-female bonds reportedly being weak by comparison (Swedell, 2002). It has been suggested that Hamadryas baboons lack close female bonds due to their reliance on scarce, widely dispersed food resources. However, there is some evidence that female-female relationships may be more flexible than initially thought, and that close relationships can form depending upon food distribution and levels of predation risk (Swedell, 2002). Socioecological theory posits that when food is clumped and defensible, intra-group competition (i.e., contest competition) increases and females are predicted to remain in their natal groups and form kin-based affiliative and agonistic relationships. Conversely, contest competition is not promoted when food is more evenly distributed, which suggests that females should be expected to disperse from their natal groups and develop weak, if any, bonds with females in neighboring groups since they would not benefit from forming kin-based alliances (Swedell, 2002).

Swedell (2002) conducted research on a population of wild female Hamadryas baboons at the Filoha field site in Awash National Park in Ethiopia and compared her results with those obtained from groups at Erer-Gota and Awash Station. She found that while Erer-Gota and Awash Station females interacted more frequently with leader males, most Filoha females interacted at least as much with other females as they did with leader males. Swedell (2002) argues that this variation is the result of variation in group size and/or food availability, and thus be indicative of behavioral plasticity in this species. In captivity, Hamadryas females have been observed establishing both hierarchical and affiliative relationships (i.e., grooming) with conspecific females, especially in the absence of male conspecifics (Stammbach and Kummer, 1982). Swedell (2002) makes the point that since other aspects of Hamadryas behavior are not significantly altered by captivity, it is possible that the female social relationships can be equally flexible in captive environments. However, there is currently little evidence of these female social relationships in the wild.

MATERIALS AND METHODS

The objective of this research was to investigate patterns of variation in allocare in extended female kin-groups of captive Hamadryas baboons in which females remain in their natal groups and consequently establish strong social bonds with related kin, the latter providing opportunities for the expression of allocare. I tested the hypothesis that allocare is strongly dependent upon the existence of extended female kin-groups in captivity. I predicted that allocare will occur in extended kin groups of mother-infant pairs and be absent in extended non-kin groups of mother-infant pairs.

❖ Study Site and Housing

The subjects of this study are housed at the North Carolina Zoo (NCZ), which is located in Asheboro, North Carolina. It is an agency of the NC Department of Environment and Natural Resources. The baboons are housed in a habitat that is composed of an exterior exhibition space as well as an interior enclosure. The exterior exhibition space is just under an acre (167 sq. meters) and is composed of a grassy meadow with several trees, as well as a climbing structure. There are artificial cliffs on three sides of the exhibit, including one area where the baboons can climb up and down the cliffs and into a small gorge.

The interior enclosure substrate is composed of a reddish earth and woodchip mixture, and a low hill provides distinct upper and lower areas (Gastil, 2014). The lower area is equipped with climbing logs and a tree limb climbing structure. The baboons access the outside area from the top of the hill, via an opening large enough for two baboons to exit the interior space. The enclosure has floor-to-ceiling windows on two sides.

The troop has access to both the indoor and outdoor spaces 24 hours a day during mild weather and can move easily between the two areas at all times of the day. During particularly cold weather and/or severe thunderstorms, the baboons are transferred into the indoor facility and remain off exhibit. The exterior exhibition space is composed of grassy, flat areas; there are also climbing structures as well as three cliffs on which the baboons can climb.

The troop is fed twice a day in the indoor enclosure where they also participate in operant conditioning exercises that are designed to facilitate visual medical inspections and treatment. The feedings occur before the NCZ opens to the public at 9:00AM and after it closes at 5:00PM. The troop is also provided a snack in the exterior exhibition space daily at approximately 2:00PM while on exhibit.

❖ Subjects

The subjects of this study are members of the largest group of captive Hamadryas baboons in North America. At the time that this study took place, there were 22 baboons in the group of which 13 were females and 9 were males, ranging in age from less than 1 year old to 30 years of age. There were ten adult females (i.e., > 4 years old), five adult males (i.e., >9 years old), one subadult female (i.e., 3-4 years old), two juvenile males (i.e., 3-4 years old), two infant males (1 year and 8 months), and 2 infant females (10 months and 8 months).

This population consisted of four one-male unites (OMUs), each headed by a dominant lead male. “Gondar” was the alpha male of the group and had the largest OMU with four females and two offspring. “Addis” lead an OMU composed of two females and two offspring. “Negelli’s” OMU also contained two females and two offspring.

“Geb” had one of the smallest OMUs with only two adult females, and “Tukio” lead only one adult female and one offspring.

For the purpose of this study, the four immature members of the group were selected to be focal subjects based on their young age and increased likelihood of being the recipients of allocare: Wiley (male, 1yr), Tinka (female, 10mos), Karamela (female, 8mos), and Zanzibar (male, 8mos) and their extended kin-group/non-kin-group affiliation

Table 1: The NC Zoo Hamadryas Group by Age

Subjects	Sex	Age in Years (as of 6/2015)
Sally	Female	30
Margie	Female	24
Matilda	Female	24
Negelli	Male	16
Addis	Male	16
Gondar	Male	16
Mendi	Female	16
Ras Mitat	Female	12
Geb	Male	10
Sudi	Female	10
Rhea	Female	10
Tukio	Male	9
Candy	Female	9
Zuri	Female	5
Meka Chini	Female	5
Tankara	Female	4
Tullu	Male	4
Babu	Male	3
Wiley	Male	2
Tinka	Female	1
Karamela	Female	1
Zanzibar	Male	1

- Hamadryas Baboon Identification Key/Taxon Report

The availability of the Hamadryas baboon identification key made possible the identification of individual subjects. The Hamadryas baboon taxon report provided information on the subject’s date of birth, parentage, and origin (Ireland, pers. comm.).

DATA COLLECTION AND RECORDING

This observational study was conducted from June 22, 2015 to September 30, 2015. Behavioral observations were recorded from a public observation area. An ethogram of relevant behaviors (Appendix A) was used to quantify social behavior using 15-minute focal animal sampling techniques (Altmann, 1974b). Data were recorded using an ethogram check-sheet (Appendix B), and 10 minute *ad libitum* notes were taken between focal observations. Four immature baboons in the population were used for this study; four subjects sampled across the 14-week study yielded approximately 45 hours of data collected per subject.

The ethogram was constructed using operational definitions that were drawn from several relevant sources, including Kummer (1968) and the Hamadryas Baboon Social Behavior Checklist from the Auckland Zoo in New Zealand (2013) as well as two unpublished M.A. theses, the foci of which are this same baboon population (Gastil, 2014; Melwani, 2012) (see also Treat, 2013).

Behaviors were coded as “states” or “events.” Borrowing from Gastil (2014), “states” are defined as mutually exclusive behaviors with continuous duration, and “events” are defined as behaviors with an insignificant duration that occurred with significant frequency during a state (Altmann, 1974b).

❖ Methods

Observations occurred at a minimum of 4 days per week and began at 9:00AM and ended at 5:00PM. 15-minute focal animal sampling techniques (Altmann, 1974b) were employed to record frequencies/duration of all behavioral interactions between the focal and conspecifics, including behavioral indicators of allocare which have been elucidated/defined in an ethogram. A stopwatch was used to begin and end each focal animal sample. Ten minute *ad libitum* observations occurred between each focal observation to ensure independence of the focal samples. Each focal animal was selected at random to eliminate observer bias. The subjects' names were recorded on individual pieces of paper, and those slips of paper were put in a cup that was shaken. A piece of paper was pulled from the cup. Observations took place during the NC Zoo's operational hours from a publicly accessible area.

DATA ANALYSES

Statistical analyses were performed using Minitab 17 (Minitab, Inc., State College, PA). Multi-and univariate statistical analyses were used to identify which variable(s) best predict variation in inter-individual mean rates of individual indicators of allocare behavior (e.g., provisioning, carrying, huddling, babysitting, etc.) The potential effects of extended kin-group vs. non-kin-group affiliation and sex on each component of allocare were tested using multivariate (multiple linear and linear regression) and univariate (t-test, ANOVA, etc.) analyses. Variables were tested for normality and equal variance. Results were then reported as means and standard deviation, with significance set at $p < 0.05$.

RESULTS

Over the course of this 14-week study, a total of 179.9 focal hours were recorded. A total of 44.5 hours were collected for Tinka, 45.25 hours for Karamela, 45.15 hours for Wiley, and 45 hours for Zanzibar. The observed behaviors were broken down into four categories: approach, affiliation, agonism, and allocare. To characterize the general social behavior of these primates, a correlation was calculated to determine if approaches led to agonistic behaviors or affiliative behaviors among the four focal subjects. Neither correlation was found to be significant (agonism: $p = 0.71$, affiliation: $p = 0.12$).

The results of an ANOVA examining variation in the mean hourly rates of observed behaviors for approach, agonism, affiliation, and allocare revealed that there were significant differences among the four focal subjects for all four behavioral categories, $p < 0.05$ (Table 2, Figure 1). Post-hoc Tukey tests revealed that Tinka was the focal subject that drove the calculated significant difference in the hourly rate of approach. Tinka's mean hourly rate of approach was 50% higher than the calculated averages for Karamela, Wiley, and Zanzibar (Table 2). Comparing Tinka's mean hourly rate of approach to Karamela's, Wiley's, and Zanzibar's, significance difference comes out to be, $p = 0.0006$, $p = 0.002$, and $p = 0.0032$ respectively (Figure 2). However, the mean differences in approach rate between Wiley and Karamela, Zanzibar and Karamela, and Zanzibar and was not significant, $p > 0.96$ for all.

Additional post-hoc analysis of the hourly rates of affiliative behaviors revealed that the hourly averages of the four animal subjects clustered into two groups. Zanzibar (Mean = 8.96, SD = 4.19) and Tinka (Mean = 8.88, SD = 3.10) in one group and Wiley (Mean = 7.36, SD = 3.81) and Karamela (Mean = 6.53, SD = 2.43) in the other group, although Wiley was borderline. The Tukey simultaneous test for differences of means found significant differences between Karamela and Tinka (p = 0.0025) and between Karamela and Zanzibar (p = 0.0016). The Tukey test also revealed that the differences of means for hourly rates of affiliative behaviors between Wiley and Tinka and Wiley and Zanzibar approached significance (See Table 5).

A Tukey test for differences of means in hourly rates of agonistic behaviors was also performed and revealed wide variation between the four subjects. Each pair of means analyzed by the Tukey test was found to be significantly different with the exception of Wiley and Zanzibar, p = 0.48 (Table 4). The Tukey test for differences of means for hourly rates of allocare behaviors revealed that while there was variation between the four focal subjects, Tinka was the outlier driving the calculated significant difference (Table 6).

❖ Between-sex Differences

Statistical analyses revealed that there were marked differences between the sexes for two of the four behavior categories studied in this population. The between-sex differences for affiliation (female: Mean = 7.70, SD = 3.02, male: Mean = 8.16. SD = 3.58) and agonism (female: Mean = 6.98, SD = 3.88, male: Mean = .75. SD = 2.54) were not significant (0.35 and 0.63, respectively) (Table 7). However, females were observed approaching conspecifics more frequently than the males (female Mean = 7.96, SD =3.35; male Mean 6.83, SD = 3.67, p=0.03) A significant difference between the sexes was also observed in the hourly rate of allocare behaviors. Female focal animals (Mean = 0.40, SD = 0.62) were recorded receiving allocare more frequently than male focal animals (Mean = 0.14, SD = 0.36). It should be noted that among the four categories of behavior, rates of allocare were the least frequently observed behavior exhibited by the focal subjects (Table 2).

- Within-sex Differences

Significant within-sex differences in the frequency of behavior was observed (Table 8, Table 9). For the females, Tinka (Mean = 9.36, SD = 3.53) exhibited a significantly higher rate of approach, affiliation, and agonism toward conspecifics than Karamela (Table 8). Both females exhibited similar rates of allocare (Table 8). The juvenile males in this population exhibited significant differences in rates of affiliation, Zanzibar, the younger of the two males, directing higher rates of affiliation (Mean = 8.96, SD = 4.19) toward conspecifics than Wiley (Mean = 7.36, SD = 2.65; Table 9). The frequency of approach, agonism, and allocare interactions were similar between the males, and not significantly so (Table 9).

- Matriline vs. Non-matriline

There was a significant effect of matriline in the frequency of behaviors exhibited by the subjects in this study, this matriline- effect being observed in Tinka, the only member of the study subjects belonging to a matriline (Table 10). The remaining three subjects in this study were not members of extended kin groups, thus the results for the non-matriline condition represent the mean rate of behavior pooled from these focal subjects (Table 10). The matriline condition (e.g., Tinka) yielded higher rates of approach, affiliation, agonism, and allocare than the nonmatriline condition (e.g., pooled results for Karamela, Zanzibar, and Wiley), which suggests that there may be an effect of extended kin group on the behavior of these focal subjects

DISCUSSION

The hypothesis that allocare would be present in this population based on the ability of females to form extended matrilines in a captive environment was only weakly supported. Allocare was the least frequently observed behavior of the four categories of behaviors recorded among these study subjects. Explanations for this result are not readily apparent, but most likely concern the older age class of the focal subjects who were juveniles rather than infants. Karamela, Zanzibar, and Tinka were all transitioning out of infancy and into the juvenile phase of development (see Sigg et al., 1982) and Wiley had already reached the juvenile phase. During Gastil's (2014) previous studies of allocare in this population Karamela, Zanzibar, and Tinka were newborns and Wiley was still an infant, likely resulting in the higher rates of allocare being observed in that study than were seen in this study.

Siggs et al. (1982) define the transition from infancy to the juvenile stage in terms of physical characteristics. The juvenile stage is divided into three phases. The Juvenile 1 phase is the same in both sexes. The head becomes more dog-like due to the growth of the snout, and individuals have a sitting height of approximately 30 cm. Individuals in the Juvenile 1 phase range in age from 1.3 years to 3 years. The Juvenile 2 phase is also the same in both sexes and is marked by more pronounced individual physiognomy. Baboons in the Juvenile 2 phase have an average sitting height of 40 cm and range in age from 3 to 4.3 years. By these definitions, Karamela, Tinka, and Zanzibar were all entering the Juvenile 1 phase while Wiley was entering the Juvenile 2 phase.

In addition to changes in physical characteristics, there are also observable behavioral changes for individuals as they transition out of infancy. As the baboons get older, they are less likely to receive allocare since they are becoming less reliant on the aid of others and are becoming more independent. Previous research on wild olive baboons (*Papio anubis*) found that, like other primate species, the mother-infant relationship begins to wane with increasing age of the infant, the most marked changes usually occurring when the infant is between 10 and 12 months of age and mothers typically begin rejecting the suckling and riding attempts of their infants (Nash, 1978). In response to this rejection, the young baboons will resort to simply sitting near their mother rather than maintaining some sort of physical contact with her. During this period of development, baboon youngsters begin initiating more play interactions with conspecifics and spend more time playing with other infants and juveniles than with adults (Owens, 1974).

The focal subjects in this study exhibited these same behaviors. Zanzibar, Tinka, and Karamela would often be observed sitting near their mothers, but usually not in direct contact. They would graze on grass in the same area as their mothers and retrieve their own food during the daily snack period at 2:00 PM rather than depending on their mothers or other conspecifics to help them.

Previous research on natal attraction in adult female baboons (*Papio cynocephalus ursinus*) found that females were more attracted to very young infants (Silk et al., 2003). Infants that were one month old were approached an average of 10 times per hour, this rate declining to 2 times per hour at 12 months of age. Adult females also made more attempts to groom the mother of a young infant (i.e., 0-2 months) than they did towards mothers of older infants.

The effect of matriline was readily apparent in the 2-fold higher rates of allocare exhibited by Tinka above those observed in the non-matriline subjects. Allocare was operationalized in this population by the behaviors “being carried/riding” and “huddling” since these were the only behaviors observed to occur in these subjects out of the array of behaviors possible in this category (Appendix A). Tinka was the only focal subject observed riding; she was observed riding on the back of her mother, but she was also seen riding on the backs of her maternal grandmother (Ras Mitat) and her aunt (Sudi). Of the four hypotheses advanced to explain the evolution of allocare, kin selection was the only hypothesis amenable to testing under these particular captive conditions. The captive environment does not lend itself to testing the benefits of philopatry because there is no choice involved concerning whether an individual stays at home or migrates, because members of this captive population cannot migrate to other territories. Provisioning of this captive troop make it unlikely that reciprocity or mutualism would explain allocare in this population as the opportunities for exchange of skills/benefits are substantially reduced in this matriline (e.g. n=1 focal). The kin selection hypothesis appears to be the most robust explanation for the, albeit, low levels of allocare observed in this study, but this finding requires further testing with a larger sample size of infants residing in matrilines.

Personality may also have contributed in shaping the behaviors observed in this baboon population, but direct tests of the putative effects of personality on behavior of the focal subjects were not possible. Previous studies of vertebrate personality have been conducted on a variety of animal species, including octopus (Mather & Anderson, 1993), cats (Feaver et al., 1986), and non-human primates (Clarke & Boinski, 1995).

Methodologies employed in these studies have not always been consistent (Itoh, 2002), but results have shown that personality can play a role in shaping the behavior of individual primates (see Freeman & Gosling, 2010 for a review). Anecdotal evidence for the existence of personality differences among the focal subjects of this study involve "my subjective impression" that Karamela appeared to be more introverted compared to the other focal subjects. She has the lowest mean rate of approach, affiliation, and agonism (Table 2), and she was frequently observed sitting apart from the troop, watching the other focal subjects play, this solitary tendency potentially explaining her lower frequency of contact with conspecifics.

Tinka, on the other hand, exhibited higher rates of agonism than those observed in the other focal subjects, and I documented a case of her "badgering" an older, high-ranking female in the troop. For example, Mendi, the second highest-ranking female of the alpha male's OMU, was observed investigating a stick. Tinka watched her do this for a brief period of time before approaching Mendi and grabbing for the stick. Initially Mendi avoided Tinka's attempts to grab the stick but then Tinka began climbing on Mendi and squealing, which alerted Ras Mitat, the highest-ranking female in the troop who is also Tinka's maternal grandmother. Mendi immediately relinquishes the stick to Tinka and withdraws from contact. Subsequent communication with the zoo staff revealed that these kinds of events were fairly common (Rives, pers. comm).

An effect of rank acquisition could be at play, but it would be difficult to tease out from the effect of matriline. Previous research on primate social hierarchies has shown that offspring tend to inherit the rank of their mothers (vervets (*Chlorocebus pygertjrus*) (Horrocks & Hunte, 1983); geladas (*Theropithecus gelada*) (le Roux et al., 2011), and maternally inherited linear dominance hierarchies have been described as characteristic of Cercopithecines (le Roux et al., 2011). Rank acquisition has been shown to be a strong influence on the rank and behavior of infants and juveniles in other species of baboons where females remain in their natal groups in the wild (yellow baboons (*Papio cynocephalus*): Lee and Oliver, 1972; chacma baboons (*Papio ursinus*): Cheney, 1977, olive baboons (*Papio anubis*): Johnson, 1987). Karamela's mother was one of the lower ranking females. This could be a contributing factor to the lack of recorded observations for agonistic behaviors. Wiley's and Zanizbar's mom were mid-ranking members of the troop, which would explain their averages. However, Tinka's lineage is much more complicated. Raz Mitat is the highest ranking female and is the mother of both of Tinka's parents, Tankara and Tukio. Because Tinka's grandmother is part of the longest matriline and the highest ranking female, it would be difficult to determine if it were rank or matriline affecting Tinka's behavior.

While the frequency of allocare behavior observed in this population was low, results of this study showed that the focal subject residing in longest matriline was the recipient of allocare at a higher average rate than those focal subjects, which were not members of extended matrilines. The effect of matriline was also evident in the frequencies of the three other behavioral categories recorded in this study. Tinka exhibited significantly higher rates of social interactions with conspecific focal subjects than those focal subjects which were not members of a matriline, although a sample size of n=1 matriline focal subject is insufficient to draw broad conclusions regarding the frequency with which allocare occurs in this population. Additional studies of captive Hamadryas baboon populations composed of a larger sample size of very young infants residing in both matrilines and non-matrilines are necessary to confirm (or not) the findings reported here.

CONCLUSION

The results of this study provide tentative evidence for the existence of allocare in this captive population of Hamadryas baboons at the NC Zoo in Asheboro, NC. The hypothesis that allocare would be observed in this population based on the presence of extended matrilines was supported, albeit, weakly since allocare was only rarely observed in this study. Nevertheless, there was a two-fold higher rate of allocare observed in the extended female-kin groups of mother-juvenile pairs than in the extended non-kin groups of mother-juvenile pairs, suggesting that the existence of strong social bonds among related kin provide opportunities for the expression of allocare even in species-atypical captive environments.

The importance of this research resides in the new insights that may be gained into the conditions under which allocare may be observed in an environment of decreased competition among group-living, hierarchical captive primate populations and how female-female relationships and competition play a role in the presence of allocare.

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APPENDIX A: HAMADRYAS BABOON (*PAPIO HAMADRYAS*) BEHAVIORAL ETHOGRAM

States: mutually exclusive behaviors which have a substantial duration (= bout) with a beginning and an end. Behaviors considered states are marked with an asterisk (*).
Events: mutually exclusive behaviors which are instantaneous or occur for a very brief time period.

I. Static/Spatial

Rest*	Any form of inactivity. May involve sitting, lying down, eyes closed (or not).
Move*	Any form of movement
Feed*	The focal animal uses their hands to bring food to their mouth.

II. Monitor/Adjust/Proximity

Glance	A brief look at a conspecific.
Approach/Contact	“A” moves towards “B” in a non-aggressive manner and touches physically contacts conspecific
Is Approached/Contact	Focal animal is moved towards by a conspecific in a non-aggressive manner and touched by a conspecific.
Withdraw/Contact	Movement away from a conspecific, breaking physical contact.
Is Withdrawn From/Contact	Focal is moved away from by a conspecific, breaking contact
Turn Away	A rotation of the body away from a conspecific
Is Turned Away From	Focal is rotated away from by a conspecific.
Follow	Focal moves in the same direction as conspecific
Is Followed	Conspecific moves in the same direction as focal

III. Social Interactions

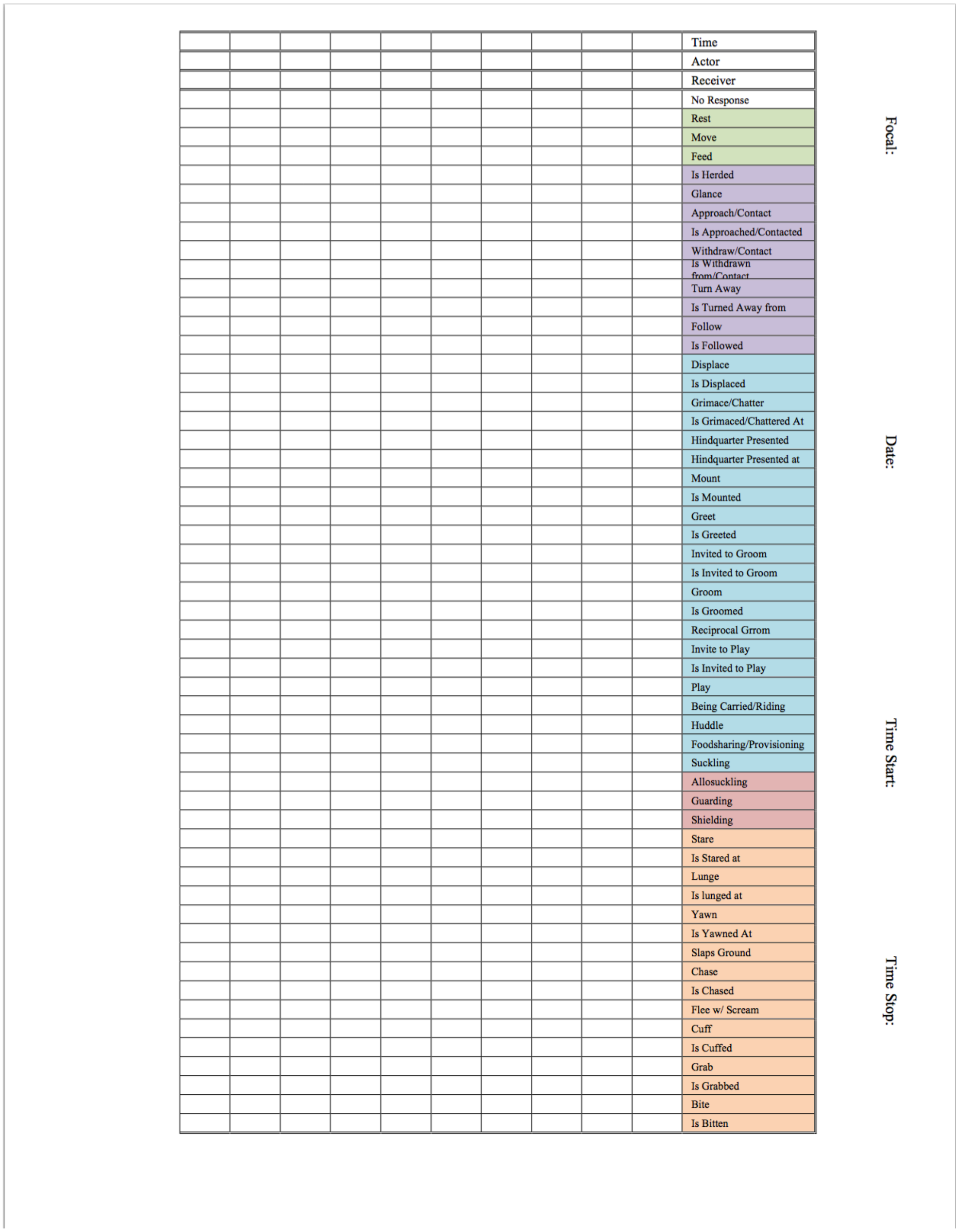
	Dominance/Submission
Displace	Moving very close, almost on top of a conspecific so that they are forced to move.
Is Displaced	Focal animal is the recipient of displacing behavior (see previous definition)
Grimace/Chatter	The bearing and clicking of teeth together, generally performed by a subordinate animal.
Is Grimaced/Chattered At	Focal is being given a warning through the bearing and clicking of teeth together by a dominant animal.
Present	Focal presents its hindquarters to a conspecific.
Is Presented	Focal animal is presented hindquarters of a conspecific
Mount	Move over back of partner facing same direction; partner’s ankles clasped by feet during full manifestation, which typically leads to thrusting.
Is Mounted	Focal animal is mounted by a conspecific?

Affiliative: behaviors that indicate a friendly relationship between conspecifics	
Greet	Focal meets and touches noses with conspecific
Is Greeted	Conspecific touches noses with the focal.
Groom	The manual separation of hair through the use of fingers and picking at coat or skin of another animal and occasionally putting lose particles into the mouth.
Is Groomed	Focal animal is the recipient of grooming behavior (see previous definition)
Reciprocal Groom	Grooms a conspecific after having been groomed
Invite to Play	Approaches a conspecific and initiates physical contact between the focal animal and another conspecific that can be rough but is not aggressively antagonistic.
Is Invited to Play	Focal animal is approached by a conspecific who initiates physical contact between the focal animal and themselves that can be rough but is not aggressively antagonistic.
Play*	Quiet rough-and-tumble wrestling

Allocare: Care that is provided by other group members and includes allomaternal care (i.e., care provided by group members other than the mother of the infant) and alloparental care (i.e., care provided by group members other than the parents of the infant.	
Being Carried/Riding	The focal animal is being carried by or riding on the back of a conspecific.
Food Sharing	Food is give to aa conspecific by another.
Huddling	An active and close aggregation of animals
Suckling/Nursing	The focal animal is positioned on the ventral area of a conspecific with the conspecific's nipple in their mouth.
Is Protected	The focal animal is shielded from danger by a conspecific. The conspecific will use their body to shield the focal.

Agonistic: behaviors that have been identified as aggressive, threatening, or confrontational	
Stare	A focused gaze at another conspecific for at least 3 seconds sometimes accompanied by eyebrows bobbing up and down
Is Stared At	Focal animal is the recipient of a stare (see previous definition)
Lunge	A sudden forward thrust of the body, typically with an arm outstretched to attack or seize a conspecific
Is Lunged At	Focal animal is the recipient of a lunge (see previous definition) by a conspecific.
Yawn	Mouth is fully open to show the canine teeth. Generally performed by adult males.
Is Yawned At	The focal animal is the target of a yawn (see previous definition).
Slaps Ground	One or two-handed forceful striking of the ground
Chase	Rapid advance towards another animal that exceeds the recipient's location at the time the action begins that is not in a play context. Eyelid flashing may be present
Is Chased	Focal animal is the recipient of chase behavior (see previous definition)
Flee w/ Scream	Rapid withdraw from a conspecific in response to aggressive behavior or an approach
Cuff	Manually striking a conspecific.
Is Cuffed	Focal animal
Grab	Use of the hands to grasp a conspecific
Is Grabbed	Focal animal is the recipient of grabbing behavior (see previous definition)
Bite	Strong unrestrained grip of the skin/ limb of another with the teeth, almost always accompanied by a scream from the recipient
Is Bitten	Focal animal is the recipient of a bite (see previous definition)

APPENDIX B: ETHOGRAM CHECK SHEET



										Time
										Actor
										Receiver
										No Response
										Rest
										Move
										Feed
										Is Herded
										Glance
										Approach/Contact
										Is Approached/Contacted
										Withdraw/Contact
										Is Withdrawn from/Contact
										Turn Away
										Is Turned Away from
										Follow
										Is Followed
										Displace
										Is Displaced
										Grimace/Chatter
										Is Grimaced/Chattered At
										Hindquarter Presented
										Hindquarter Presented at
										Mount
										Is Mounted
										Greet
										Is Greeted
										Invited to Groom
										Is Invited to Groom
										Groom
										Is Groomed
										Reciprocal Grrom
										Invite to Play
										Is Invited to Play
										Play
										Being Carried/Riding
										Huddle
										Foodsharing/Provisioning
										Suckling
										Allosuckling
										Guarding
										Shielding
										Stare
										Is Stared at
										Lunge
										Is lunged at
										Yawn
										Is Yawned At
										Slaps Ground
										Chase
										Is Chased
										Flee w/ Scream
										Cuff
										Is Cuffed
										Grab
										Is Grabbed
										Bite
										Is Bitten

Focal:

Date:

Time Start:

Time Stop:

APPENDIX C: TABLES

Table 1: The NC Zoo Hamadryas Group by Age

Subjects	Sex	Age in Years (as of 6/2015)
Sally	Female	30
Margie	Female	24
Matilda	Female	24
Negelli	Male	16
Addis	Male	16
Gondar	Male	16
Mendi	Female	16
Ras Mitat	Female	12
Geb	Male	10
Sudi	Female	10
Rhea	Female	10
Tukio	Male	9
Candy	Female	9
Zuri	Female	5
Meka Chini	Female	5
Tankara	Female	4
Tullu	Male	4
Babu	Male	3
Wiley	Male	2
Tinka	Female	1
Karamela	Female	1

Table 2: *Summary Statistics for Hourly Rates of Observed Behaviors*

Behavior	Mean +/- SD				p-value
	Karamela	Tinka	Wiley	Zanzibar	
Approach	6.56 +/- 2.49	9.36 +/- 3.53	6.78 +/- 3.81	6.88 +/- 3.56	**0.0002**
Affiliation	6.53 +/- 2.43	8.88 +/- 3.10	7.36 +/- 2.65	8.96 +/- 4.19	**0.0003**
Agonism	4.57 +/- 1.91	9.38 +/- 3.87	7.12 +/- 2.80	6.29 +/- 2.19	**<0.0001**
Allocare	0.37 +/- 0.57	0.43 +/- 0.68	0.13 +/- 0.34	0.16 +/- 0.38	**0.0085**

Table 3: *Tukey Simultaneous Tests for Differences of Means for Hourly Rates of Approach Behaviors*

	Karamela	Tinka	Wiley	Zanzibar
Karamela	--	--	--	--
Tinka	**0.0006**	--	--	--
Wiley	0.99	**0.002**	--	--
Zanzibar	0.97	**0.003**	0.99	--

Table 4: *Tukey Simultaneous Tests for Differences of Means for Hourly Rates of Agonistic Behaviors*

	Karamela	Tinka	Wiley	Zanzibar
Karamela	--	--	--	--
Tinka	**<0.0001**	--	--	--
Wiley	**0.0001**	**0.0009**	--	--
Zanzibar	**0.02**	**<0.0001**	0.48	--

Table 5: *Tukey Simultaneous Tests for Differences of Means for Hourly Rates of Affiliative Behaviors*

	Karamela	Tinka	Wiley	Zanzibar
Karamela	--	--	--	--
Tinka	**0.0025**	--	--	--
Wiley	0.58	0.09	--	--
Zanzibar	**0.0016**	0.99	0.08	--

Table 6: *Tukey Simultaneous Tests for Differences of Means for Hourly Rates of Allocare Behaviors*

	Karamela	Tinka	Wiley	Zanzibar
Karamela	--	--	--	--
Tinka	0.93	--	--	--
Wiley	0.12	**0.02**	--	--
Zanzibar	0.20	**0.05**	0.99	--

Table 7: *Between-sex Differences in Rate of Social Interactions*

Behavior	N	Mean +/- SD		p-value
		Female	Male	
Approach	92	7.96 +/- 3.35	6.83 +/- 3.67	**0.0308**
Affiliation	92	7.70 +/- 3.02	8.16 +/- 3.58	0.3480
Agonism	92	6.98 +/- 3.88	6.75 +/- 2.54	0.6270
Allocare	92	0.40 +/- 0.62	0.14 +/- 0.36	**0.0008**

Table 8: *Within-sex Differences in Rate of Social Interactions for Females*

Behavior	N	Mean +/- SD		p-value
		Karamela	Tinka	
Approach	92	6.56 +/- 2.49	9.36 +/- 3.53	**<0.0001**
Affiliation	92	6.52 +/- 2.43	8.88 +/- 3.10	**0.0001**
Agonism	92	4.58 +/- 1.91	9.38 +/- 3.87	**<0.0001**
Allocare	92	0.37 +/- 0.57	0.43 +/- 0.68	0.6190

Table 9: *Within-sex Differences in Rate of Social Interactions for Males*

Behavior	N	Mean +/- SD		p-value
		Wiley	Zanzibar	
Approach	92	6.78 +/- 3.81	6.88 +/- 3.56	0.9027
Affiliation	92	7.36 +/- 2.65	8.96 +/- 4.19	**0.0312**
Agonism	92	7.12 +/- 2.80	6.29 +/- 2.19	0.1160
Allocare	92	0.13 +/- 0.34	0.16 +/- 0.38	0.7023

Table 10: *Differences in Rate of Social Interactions for Matriline vs. Nonmatriline*

Behavior	N	Mean +/- SD		p-value
		Matriline	Nonmatriline	
Approach	92	9.35 +/- 3.53	6.74 +/- 2.05	**<0.0001**
Affiliation	92	8.88 +/- 3.10	7.62 +/- 2.07	**0.0236**
Agonism	92	9.38 +/- 3.87	5.99 +/- 1.43	**<0.0001**
Allocare	92	0.43 +/- 0.68	0.22 +/- 0.26	**0.0489**

APPENDIX D. FIGURES

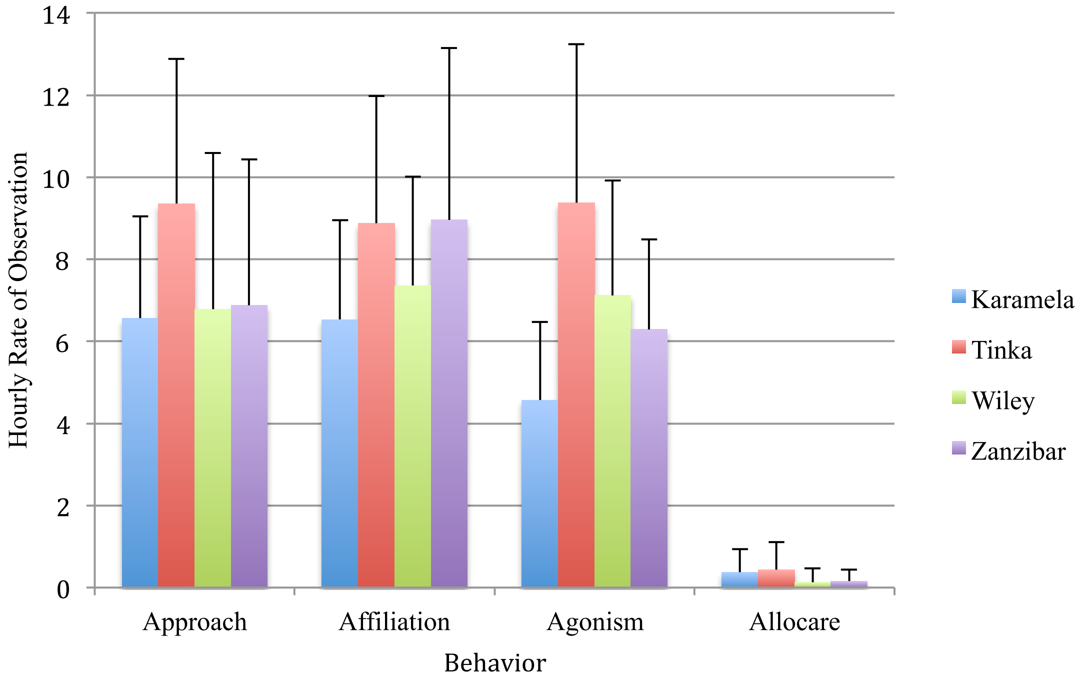


Figure 1: *Summary Statistics for Hourly Rates of Observed Behaviors*

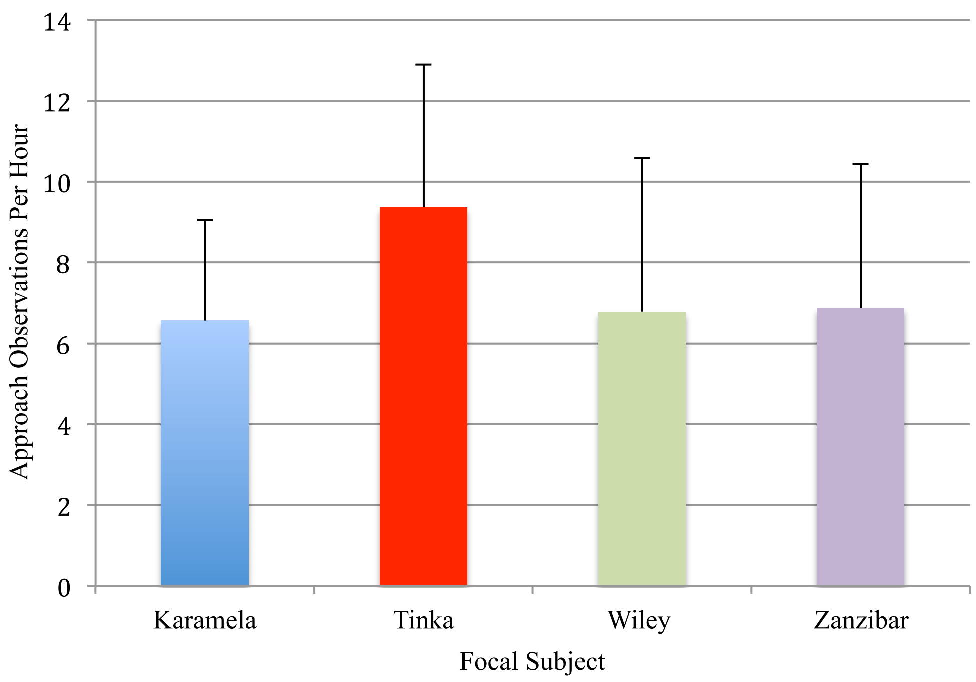


Figure 2: *Average Hourly Rates of Approach Per Focal Subject*

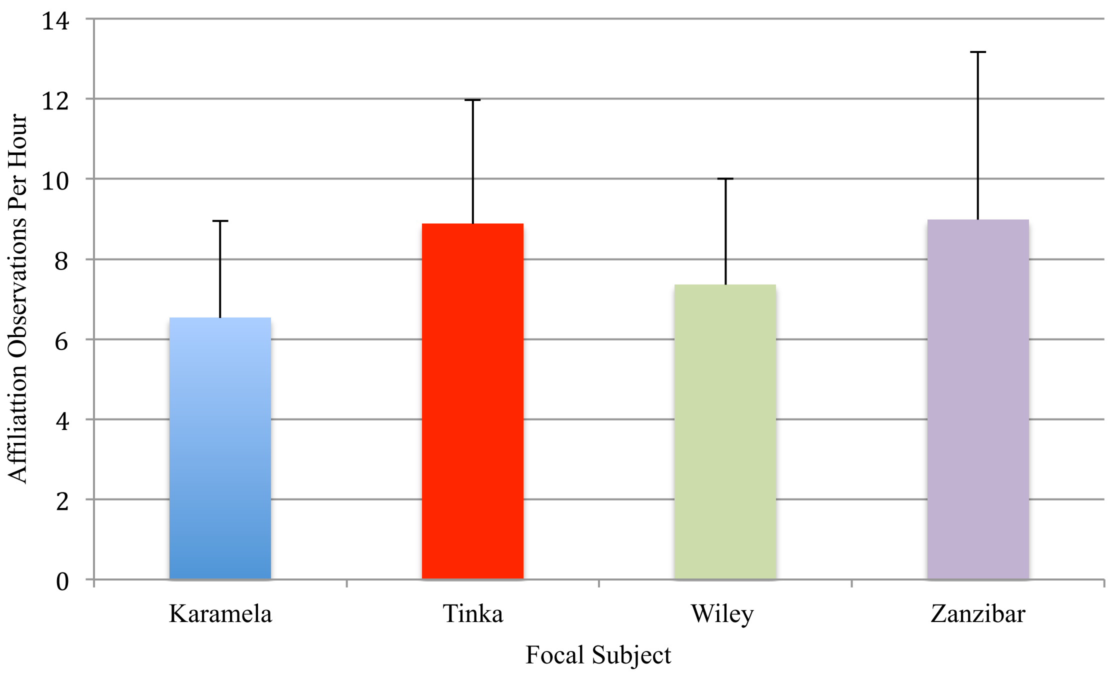


Figure 3. *Average Hourly Rates of Affiliation Per Focal Subject*

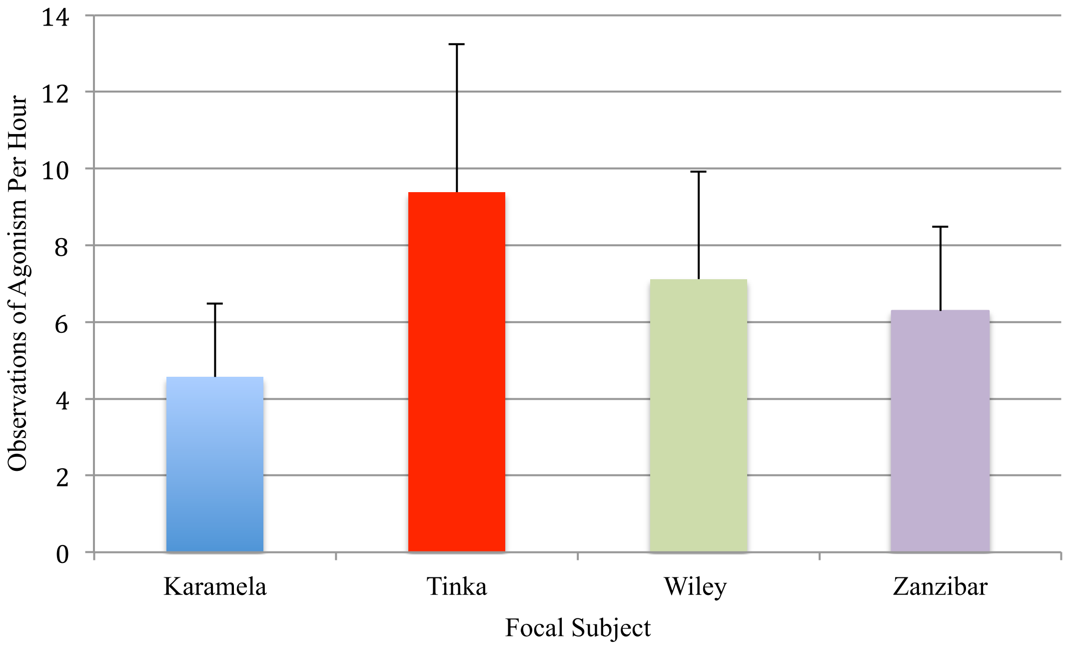


Figure 4: *Average Hourly Rates of Agonism Per Focal Subject*

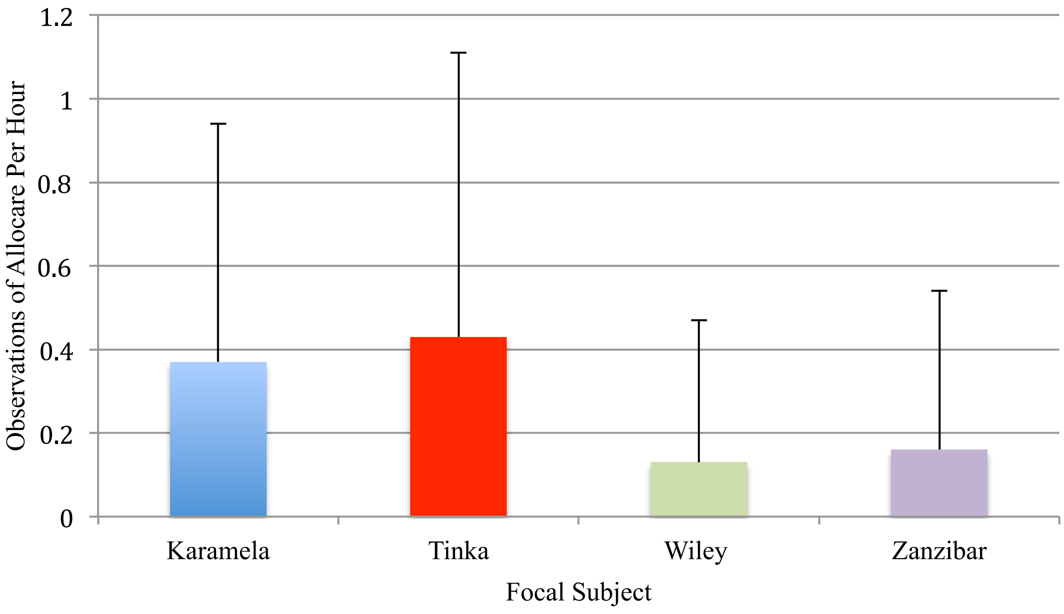


Figure 5: *Average Hourly Rates of Allocare Per Focal Subject*

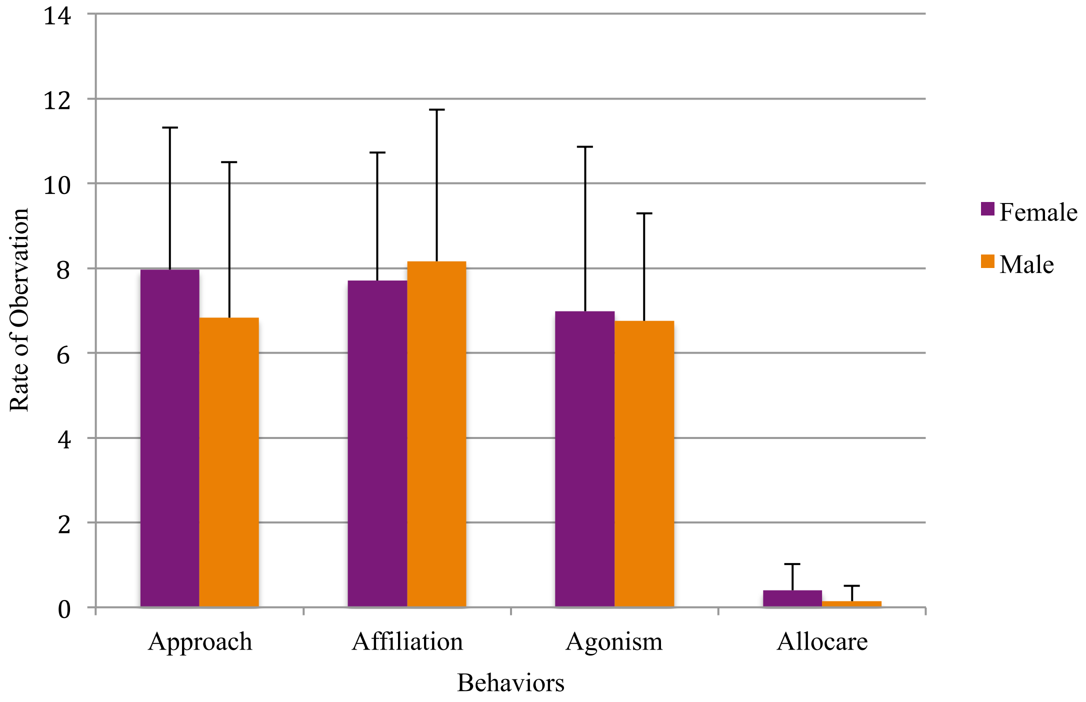


Figure 6: *Between-sex Differences in Rate of Social Interactions*

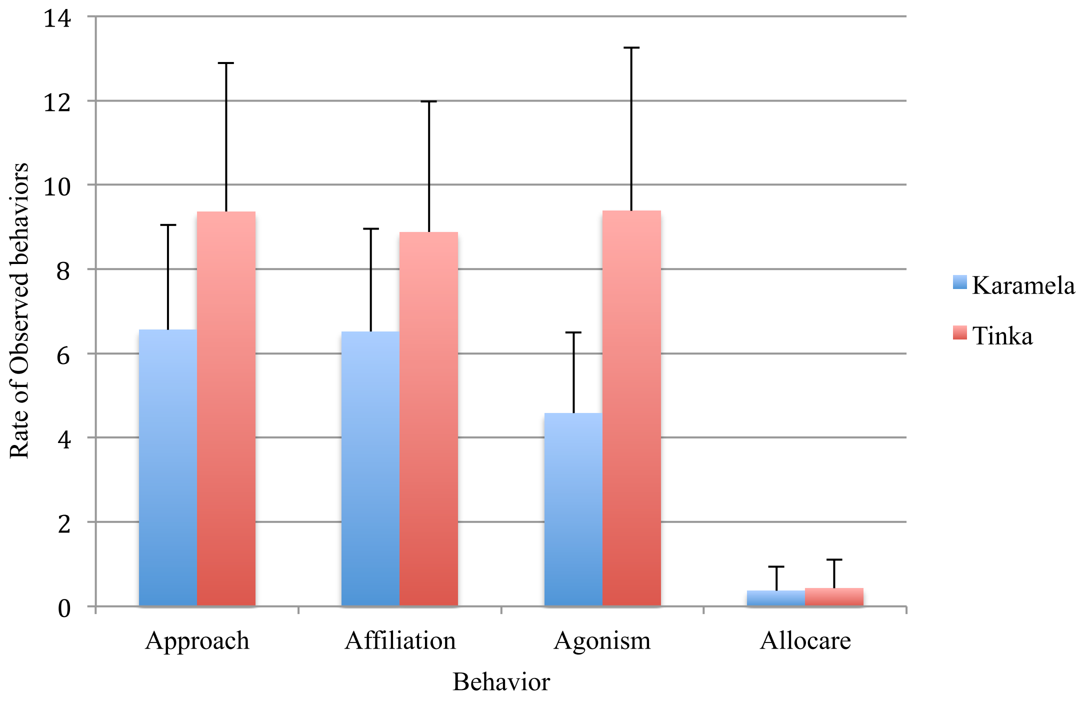


Figure 7. *Sex Differences Between Females in Rate of Social Interaction*

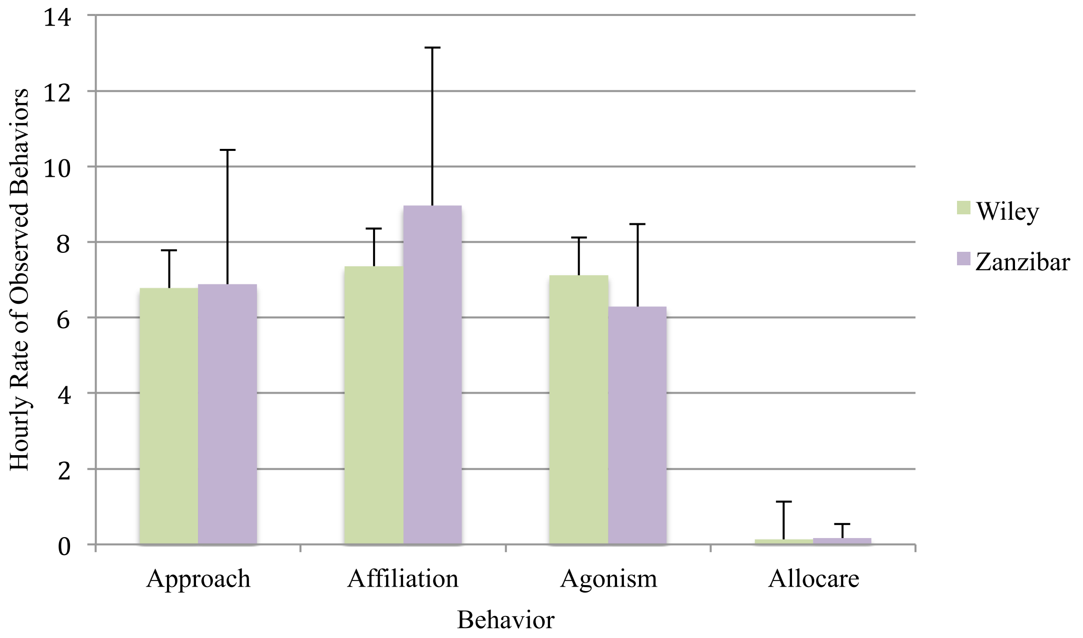


Figure 8. *Sex Differences Between Males in Rate of Social Interaction*

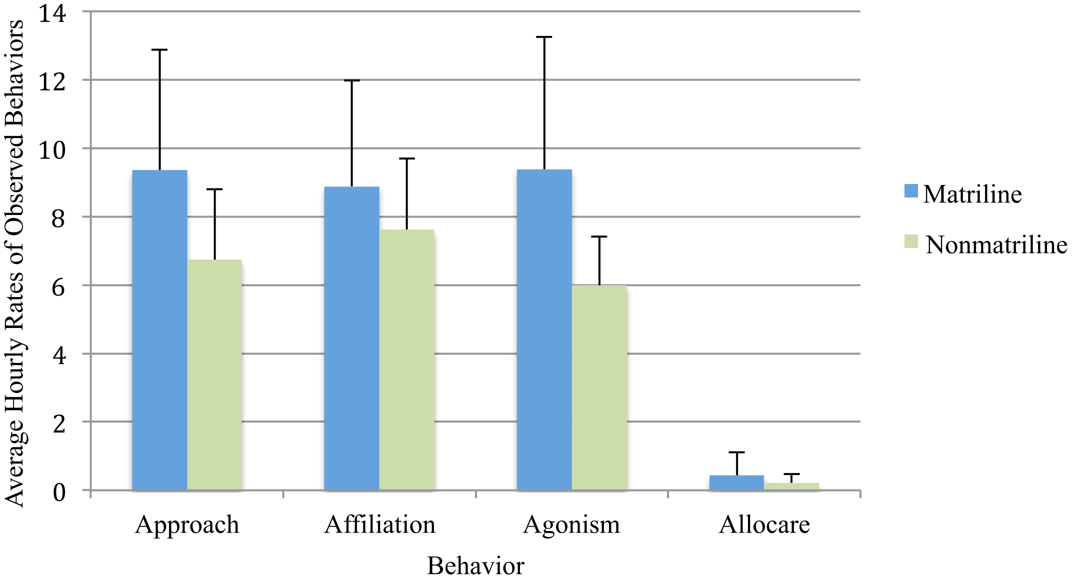


Figure 9. *Differences in Rate of Social Interactions for Matriline vs. Nonmatriline*