BEHAVIOR AND SOCIOENDOCRINOLOGY OF BONOBOS (*PAN PANISCUS*): MECHANISMS THAT CONTRIBUTE TO THE EVOLUTION AND MAINTENANCE OF SOCIAL STRUCTURE IN THE OTHER *PAN* SPECIES

by

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A DISSERTATION

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DISSERTATION ABSTRACT

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Title: Behavior and Socioendocrinology of Bonobos (*Pan paniscus*): Mechanisms That Contribute to the Evolution and Maintenance of Social Structure in the Other *Pan* Species

Research into the origins of our own social behavior begins with understanding how environmental elements lead to complex social interaction. Social structure emerges from these interactions as a bottom-up process, whose patterning constitutes the very framework of a society. Studies of behavioral mechanisms are important in determining the full repertoire that results in the social and dominance structures of a species. Hormones such as oxytocin and cortisol facilitate and fluctuate in response to social interactions and measuring their relative values among individuals is a valuable tool in testing functional hypotheses of behavioral mechanisms. The objective of this dissertation is to investigate several fundamental, under-, or previously unstudied behavioral mechanisms and hormonal correlates that shape the unique social system of bonobos.

The first study describes the pattern of expression of harassment behavior among immatures and tests predictions generated by the Exploratory Aggression and Rank Improvement hypotheses. Results demonstrate that immatures use harassment to test the nature of existing inter-individual relationships and to explore the parameters of aggressive behaviors and furthers our understanding of juvenile development of aggression and integration into the dominance hierarchy. The second study describes the pattern of occurrence of infant handling and tests predictions generated by several functional hypotheses, including examining the relationship between oxytocin and handling behaviors. Results show a significant sex difference in expression of handling where, during adolescence, male interest in infants sharply declines whereas females continue to handle infants, the expression of which was correlated with oxytocin. These results primarily support the Learning-to-Mother hypothesis and provide insight into the role oxytocin may play in facilitating care-giving behaviors in young females. The final study explores the patterning of female sexual behavior and male aggression, and investigates whether male constraint of female choice imposes a cost to females through induction of a stress response. Results show that while females exercise unconstrained mate choice through proceptive behaviors, males influence female receptivity through aggression and sexual coercion, shedding light on the degree to which rank related asymmetry in male mating success reflects female choice vs. constraint of choice.

This dissertation includes previously published and unpublished co-authored material.

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Jaeggi, A. V., Boose, K. J., White, F. J., & Gurven, M. (2016). Obstacles and catalysts of cooperation in humans, bonobos, and chimpanzees: behavioural reaction norms can help explain variation in sex roles, inequality, war and peace. *Behaviour*, *153*(9-11), 1015-1051.

White, F. J., Waller, M., Boose, K., Merrill, M. Y., & Wood, K. D. (2015). Function of loud calls in wild bonobos. *Journal of Anthropological Sciences*, *93*, 1-13.

Boose, K. J., White, F. J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American journal of primatology*, *75*(9), 917-926.

White, F. J., Waller, M. T., & Boose, K. (2013). Evolution of primate peace. *War, peace and human nature: The convergence of evolutionary and cultural views*, 389-405.

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For my boys

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CHAPTER I

INTRODUCTION

THEORETICAL BACKGROUND

> *"In considering structure, to limit discussion to relationships between actors in their capacity of playing roles relative to one another, where playing roles refers to the occupancy of a particular position in the society, is to consider only part of the whole, and to seek for principles whose pure expression is always confounded by that of others."*
>
> Hinde, 1976, 'Interactions, relationships, and social structure.'

The Socioecological Synthesis

The core principles of the theory of evolution by natural selection is that given variation, heritability of that variation, and differential reproduction as a consequence of that variation, those traits that yield greater relative reproductive success of their bearers will tend to be retained and spread, for that reason, through a population. Organisms will thus compete for access to resources that enable them to survive and reproduce within a particular environment (Darwin 1859). This competition for limited resources pits individuals of the same species, both within and between groups, against each other in a struggle for both survival and relative reproductive success. However, despite this inherent competition between individuals, cooperation, in one form or another, is evident across the whole of *Kingdom Anamalia*. Cooperative action ranges from genes interacting in a genome (Frank 1995) to the emergent property of social structure that arises out of individuals living together within a society (Watts 2010).

At the level of the individual organism, humans are among the cooperative outliers in the animal world. Research into the origins of our social behavior begins with an understanding of how elements of the environment lead to complex social interaction. Studies on primate behavioral ecology have demonstrated the importance of understanding the diversity of behavior of our closest relatives for shedding light on our own species' evolutionary trajectory. After nearly 60 years of work, the Socioecological Synthesis (SES) has emerged as the primary model for generating predictions about the ecological conditions that give rise to the variety of social systems seen within the Primate Order. The SES seeks to unify the core parameters that account for this behavioral diversity: 1) group living with particular emphasis on female group formation; 2) constraints on group size; 3) male distribution around female grouping patterns; 4) types of dispersal and competitive regimes; 5) the nature of social relationships within a group; and 6) the resulting higher order social structure that is characteristic of a species, genus, or clade. According to the SES, living in a group is, for most species, the foundation for complex social structure (Fig. 1.1).

Compared to other mammals, primates share a number of unique characteristics, particularly the Order's high level of sociality. Nearly all species of haplorrhines (the clade containing tarsiers, old world monkeys, and apes), and many genera of strepsirrhine (the clade containing lemurs, lorises, galagos, pottos, sifakas, and indris), live in stable social groups consisting of multiple males and females (Smuts et al. 1987). Within the broad context of evolutionary theory, group living depends on the benefits afforded to individuals in groups (e.g., reducing predation risk) outweighing the costs of sharing resources and dealing with intra-group conflicts. The SES predicts group living under a particular set of risks and resource distributions that act as important evolutionary pressures in primates. Although readily tested among short-lived species, the long lives of primates have made it difficult to test predictions of the SES model directly. Nevertheless, primates are subject to the same principles of evolution by natural selection and their distinctive attributes can be studied within this framework. For example, rather than obstacles to understanding the underlying selective processes, the behavioral flexibility characteristic of cognitive sophistication across primates is based on suites of adaptations to the complex social and ecological environments faced by these species. Additionally, organisms with few offspring are inherently subject to unique pressures that can be catastrophic to their net fitness, namely predation and infanticide. In general, the application of the SES over the last four decades has given shape to 3 key evolutionary agents shaping the evolution of group living in primates: 1) food resource characteristics; 2) the intrinsic threat of predation; and 3) avoidance of sexual coercion and infanticide (Fig. 1.1).

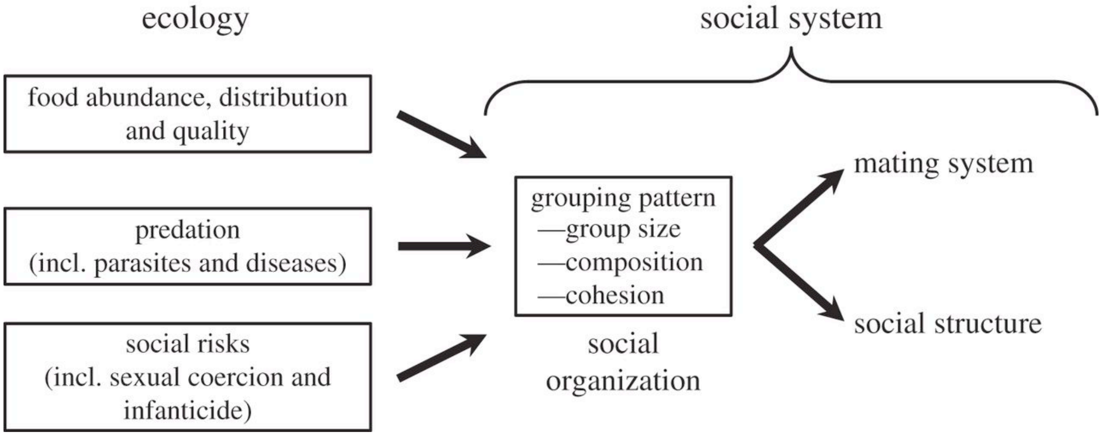

Fig. 1.1. Flow chart of the Socioecological Synthesis

Research on the evolutionary agents driving the group living in primates has focused primarily on the relationship between female aggregation and dispersal around food resources. Wrangham (1980) posited that spatial and temporal variance in food distribution and corresponding differences in the intensity of feeding competition could account for the differences in group size between species. He also suggested that differences in female social relationships and dispersal patterns could be tied to features of feeding competition (Wrangham 1980). He hypothesized that where the distribution of resources is patchily distributed, competition for these feeding patches will be frequent and intense. Selection would then favor the formation of dominance hierarchies and resource defense by groups of philopatric females who share not only the benefits of the spoils but gain additional inclusive fitness benefits by facilitating food access to close female kin and their progeny (Wrangham 1980). In contrast, then, where food resources are of low value or are evenly distributed in the environment, feeding competition will be less intense and the benefits of resource defense via the construction of female philopatric groups would be reduced (Wrangham 1980). Under this scenario, dominance relations between females would be less consistent, the payoff associated with cooperating with female relatives would be low and thus, females would be more likely to disperse into smaller groups with less feeding competition (Wrangham 1980). Collectively, these ideas became known as the Between-Group-Contest (BGC) competition component of the SES.

This brings up the questions of why there are groups with multiple males, and why do so many primate species have essentially stable associations between males and females? Permanent associations between males and females are unusual among mammals. Because females invest more heavily in offspring (primarily through the energetics involved in gestation and lactation) and are generally limited by their access to food resources, males typically compete for access to available fertile females, thus making females the limiting resource for male reproductive success (Trivers 1972). One consequence of this asymmetry in parental investment is that variations in group composition across primate species may best be understood in terms of the connection between female sociality and male mating strategies, whereby males follow the distribution of females (Bradbury and Vehrencamp 1977 ; Emlen and Oring 1977; Wrangham 1980; Clutton-Brock 1989). The spatial distribution of females has been shown to be a reliable predictor of the number of males in a group (Andelman 1986 ; Dunbar 1988 ; Altmann 1990 ; Janson 1992) and Andelman (1986) was first to demonstrate that the number of males per group across a range of cercopithecine species was correlated with the number of females. Subsequent research corroborated these findings (Dunbar 1988; Altman 1990), showing correlations between numbers of females and males for a range of species, leading Altmann (1990) to famously conclude, “primate males go where the females are.”

In many primate species, permanent associations between males and females are thought to be the result of a high risk of infanticide (van Schaik and Kappeler 1997). Infanticide functions as an effective sexual strategy, whereby males are able to increase their fitness by killing the dependent offspring of rival males, ending the mother's lactational amenorrhea and thus bringing her into estrous sooner than she otherwise would (Hrdy 1974). On this view, males stay in a group, even when the mating season has ended, to protect their offspring against attacks from other males. The conditions that give rise to infanticide are associated with male monopolization of females because males will evolve alternate strategies to access females, including the use of infanticide. Given the extreme fitness cost of infanticide for mothers, females are expected to evolve counterstrategies to reduce that risk (Hrdy 1979). Polyandrous, or promiscuous, mating has been proposed as a counterstrategy that functions to confuse paternity among the available males (Hrdy 1979; van Schaik et al. 1999). Supporting this hypothesis is the observation that non-conceptive female receptivity is highest in species with a high degree of infanticide (Soltis 2002; Paul 2002). Additionally, under contexts of high mating skew, primate males will often engage in other forms of intersexual conflict, such as sexual coercion, where male directed aggression drives female proceptive sexual behavior (e.g. chimpanzees: Muller et al. 2011). As expected, this leads to inter-sexual competition, because as the principles of parental investment theory predict, females are expected to express mate choice by mating with the highest quality male available (Trivers 1972). Studies determining the degree to which male directed aggression influences female proceptivity and receptivity are thus important for our understanding of the socioecological parameters that give rise to female choice and male constraint of choice.

Just as resource distribution and infanticide risk drive the formation and composition of primate groups, these factors also influence the types of social relationships within and between communities. When within-group competition is strong, selection will favor traits that lead to success in aggressive interactions (Janson 1985). This is particularly the case for females, whose reproductive success is closely tied to their ability to acquire food resources (Janson 1985). Because aggressive interactions entail costs, even among physically powerful individuals, selection is expected to favor the formation of dominance hierarchies as a mechanism to regulate access to resources while, simultaneously, minimizing the costs associated with constant aggressive interaction between individuals (de Waal and Luttrell 1989).

De Waal (1986) has hypothesized that evidence of this aggression reduction function of dominance hierarchies can be found in the evolution of formalized signals of dominance and submission in species with clear and linear hierarchies. Conceptually, de Waal (1986) likens these signals to a type of 'peace agreement' whereby when individuals compete over a resource, instead of costly physical altercation, each flashes the appropriate signal (of dominance or submission) that is the product of their previously determined relationship. Stability in dominance hierarchies is achieved via agonistic support of relatives in contests and reciprocal coalitions with non-kin (Chapais 1992). Furthermore, primates are unique among mammals for maintaining long-term, and often equitable, social bonds with conspecifics. Enduring relationships, however, inevitably involve contests over limited resources, including access to mates, the outcome of which can significantly impact fitness. These recurring and dynastic competitive interactions are the mechanism by which dominance and submission between individuals is established, and in turn, defines the nature of social relationships within a group (Hinde 1983). Studies detailing the agonistic interactions among all individuals, including immatures, across a variety of contexts are therefore necessary to accurately describe dominance in a species.

Becoming fully integrated into the dominance hierarchy is a developmental process of particular importance in species where dominance rank confers fitness-related benefits, such as mating success in males and access to resources in females. Acquiring the social skills necessary to navigate the complexities of group living is one factor thought to contribute to the slow life histories that characterize primates as a clade. Life history theory posits that the energy extracted from the environment is finite and cannot be allocated for multiple functions at the same time (Charnov 1979, 1991; Stearns 1992). Natural selection therefore is predicted to produce age and context specific tradeoffs among growth, maintenance, and reproduction (Charnov 1979, 1991). The extended period of juvenility (growth) in primates is posited to have been selected for to provide time for brain development to learn critical species-specific social, foraging, and mating and/or parenting skills (Harvey and Clutton-Brock 1985). For example, successful rearing of offspring in primates is dependent on juvenile females having the opportunity to learn and gain valuable experience practicing and watching other females perform maternal behaviors (Harlow and Harlow 1965; Lancaster 1971). Studies that give special attention to the behavioral mechanisms of juveniles and adolescents are therefore valuable for understanding the full behavioral repertoire of a species and the resulting social structure that develops from interactions among *all* individuals within a group. Social structure emerges from these interactions as a bottom-up process, whose patterning constitutes the very framework of a society (Hinde 1976) (Fig. 1.2).

The Genus *Pan*

The earliest comparison of our two closest extant relatives was detailed by Robert Yerkes in his book Almost Human, by mistake. Yerkes had assumed the young male he named Prince Chim and the female he named Panzee both belonged to the species *Pan troglodytes*, the common chimpanzee. He describes Prince Chim as an intellectual genius, alert, adaptable, and agreeable in disposition in comparison to the female youngster, Panzee. We now know Prince Chim was a bonobo, *Pan paniscus*, and that Yerkes had given the first accounts of behavioral differences between chimpanzees and bonobos. Decades later, Jane Goodall would conduct her pioneering work on the wild chimpanzees of Gombe, setting off an avalanche of studies on the species who would go on to redefine the meaning of being human. Although bonobos were formally recognized as a separate species within the *Pan* genus in 1929, detailed investigations into their behavior and ecology wouldn't come until much later, when researchers Kano, Badrian and Badrian, White, Idani, and Furuichi began publishing their observations from wild field sites. Bonobos are endemic to the Congo basin, a region with dense vegetation that has been plagued by human conflict over the last several decades. For these reasons, observations of wild bonobos are difficult and continue to lag behind the field studies of chimpanzees through to the present day.

Nevertheless, researchers are steadily working towards establishing a set of ecological parameters that explain the observed variation in behavior across the *Pan* genus. Early comparative research detailed significant differences in dominance, aggression, inter-community interactions, and use of sociosexual behavior (Kuroda 1979; Thompson-Handler et al. 1984; Kano 1992; White 1996; Nishida 1997). More recently, differences across bonobo field sites (ex. Lomako: White 1992, 1996; Lui Kotal: Hohmann and Fruth 2003) demonstrate the importance of expanding the breadth of information we have on bonobos to gain the full picture of their behavioral repertoire and the ecological conditions that give rise to it. Chimpanzees occupy a range of habitats across equatorial Africa and show marked behavioral differences across the populations that inhabit different regions (see Stumpf 2011, Table 20.3 and Fig. 20.1, ppg. 342-345). This has led some researchers to conclude that these observed behavioral differences are primarily driven by ecology and not tied to species-specific behavioral repertoires (see Stanford 1998).

Both chimpanzees and bonobos are male philopatric and exhibit a multi-male multi-female grouping pattern with fission-fusion community structure (Nishida

1968; White 1988; Kano 1992). Both species are large bodied, ripe fruit specialists who derive protein from both plant and animal sources (Kano 1992; Goodall 1986). Although consumption of terrestrial-herbaceous-vegetation (THV), social insects, and vertebrates varies considerably across chimpanzees and bonobo field sites, both species are primarily frugivorous (Wrangham et al 1998; Conklin-Brittain et al. 1998). There are, however, key differences in chimpanzee and bonobo habitats that may have shaped female spatio-temporal distribution. For example, White (1996) demonstrated that bonobo habitats exhibit less seasonal variability in food availability relative to what has been observed across chimpanzee field sites and, therefore, experience reduced variability in feeding competition, allowing females to associate more frequently and in greater party sizes.

These differences in ecology are also thought to impact reproductive parameters within the genus. Greater party sizes and more permanent associations between males and females in bonobos likely reduce the risk of infanticide (Kano 1992; Stanford 1998) compared to chimpanzees, who are known to kill infants both within and between communities (see Arcadi and Wrangham 1999). Among female chimpanzees, dispersing copulations across all of the male group members is thought to confuse paternity of their offspring and has been conceptualized as a counter-strategy to infanticide, although females may also concentrate copulations with the alpha male during times when conception is most likely (Stumpf and Boesch 2006). In response, because chimpanzee dominance is sex based, males may use sexually coercive aggression directed at females to constrain female choice (Muller et al. 2009; 2011). In bonobos, numerous studies on inter-individual relationships in bonobos have demonstrated that females can occupy the highest rank positions within the dominance hierarchy (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016) and that females form strong bonds with both males and females (White1998; Hohmann et al. 1999). Mating success and paternity skew are high among male bonobos (Boose et al. 2012; Surbeck et al. 2017), but the degree to which this skew is the result of female choice vs. male constraint of female choice is not known.

Finally, bonobo habitats have less variation in seasonality of food availability, which may also contribute to the slightly lower inter-birth-intervals (IBI) seen in bonobos compared to chimpanzees (Nishida 1990; Furuichi et al. 1998; White et al. 2008). Coupled with the inferred low risk of infanticide, opportunities for individuals to interact with infants may be greater in bonobos than in chimpanzees. The function of interactions with infants in bonobos and the impact of these relationships on social and dominance structures, however, has gone largely unstudied in this species.

HORMONAL REGULATION OF BEHAVIORAL MECHANIMS

Natural selection is expected to have shaped hormonal responses to different life and environmental contexts in ways that maximize reproductive success. The degree to which the hormonal response is plastic can vary by taxa, with primates being more flexible as a clade than other mammals. Investigations into the socioendocrinology of primates, therefore, can shed light on the different biological pathways that regulate and facilitate complex sociobehavioral mechanisms. In particular, the hormones oxytocin and cortisol are known to facilitate, and fluctuate in response to, social interactions. Studies measuring the association between levels of these hormones and social behavior within a group therefore provides a valuable tool for testing functional hypotheses about behavior.

Oxytocin

Oxytocin (OT), along with other neuropeptide hormones, functions as a modulator of complex social behavior and social cognition in mammals (Lim et al. 2006). Produced by the hypothalamus and stored and secreted by the pituitary gland, OT acts primarily as a neuromodulator in the brain where, once released, is not immediately reabsorbed or broken down into a metabolite and diffuses into the cerebrospinal fluid where it influences neurons in several areas of the brain. OT has long been recognized for its functions in several aspects of reproduction including parturition, lactation, and mating (Fuchs et al. 1982; Caldwell et al. 1986; Smith 1989; Witt and Insel 1991) and has also been associated with the regulation of social behaviors (see Benarroch 2013; Feldman 2012; Meyer-Lindenberg et al. 2011 for review) such as anxiety and affiliation (Insel 1992; Insel and Winslow 1991; Witt et al. 1992), interpersonal trust (Van IJzendoorn and Bakermans-Kranenburg 2012), recognition of emotions and empathy (Rodrigues et al. 2009; Hurlemann et al. 2010; Lischke et al. 2012; Perry et al 2013), pair bonding in monogamous species (Insel 1992; Insel and Hulihan 1995; Ross et al. 2009;

Snowden et al. 2010; Schneiderman et al. 2012), and social bonding and food sharing in chimpanzees (Crockford et al. 2013; Wittig et al. 2014).

More recently, research has begun to focus on the role of OT as a key neuromodulator of caregiving, responsible for the facilitation and maintenance of maternal behaviors (Pedersen 1997; Strathearn 2011; Feldman 2012; Pedersen 2013; Kim et al. 2014). Further studies using animal models have significantly advanced our understanding of the neuroendorine pathways of OT mediated maternal behaviors. For example, injection of OT stimulates the onset of species-specific maternal behaviors in rats (Pedersen and Prange 1979). In mice, variations in lactation-induced OT levels have been found to correspond to variations in maternal behaviors (Francis et al. 2000) and administration of OT has been found to suppress rates of infanticide and simultaneously increase care-giving behaviors (McCarthy et al. 1986; McCarthy 1990). In female sheep (ewes) central injection of OT has been found to rapidly stimulate species typical maternal responses (Kendrick et al. 1987), while the administration of peridural anesthesia, which blocks the normal rise in cerebrospinal fluid (CSF) concentrations of OT, was found to inhibit onset of maternal behaviors (Levy et al. 1992). In rhesus macaques, researchers have found that variations in maternal behaviors, such as time spent grooming and nursing, are associated with variations in circulating OT (Maestripieri et al. 2009). OT has also been implicated in the modulation of maternal behaviors in humans, particularly during pregnancy and the postpartum period. For example, peripheral OT levels rise and remain high in pregnant and parturient women (Feldman et al. 2007; Levine et al. 2007; Gordon et al. 2008, 2010) relative to non-pregnant women (Feldman et al. 2007; Gordon et al. 2008). Researchers have also found that OT levels during pregnancy are predictive of maternal behaviors such as infant gaze, vocalizations, positive affect, and affectionate touch during the postpartum period (Feldman et al. 2007) and mothers who exhibit a pattern of rising OT during pregnancy and the early postpartum period self-reported stronger attachment to offspring (Levine et al. 2007). In addition, higher OT levels have found to be associated with greater infant affect synchrony and social engagement (Feldman et al. 2010). The results of these studies indicate that OT may function in a state vs. trait manner, ready to influence the onset and facilitation of maternal behaviors when the context of providing care-giving behaviors to infants arises.

Cortisol

Cortisol is a glucocorticoid hormone produced by the adrenal glands that modulates the body's response to external stressors. Stressors are elements of an organism's environment that perturb an individual's physiological or behavioral homeostasis (Selye 1975). The physiological mechanism behind the induction of a stress response has been well studied in animals, including primates (see Sapolsky et al. 2000). Upon perception of a stressor, the hypothalamus-pituitary-adrenal axis (HPA) is activated, causing a cascade of neuroendocrine events whereby the hypothalamus releases corticotropin-releasing hormone (CRH), which causes the anterior pituitary to secrete adrenocorticotropic hormone (ACTH) into the circulatory system. ACTH is taken up by the adrenal gland where it stimulates the secretion of glucocorticoids which function to facilitate bringing the body back to homeostasis. Best known for its role in the 'fight-or-flight' response, cortisol up-regulates gluconeogenesis (the metabolism of fat, carbohydrates, and protein into glucose), increasing energy production when an individual is faced with a stressor. At the same time, processes that are not required for immediate survival are down-regulated and only when the external stressor has been resolved, will cortisol levels return to baseline. When chronically elevated, however, cortisol can have deleterious effects on several systems in the body including immune functioning, cognitive performance, and sleep patterns (ex. Dickerson et al. 2004) and chronic exposure to stressors can, therefore, impose a significant fitness cost.

As discussed above, competition for both food and mates are inherent features of group-living species and aggressive behavior associated with this competition can induce a stress response. This response is detectable through the relative changes in an individual's circulating level of cortisol and has been demonstrated in a number of primate species (Sapolsky 2005, see Anestis 2010). Variation in cortisol levels between individuals within a group have been associated with acquiring and maintaining rank as well as aggression received by subordinate individuals (e.g., Surbeck et al 2012). Researchers have also demonstrated that the sexually coercive aggression female chimpanzees receive from males (Muller et al. 2011) is costly to females in terms of the induction of a stress response (Muller et al. 2007), suggesting a negative impact on fitness. Measuring variation in cortisol levels in response to social stressors is, therefore, a valuable tool in assessing the relative importance and impact of agonistic interactions on inter-individual relationships.

DISSERTATION OBJECTIVES

There are few longitudinal and multidimensional examinations of one of our closest relatives, the bonobo (*Pan paniscus*). The objective of this dissertation is to use five consecutive years of data collection to investigate several under-studied or previously unstudied behavioral mechanisms that shape the unique social system of what has been called the other *Pan* species.

1. **Mechanisms of Development**:
    a. *Harassment*: to assess the functional nature of this mechanism and its role in facilitating the entry of juveniles and adolescents into the adult dominance hierarchy, I will describe the expression of harassment behaviors and test the predictions generated by the Exploratory Aggression and the Rank Improvement hypotheses
    b. *Infant Handling*: to better understand this frequently occurring but not yet studied behavioral mechanism in bonobos, I will describe the patterning of expression of infant handling, test predictions generated by six functional hypotheses to account for infant handling, and determine the relationship between infant handling and oxytocin, a known facilitator of maternal behaviors
2. **Mechanisms of Mating**:
    a. Female *proceptivity* and *receptivity*: to establish clearer picture of female choice in bonobos, I will examine the pattern of expression of

these behavioral mechanisms and their relation to male directed aggression

b. *Sexual coercion*: to more fully understand the degree to which rank related asymmetry in male mating success reflects female choice vs. constraint of choice, I will describe male directed aggression in the context of mating and will examine the impact of sexual coercion on the stress response of females

METHODS

Study Population

All data were collected on the captive group of bonobos housed at the Columbus Zoo and Aquarium (CZA) in Columbus, Ohio, USA during five study periods: 2011 (June 23 – August 29), 2012 (May 20 – July 13), 2013 (April 14-June 16), 2014 (June 3-July 10), and 2015 (August 27-September 14). Over the course of these five study periods, CZA had a total of 11 females and 8 males, whose sex and age class distributions changed over time (see Table 2.1, 3.2, and 4.1). The bonobos were housed in a complex of areas consisting of two large indoor public viewing exhibits (54.8 m^2 each) with multiple climbing structures, two off-exhibit indoor enclosures (22.6 m^2 each), two off-exhibit outdoor enclosures (18.5 m^2 each) and a large naturalistic outdoor public viewing exhibit (57.9 m x 45.7m, 2647.7 m^2) with grass, mature trees, and an artificial stream and waterfall. During the summer months of each study period, the bonobos were released into the outdoor exhibit each morning at approximately 0730 hr and were brought back into the indoor enclosures at approximately 1900 hr. The bonobos were rarely brought inside between these hours, except for extenuating circumstances (i.e. dangerous inclement weather or an emergency). Each night the party that occupied the outdoor exhibit was brought into one of the indoor enclosures and the outdoor exhibit remained empty until the following morning. The bonobos were fed each morning and evening at approximately 0730 and 1900 hr. Additional supplemental enrichment feedings were sometimes given throughout the day.

The keepers at CZA managed the bonobos to simulate the species typical fission-fusion process of variable party composition. In the morning, bonobos were allowed access to each other and parties were set based mostly on individual bonobo association preferences rather than parties that were predetermined by the keepers. Most individuals had equal access to each other, but some of the adult males were never allowed to be together because of previous conflicts that had resulted in serious injury (Jimmy and Donnie and Bila-Isia and Donnie). This management process usually resulted in three parties that lasted for 2–3 days. Parties rarely changed on a daily basis or continued unchanged for m ore than 4 days. Each sub-group typically occupied different public display areas.

Individual age classifications were assigned based on the descriptions of age-class characteristics of bonobos detailed by Thompson-Handler et al. (1984). For example, Thompson-Handler et al. (1984) described an infant as an individual that ‘keeps in frequent proximity to mother; commonly rides ventrally but also may ride dorsally during progression; nurses frequently;’ a juvenile as an individual ‘no more than half size of adult; generally independent but closely associate with mother and occasionally seen to cling; development of secondary sexual characteristics slight;' an adolescent female as 'smaller than adult animals, genital swellings small at all times observed;' an adolescent male as 'smaller and more gracile than adult (approximately three-quarters size), scrotum not fully pendant;' an adult female as 'feull size (slightly smaller than large males), genital swellings developed;' and an adult male as 'full size, scrotum fully pendant' (p. 349). Individuals were therefore categorized according to the following: 0-2 years = infant; 3-7 years = juvenile; 8-9 years = adolescent I; 10-12 years = adolescent II; and >13 years = adult. These age classes vary slightly from what was reported for a wild population (Kano 1992) and reflect the accelerated development that can occur in captivity where food resources are rich and abundant. Additionally, adolescents were split into two developmental categories: 1) adolescent I, where individuals begin to display the physiological characteristics associated with the transition of puberty such as ano-genital swelling in females and expansion in testicle size in males, but where both sexes are generally still non-fertile (Marson et al. 1991; Stumpf 2011); and 2) adolescent II, where female ano-genital swellings are accompanied by menstruation and fertility, and where males undergo a significant growth spurt, including testicles that become larger, more pendulous, and are considered to be fully functioning. In the wild, females younger than 10 years are generally assumed to exhibit adolescent sterility and are therefore considered to be non-fertile (Marson et al. 1991; Stumpf 2011). In captivity, however, observations show that females can reach menarche as early as 9 years and can give birth during adolescence (Boose, unpublished data). Furthermore, adolescent males have been observed copulating with ejaculation (Boose, unpublished data).

Behavioral Observations

Daily observations at CZA usually began around 0730 hours and ended sometime between 1300 – 1700 hours and resulted in a total of 1819 observation hours of the course of five study periods (2011, 2012, 2013, 2014, and 2015). All behavioral data were collected by K. Boose using focal follows and all occurrence sampling of predetermined behavioral events (e.g., agonistic interactions such as conflicts and harassment of adults by immatures).

Hormonal Analyses

Urine collection and storage. Urine samples were collected in accordance with CZA's existing urine collection protocol using either a free catch method where individual subjects urinated through the mesh caging directly into a collection cup, or, where urine was pipetted directly off a clean floor surface immediately after a subject urinated into a plastic cryo tube. All subjects were previously trained to urinate on command (i.e., present genitals and urinate in exchange for a small food reward). Samples were then immediately frozen and stored at -20°C until they were packed on dry ice and shipped overnight to the Snodgrass Human Biology Research Laboratory at the University of Oregon in Eugene, OR where they were stored at -80°C until time of analyses.

Measurement of cortisol. To avoid multiple freeze-thaw cycles, each sample was first brought to room temperature and 0.5 ml was aliquoted into several cryo tubes. Thawed samples were then diluted (1:20) in assay buffer supplied in the 96-well Detect X Cortisol Enzyme Immunoassay Kit from Arbor Assays™ (catalog no. K003-H5) and assayed according to the kit manufacturer's instructions. The manufacturer of this kit reported the detection limit for this assay as 45.4 pg/ml. To control for variation in the amount and concentration of voided urine, all samples were assayed for creatinine concentrations (Seltzer and Ziegler 2007) using the DetectX™ Creatinine Urinary Detection Kit from Arbor Assays. The manufacturer listed the detection limit for this assay as 0.037 mg/dL. Samples run for creatinine were diluted (1:20) and run according to the kit manufacturer's instructions. All plates were read using a BioTek™ microplate reader and analyzed with Gen5™ software version 2.0.

Measurement of oxytocin. To avoid multiple freeze-thaw cycles, each sample was first brought to room temperature and 0.5 ml was aliquoted into several cryo tubes. Thawed samples were then diluted (1:4) in assay buffer supplied in the 96-well Oxytocin Enzyme Immunoassay Kit from Enzo Life Sciences™ (catalog no. 901-153A) and assayed according to the kit manufacturer's instructions. The manufacturer of this kit reported the detection limit for this assay as 15.0 pg/ml. To control for variation in the amount and concentration of voided urine, all samples were assayed for creatinine concentrations (Seltzer and Ziegler 2007) using the DetectX™ Creatinine Urinary Detection Kit from Arbor Assays. The manufacturer listed the detection limit for this assay as 0.037 mg/dL. Samples run for creatinine were diluted (1:20) and run according to the kit manufacturer's instructions. All plates were read using a BioTek™ microplate reader and analyzed with Gen5™ software version 2.0.

Data Analyses

Frequency data were compared using G Tests of Goodness of Fit with Williams correction applied and G Tests of Independence. Rank order correlations were performed using Pearson and Spearman rank order correlations (Sokal and Rohlf 2012). Two way ANOVA's and paired *t*-tests were used to compare variance between individuals and groups. Dominance rank among adults was determined from the direction and outcome (e.g., fleeing upon aggression) of a decided agonistic event and displacement matrix and analyzed using R (version 3.3.1). Linearity in the dominance rank of adults was found to be complete and significant (Landau's h = 0.476, p <0.01) and adults were ordered into a linear dominance hierarchy and assigned a unique rank number where 1 represents the highest-ranking individual.

STATEMENT OF CONTRIBUTION

This dissertation includes previously published and unpublished material co-authored by Frances White, Josh Snodgrass, and Audra Meinelt. Chapter II, *Harassment of Adults by Immatures in Bonobos (*Pan paniscus*): testing the Exploratory Aggression and Rank Improvement hypotheses*, has been published in the journal *Primates* (Boose and White 2017); Chapter III, *Non-Maternal Infant Handling in Bonobos (*Pan paniscus*): oxytocin and support for the Learning-to-Mother hypothesis*, includes co-author contributions identified in the beginning of the chapter; and Chapter IV, *Female Choice in Bonobos (*Pan paniscus*): evidence of male constraint and coalitionary sexual coercion*, also includes co-author contributions as detailed in the beginning of the chapter.

BRIDGE TO CHAPTERS II, III, AND IV

The purpose for this chapter was to provide a brief overview of the relevant theoretical background of behavioral ecology and socioendocrinology that frame the studies presented in the following chapters (II, III, IV) of this dissertation. The behavioral mechanisms presented in this dissertation are rooted in the evolutionary framework of the Socioecological Synthesis, particularly the way in which inter-individual interactions, determined from phylogenetic and ecological history, shape social and dominance structures in bonobos. Furthermore, hormones, such as oxytocin and cortisol, modulate an individual's response to the social environment and are a valuable tool in the assessment of the relative importance and function of behavioral mechanisms.

Chapter I also provided an overview of the study population, observational methods, and hormonal and data analyses for this dissertation. As discussed here in this chapter, all data were collected on the Columbus Zoo bonobo colony in Columbus, Ohio. During the course of the study periods of this dissertation, the Columbus Zoo maintained a large population of 11 female and 8 male bonobos, ranging in ages from 0-36 years, using a fission-fusion style of management similar to what occurs naturally in the wild. This husbandry style provided an opportunity to collect both naturalistic and detailed behavioral and hormonal data on a species that has been historically difficult to study in detail in the wild.

CHAPTER II

HARASSMENT OF ADULTS BY IMMATURES IN BONOBOS (*PAN PANISCUS*): TESTING THE EXPLORATORY AGGRESSION AND RANK IMPROVEMENT HYPOTHESES

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INTRODUCTION

The infants, juveniles, and adolescents of many species of non-human primates are known to exhibit a type of behavior where they routinely pester adult group members, often provoking an aggressive response (e.g., baboons: Rowell, 1967; langurs: Dolhinow, 1972; java monkeys: de Waal, 1977; vervets: Bramblett, 1978; and chimpanzees: deWaal and Hoekstra, 1980, Pusey 1990, Nishida et al. 1999). Observations of such behavior by immatures range from mild aggression, such as throwing sand, dirt, and branches at adults (de Waal and Hoeskstra 1980) to more aggressive contact, such as jumping onto resting adults and biting, kicking, and pulling their hair (van Lawick-Goodall 1968) and/or tails (Bramblett 1978). Although referred to in the literature with a variety of terms, including ‘bothering,’ ‘teasing,’ ‘annoying,’ ‘provocative,’ ‘quasi-aggression,’ and most recently as ‘harassment,’ the central feature of these behaviors is the potentially harmful or unpleasant stimuli it provides to the recipient (Adang 1984).

The first accounts of what could be described as harassment of adults by immatures in chimpanzees come from Hebb and Thompson’s (1954) early descriptions of “anger” in a captive group and from van Lawick-Goodall’s (1968) studies of the wild chimpanzees of Gombe, where young juveniles in both studies were observed aggressively pestering resting and grooming adults. De Waal and Hoeskstra (1980) remarked in their study of the contexts of aggression in chimpanzees, that juveniles and infants would regularly tease adults, who would often respond with aggression. Although such mentions of harassment behaviors were somewhat common, it was not until Adang’s (1984, 1985) studies of the Arnhem group of chimpanzees that the ethology and contextual parameters were formally described. Initially calling the behavior ‘*quasi-aggression*,’ because it had “elements in common with both play and aggression,” Adang (1984, 1985) defined harassment by immatures as any type of aggressive bothering behavior directed at adults irrespective of the response generated. Adang (1985) noted that “individuals responded in many ways, including occasional punishment in the form of retaliation.” He further differentiated harassment from other forms of immature aggression by identifying the context as “spontaneous and ... that [which] does not occur in close temporal association with conflict between any individuals in the group” (Adang 1984). Harassment by immatures, therefore, poses an interesting evolutionary question because of the inherent risks associated with retaliation, particularly when an adult target directs aggression toward smaller immature individuals.

Addressing this question of adaptive significance, Adang (1984, 1985) explored the mechanistic properties of harassment by investigating the type of behavior performed by immatures and the response behavior of targets at Arnhem. He found that all immatures harassed adults and directed their behaviors mostly at individuals outside of their immediate subgroup, consisting of their mother and closely associated female(s) that provided a degree of allo-maternal care (Adang 1984). Although all adults in the group were targets, he observed that males were more likely to receive mild aggression such as 'bluff-like' behaviors while females more frequently received behaviors with physical contact, such as hitting and kicking. Adang (1984) also found that certain responses to harassment were reinforcing in nature where the amount of harassment a target received was dependent on the type of response given. He observed that harassment would continue for longer if the target responded in an agonistic way (either aggressively or submissively) whereas friendly behaviors and ignoring the immature generally resulted in the cessation of harassment. From these results, Adang (1984, 1985) hypothesized that harassment is a form of social exploration used by immatures to learn about and refine aggressive behaviors, and to acquire information about the relationship between the actor and lesser-known individuals.

Currently referred to as the Exploratory Aggression hypothesis, Adang (1985) proposed two functional forms of exploratory aggression: 1) investigating authority and 2) reducing uncertainty. Investigating authority functions mainly as a way for immatures to acquire knowledge about the parameters of dominance by directing mild forms of harassment behavior at high-ranking group members (i.e., male chimpanzees) and to explore the properties of physical contact aggression by directing these types of harassment behaviors at lower-ranking group members (i.e., female chimpanzees) (Adang 1985). The second functional form, reducing uncertainty, is expressed in a manner similar to the way in which immatures learn about and explore the physical world (Adang 1985). In reference to the observation by Seligman (1975) that animals attempt to control their environment and to predict events before they happen, Adang (1985) hypothesized that immatures use harassment to reduce existing uncertainty in relationships by either controlling or predicting the response of targets. Both submissive and aggressive reactions provide information about dominance relationships that immatures can use to predict the behavior of targets. Eliciting submission may also reflect an immatures ability to control the response of the target (Adang 1985). Ignoring or making friendly contact with an immature, however, does not provide information about dominance relationships and is, therefore, not implicitly reinforcing in the context of harassment (Adang 1985). The Exploratory Aggression Hypothesis (1984, 1985) was initially formulated to describe harassment of adults as a mechanism through which infants and juveniles reduced relationship uncertainty, although Adang (1986) noted that as individuals matured, these behaviors might be used as a means for adolescents to exercise control (i.e., elicit submission) over adults as they begin to establish dominance.

Harassment of adults by immatures has also been documented in wild chimpanzees at the Gombe (Pusey 1990) and Mahale (Nishida et al. 1999) field sites. Contextualized as a threatening behavior, researchers at both sites recorded juvenile males spontaneously aggressing adult females, mainly through display-type behaviors such as waiving branches and throwing stones, and noted that these behaviors increased in frequency as the males matured into adolescence (Pusey 1990; Nishida et al. 1999). It was not until a later study at Mahale, however, that the behavior was specifically addressed between immature males and adult females (Nishida 2003). Referred to as the Rank Improvement hypothesis by Nishida (2003), responses in this study were classed as either 'ignore' or 'not ignore,' and as either 'retaliate' (which included both aggressive and submissive behaviors) or 'not retaliate.' Nishida (2003) reported that duration of harassment was longer when targets reacted to harassment than when they did not react. Although adult female targets frequently ignored juvenile males, they mostly responded with defensive and avoidance behaviors when harassed by adolescent males (Nishida 2003). In addition, immature males harassed more frequently than did females and targeted adult females significantly more than adult males (Nishida 2003). Evidence of adolescent male chimpanzees dominating females as a precursor to entering the male dominance hierarchy is well known (Goodall 1986; Nishida 1990) and harassment at Mahale was, therefore, interpreted as a mechanism of rank improvement used primarily by immature males as a means to outrank adult females (Nishida 2003).

Harassment of adults by immatures, to our knowledge, has only been investigated in detail in chimpanzees (captivity: Adang 1984, 1985; wild: Nishida 2003). Despite small differences in definitions and composition of study groups, there are general consistencies between the Arnhem and Mahale studies in the pattern of responses to harassment that can shed light on how harassment functions within a particular social system. Results from both sites showed that immatures frequently harass adult group members and that continuation of harassment was dependent on the type of response given by the target (Adang 1984, 1985; Nishida 2003). Additionally, females from both sites were targeted more than males and responded more frequently with agonism whereas males responded more with neutral behaviors (Adang 1985, Nishida 2003). These results suggest that harassment in chimpanzees is influenced by the sex-based dominance structure of the species, where the lower ranking sex (females) is targeted more frequently and responds in a manner consistent with harassment as a challenge to their dominance status. In order to examine the degree to which this pattern is dependent on social system and to test the assumptions of the Exploratory Aggression and Rank Improvement hypotheses, detailed observations of harassment in species with markedly different social structures are needed.

The purpose of this study, therefore, is to describe the pattern of harassment of adults by immatures in bonobos and to discuss the proposed functions of the two competing hypotheses within the context of the bonobos' unique social system. Instances of adolescent males provoking adult males with harassment behaviors have been observed in the wild population at Wamba (Furuichi 1997). Furuichi (1987) described these exchanges as 'play-like agonistic interactions' (p. 862) and considered them to be similar to the quasi-aggressive behaviors of chimpanzees reported by Adang (1985). Harassment of adults by immatures, however, has not yet been studied in detail in this species. Bonobos, like chimpanzees, are male philopatric and exhibit a multi-male multi-female fission-fusion community structure (Nishida 1968; White 1988; Kano 1992). There are, however, distinct differences between the two species, particularly in the types of social bonds displayed and complexity within the dominance hierarchy. Female bonobos, unlike female chimpanzees, form strong bonds with both males and females (White 1998; Hohmann et al. 1999) and can occupy the highest rank positions (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016). In chimpanzee communities, sex plays a defining role in the group dominance hierarchy where each male out-ranks each female (Goodall 1986; Nishida 1990). In bonobos, male rank can be heavily influenced by factors other than sex, which can result in variable dominance status (Kano 1992; Furuichi 1997; White and Wood 2007; Surbeck et al. 2011). We therefore expect that the patterning of harassment behavior in bonobos will reflect these similarities and differences to chimpanzees.

Definition of Terms

The following definitions are based on those originally given by Adang (1984, 1985) and reported by Nishida (2003) to describe harassment and response behaviors:

- **Immature harassment of adults**: from here on referred to as *harassment*, is any deliberate bothering or teasing type of aggression performed by immatures and directed at adults, irrespective of the response of the target individual and without any apparent cause or source of provocation. Although the term ‘harassment’ can be used to describe other types of aggressive behaviors in various contexts, such as ‘sexual harassment’ (e.g., Clutton-Brock and Parker 1995; van Schaik et al. 2004; bonobos: Hohmann and Fruth 2003), food ‘sharing under pressure’ (e.g., Stevens 2004), and harassment of immigrants (Pusey 1980, Watts 1992), the term ‘harassment,’ for the purpose of this paper, will refer exclusively to the above definition. Following Adang’s (1984) description, harassment type behaviors performed with a ‘play-face’ (or exhibiting any of the play behavior patterns described by Palagi (2006, see Table 3)), those performed as a direct response (within 2 minutes) of an aggressive initiative, or within 2 minutes of an agonistic event, and those directed towards individuals engaged in copulation or socio-sexual behavior were not scored as harassment.

  1. *Actor* – the ‘harasser,’ an immature performing harassment behaviors directed at an adult
  2. *Target* – an adult receiving harassment behaviors from an immature

- Harassment behaviors were further categorized based on the qualitative features originally described by Adang (1984):
  1. *Mild aggression*
     a. ‘bluff-like’: charging, dragging branches, swaying, stamping ground, etc.
     b. ‘swinging object’: manually wielding an object in the direction and proximity (within 2 meters) of the target
     c. ‘throwing object’: tossing an object (grass, dirt, wood-wool, branches/leaves, etc.) at a target
  2. *Physical contact aggression*: biting, hitting, kicking, pulling the hair, etc. of a target.

- **Responses to harassment**:
    1. *Agonistic* – responses that indicate either a submissive or aggressive position by the responding target (Scott and Fredericson 1951; Hinde 1966).
        1. Aggressive: counter-attack type responses such as chase, charge, hit, bite, etc., performed with tense and brusque movements indicative of aggression
        2. Submissive: defensive type responses such as fleeing, screaming, gesturing, baring-teeth, presenting rump, etc., indicative of submission and performed without expressing any sign of aggression
    2. *Neutral* – responses that do not overtly indicate a submissive or aggressive position by the responding target
        1. Ignore: no apparent reaction to harassment or a small response such as watching or facing away from harasser
        2. Avoid: leave the proximity of the harasser or to crouch, parry, or flinch without expressing aggression or submission
        3. Affiliative: friendly contact with the harasser such as playing, grooming, presenting for copulation or socio-sexual behavior such as genito-genital rubbing ('gg rubbing') without expressing signs of submission

HYPOTHESES AND PREDICTIONS

As discussed above, there are two competing, but not mutually exclusive, hypotheses on the function of harassment behavior. Each generates a slightly different set of predictions.

Hypotheses

- The ***Exploratory Aggression*** hypothesis describes harassment as a mechanism used by immatures to learn about the parameters of aggression and dominance behavior (i.e., investigate authority) and to acquire information about novel, complex, or unpredictable relationships (i.e., uncertainty reduction) (Adang 1984, 1985).
- The ***Rank Improvement*** hypothesis describes harassment as a mechanism of dominance acquisition used by immatures to outrank adults (Nishida 2003).

Predictions

The ***Exploratory Aggression*** hypothesis (Adang 1984, 1985) predicts that:

1. All adults will be targets of harassment but immatures will less frequently direct harassment toward his/her own mother, and toward adult females that provide him/her allo-maternal care.
2. Type of harassment behavior performed by immatures will be dependent on the dominance rank of the target where lower ranking adults will more

frequently receive physical contact aggression and higher-ranking adults will more frequently receive mild aggression.

3. Continuation of harassment will be dependent on type of response behavior where both aggressive and submissive responses will elicit continuation of harassment more frequently than will neutral responses because aggressive and submissive responses present greater opportunity for immatures to learn how to control (i.e., elicit submission) and/or predict (i.e., elicit aggression) the behavior of targets, than do neutral responses.

The ***Rank Improvement*** hypothesis (Nishida 2003) predicts that:

1. Immatures will not harass adults they already outrank. Frequency of harassment, however, will be negatively correlated with the dominance rank of adults because immatures use harassment to ascend the dominance hierarchy.
2. Aggressive responses will elicit harassment more frequently from immatures than will submissive responses because submissive responses indicate submission from the target and aggressive responses indicate dominance or incomplete submission from the target. Neutral responses will not elicit harassment that differs from expected frequency values because neutral responses do not indicate dominance or submission from the target.
3. We further predict that type of response to harassment will be dependent on:

a. dominance rank of the target where lower-ranking targets will respond more frequently with agonistic (aggressive and submissive) behaviors and higher-ranking targets will respond more frequently with neutral behaviors because lower-ranking targets are more likely to perceive harassment as a threat to their rank status; and
b. the age-class of the immature where older (i.e., adolescent) individuals will more frequently elicit agonistic (aggressive and submissive) responses and younger (i.e., juvenile and infant) individuals will more frequently elicit neutral responses because older immatures are more likely to represent a threat to the target's rank status.

Additional prediction:

As discussed above, female bonobos can hold positions of power within the group (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016). Performance of harassment by immatures may, therefore, be biased toward immatures with high-ranking mothers and we predict that frequency of harassment performed will be correlated with the dominance rank of adult females with offspring in the group.

METHODS

Subjects and Housing

All data were collected on the captive group of bonobos housed at the Columbus Zoo and Aquarium (CZA) in Columbus, Ohio, USA during 2011 (June 23 – August 29) and 2012 (May 20 – July 13). Daily observations usually began around 0730 hours and ended sometime between 1300 – 1700 hours resulting in 909 observation hours. At the time of the study, CZA had 8 females and 8 males that were housed in a complex of areas consisting of two large indoor public viewing exhibits (54.8 m^2 each) with multiple climbing structures, two off-exhibit indoor enclosures (22.6 m^2 each), two off-exhibit outdoor enclosures (18.5 m^2 each) and a large naturalistic outdoor public viewing exhibit (57.9 m x 45.7m, 2647.7 m^2) with grass, mature trees, and an artificial stream and waterfall. The keepers at CZA managed the bonobos to simulate the species typical fission-fusion process of variable party composition. In the morning, bonobos were allowed access to each other and parties were set based mostly on individual bonobo association preferences. During this study period most individuals, with the exception of two of the adult males (Jimmy and Donnie), had equal access to each other and all immatures had abundant opportunity to interact with all adults. This management process usually resulted in three parties that lasted for 2-3 days, and rarely changed on a daily basis or exceeded 4 days.

Age Classifications

Individual age classifications were assigned based on the descriptions of age-class characteristics of bonobos detailed by Thompson-Handler et al. (1984). For example, Thompson-Handler et al. (1984) described an infant as an individual that ‘keeps in frequent proximity to mother; commonly rides ventrally but also may ride dorsally during progression; nurses frequently’ (p. 349). Individuals were therefore categorized according to the following: 0-2 years = infant; 3-7 years = juvenile; 8-9 years = adolescent I; 10-12 years = adolescent II; and >13 years = adult. These age classes vary slightly from what was reported for a wild population (Kano 1992) and reflect the accelerated development that can occur in captivity where food resources are rich and abundant. Additionally, adolescents were split into two developmental categories: 1) adolescent I, where individuals begin to display the physiological characteristics associated with the transition of puberty such as ano-genital swelling in females and expansion in testicle size in males, but where both sexes are generally still non-fertile (Marson et al. 1991; Stumpf 2011); and 2) adolescent II, where female ano-genital swellings are accompanied by menstruation and fertility, and where males undergo a significant growth spurt, including testicles that become larger, more pendulous, and are considered to be fully functioning. During the 2011 season there were 2 infants (1 male, 1 female), 3 juveniles (1 male, 2 female), 2 adolescent I’s (1 male, 1 female), and 1 adolescent II (male). During the 2012 season two individuals changed age class where 1 juvenile female became an adolescent I and 1 adolescent I female became an adolescent II. For both the 2011 and 2012 seasons there were 4 adult males and 4 adult females (Table 1).

Table 2.1. Group composition and age class assignments of the CZA bonobo colony (2011-2012)

				Age Classes	
Subject	Birth Year	Sex	Adult Rank	2011	2012
Unga	1993	F	1	Adult	Adult
Ana Neema	1992	F	2	Adult	Adult
Donnie	1993	M	3	Adult	Adult
Susie[a]	1982[b]	F	4	Adult	Adult
Lady[a]	1982[b]	F	5	Adult	Adult
Jimmy[a]	1979[b]	M	6	Adult	Adult
Maiko	1984	M	7	Adult	Adult
Toby[a]	1979[b]	M	8	Adult	Adult
Bila Isia	2001	M	--	Adol II	Adol II
JoT	2002	F	--	Adol I	Adol II
Gander	2003	M	--	Adol I	Adol I
Lola	2004	F	--	Juv	Adol I
Gilda	2006	F	--	Juv	Juv
Jerry	2008	M	--	Juv	Juv
Mary Rose	2010	F	--	Inf	Inf
Wilbur	2010	M	--	Inf	Inf

Note: [a]Wild caught individuals; [b]estimated birth year.

Behavioral Observations

Data were collected using focal follows and all occurrence sampling of agonistic and harassment events (Altman 1974). A bout of harassment was considered terminated when the actor ceased performing harassment behaviors for 2 minutes. To examine the interaction between response type and likelihood of receiving further harassment, bouts were also scored as either ‘continued,’ where the actor continued harassment after the initial response of the target, or ‘discontinued,’ where the actor ceased harassment immediately after the initial response of the target. Initial response to harassment was scored as the first type of behavior exhibited by the target in response to receiving harassment. If no response was recorded within 10 seconds of the onset of harassment behavior, then 'ignore' was scored as the initial response (Adang 1984).

Data Analyses

Frequency analyses. Frequency data were compared using *G* Tests of Goodness of Fit with Williams correction applied (G_{gof}) and *G* Tests of Independence (G_{toi}) (Sokal and Rohlf 2012). Expected frequencies (E_{freq}) of harassment and response behaviors were calculated by dividing the number of individuals in a given age and/or sex class observed performing the behavior (N_c) by the total number of individuals in a given age and/or sex class (N_t) and multiplying this number (N_c/N_t) by the total number of behaviors recorded (B):

$$E_{freq} = (N_c/N_t) \text{ x } B$$

Rank analyses. Pearson correlations were used to test rank effects and correlations between recorded behaviors. Dominance rank among adults was determined from the direction and outcome (e.g., fleeing upon aggression) of a decided agonistic event and displacement matrix and analyzed using R (version 3.3.1). Linearity in the dominance rank of adults was found to be complete and significant (Landau's $h = 0.476$, $p <0.01$). Individuals were, therefore, ordered into a linear dominance hierarchy and assigned a unique rank number where 1 represents the highest-ranking individual and 8 represents the lowest-ranking individual (Table 2.1).

All immatures had mothers in the group and some females had >1 immature offspring. The amount of harassment behaviors performed was averaged across all of a female's immature offspring (for females with >1 immature offspring) in order to investigate the relationship between harassment performed and dominance rank of the actor's mother. All other analyses were run using BIOMstat (version 3.30t).

RESULTS

General Pattern of Harassment in Bonobos

A total of 1140 agonistic events between all age-sex classes were recorded during the 2011 and 2012 seasons and 489 of these events were between an immature and an adult. 413 of these immature-adult agonistic events fulfilled the specific definition of harassment, given by Adang (1984) and described in the introduction of this paper, and were therefore classed as harassment by an immature toward an adult (Fig. 2.1). Of the 413 harassment events, 279 were categorized as 'mild aggression' and 134 were categorized as 'physical contact aggression' (Table 2.2). Harassment escalated into a conflict between the actor and target in 14 of the 413 recorded events.

Table 2.2. Distribution of type of harassment behavior received by sex of target

	Target Sex	
Type of Harassment Behavior	Male	Female
Mild Aggression		
'bluff-like'	94	38
'swinging object'	72	13
'throwing object'	52	10
Total	218	61
Physical Contact Aggression		
'bite' 'hit' 'kick' 'pull hair' *etc.*	84	50
Total	302	111

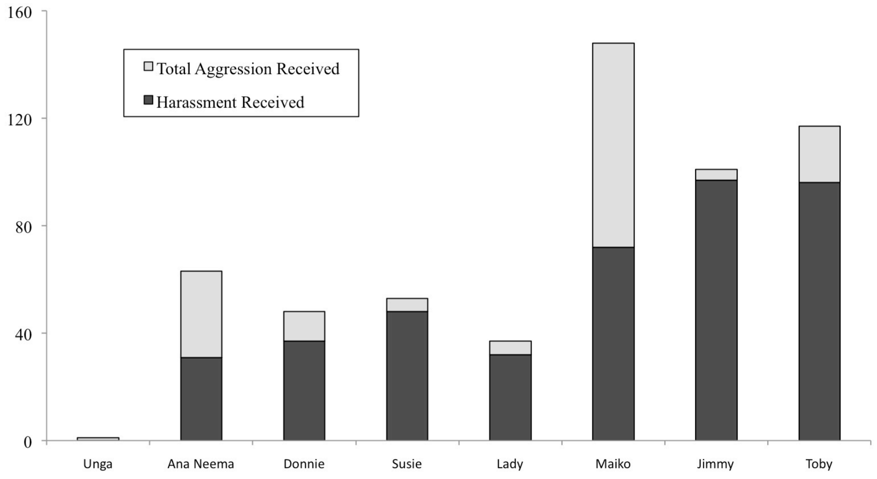


Fig. 2.1. Distribution of total aggression and harassment received by target

Actors. All immature individuals (N=8) were observed performing harassment behaviors and there was no significant correlation ($r = 0.384$, $df = 3$, $p = 0.190$) between harassment performed and dominance rank of the mother. Therefore, assuming an equal likelihood in performance, frequency of harassment did not show an expected distribution between the age or sex classes. Adolescent I performed harassment significantly more frequently than did adolescent II, juveniles, and infants ($G_{gof} = 193.818$, $df = 3$, $p < 0.001$; Fig. 2.2, Table 2.3). We also found that males performed harassment significantly more frequently than did females ($G_{gof} = 67.226$, $df=1$, $p<0.001$; Fig. 2.2).

Table 2.3. Harassment performed and type of response elicited by age-class of actor

		Harassment Performed		Response Type Elicited		
				Neutral	Agonistic	
Actor Age-Class		observed	expected		submissive	aggressive
Adol II	N=2	37	82.6	12	11	14
Adol I	N=3	252	123.9	61	124	67
Juvenile	N=3	99	123.9	58	16	25
Infant	N=2	25	82.6	16	2	7

Targets. All adults received harassment from immatures with the exception of the alpha female (Unga). We could not fully test the prediction that immatures direct more harassment toward individuals outside of a ‘sub-group’ (as defined by Adang (1984)) because all immatures had equal access to all the adults in the group and no adult females were observed engaged in allo-maternal care. However, immatures were never observed directing harassment behaviors at their own mother. For 5 of the 8 adults in the group, harassment constituted the majority (>50% of the total) of aggressive initiatives they received (Fig. 2.1) and males were targets of harassment significantly more frequently than were females ($G_{gof} = 91.674$, $df = 1$, $p < 0.001$; Fig. 2.2).

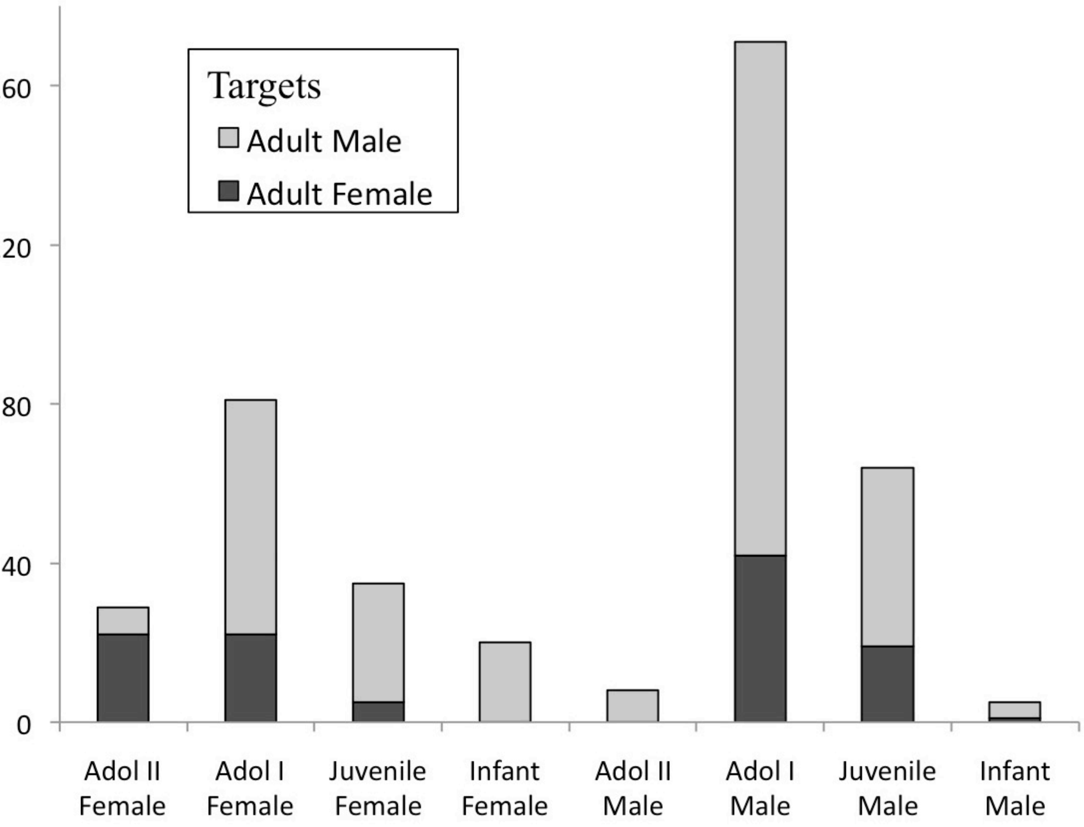


Fig. 2.2. Distribution of harassment given and received by age-sex class

Responses of Adults to Harassment

We found that the overall pattern of response to harassment did not follow an expected frequency distribution based on equal likelihood in type of response behavior. Agonistic responses occurred significantly more frequently than did neutral responses ($G_{gof} = 34.737$, $df = 1$, $p < 0.001$). The frequency of harassment received was significantly positively correlated with both aggressive ($r = 0.771$, $df = 6$, $p < 0.01$) and submissive ($r = 0.766$, $df = 6$, $p < 0.01$) responses but there was no correlation with neutral responses ($r = 0.089$, $df = 6$, $p = 0.236$). Continuation of harassment was found to be dependent on type of initial response where both aggressive and submissive responses were followed by continued harassment significantly more frequently than were neutral responses ($G_{toi} = 83.98$, $df = 2$, $p < 0.001$; Fig. 2.3). The type of response elicited was found to be dependent on the age class of the actor, where both adolescent I and II elicited agonistic responses significantly more frequently than neutral responses and both juveniles and infants received neutral responses significantly more frequently than agonistic responses ($G_{toi} = 45.217$, $df = 3$, $p < 0.001$; Table 2.3).

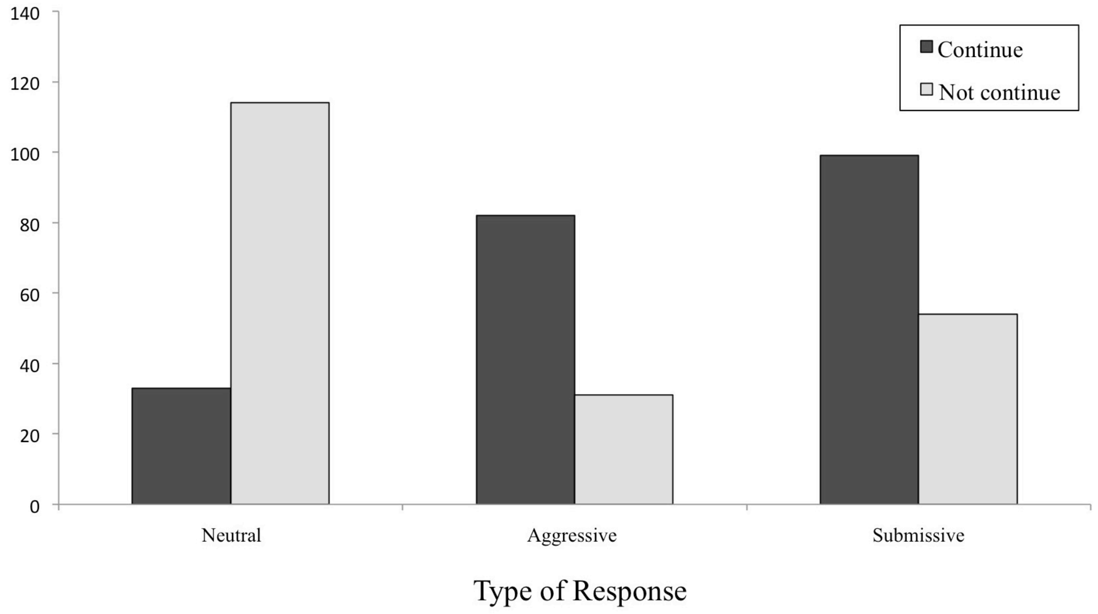


Fig. 2.3. Distribution of continuation of harassment received by type of response given

Rank Effects

We found that the total amount of harassment each target received was significantly negatively correlated with target rank (*r* = 0.869, *df* = 6, *p* < 0.001; Fig. 2.4). Furthermore, although no relationship was found between rank of the target and amount of neutral responses given (*r* = 0.020, *df* = 6, *p* = 0.732), a significant negative correlation was found between rank of the target and amount of agonistic responses (*r* = 0.868, *df* = 6, *p* < 0.001; Fig. 2.5). We also found that type of harassment behavior received was dependent on the target's rank where high-ranking individuals received mild aggression significantly more frequently than physical contact aggression and lower-ranking individuals received physical contact aggression significantly more frequently than mild aggression (G_{toi} = 71.03, *df* = 7, *p* <0.001). The only immatures to elicit submission from adults during a decided non-harassment agonistic event were the two individuals classed as Adolescent II (Bila-Isia and JoT). Both Bila-Isia and JoT, however, continued to direct harassment behaviors at these lower-ranking adults (Maiko and Toby; Susie, Maiko, and Toby respectively).

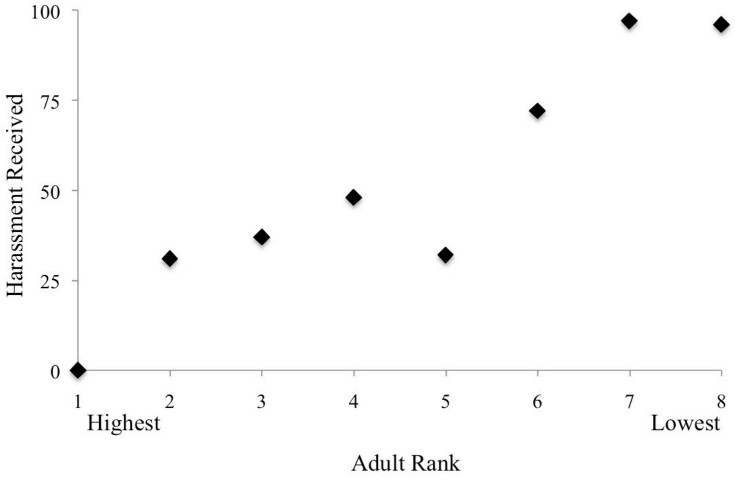


Fig. 2.4. Harassment received by rank of target

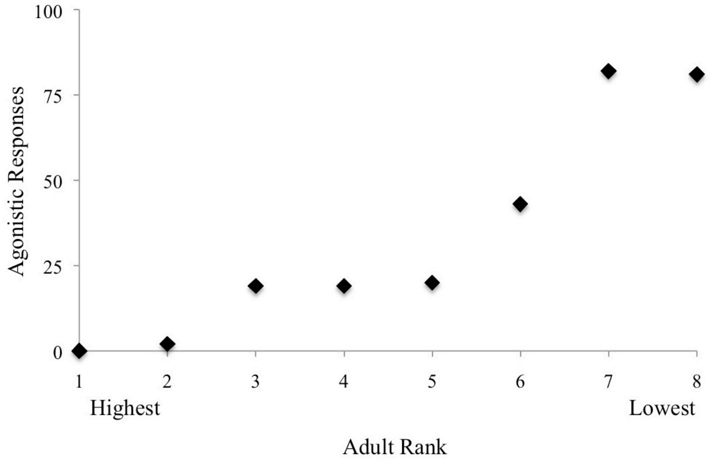


Fig. 2.5. Agonistic responses by rank of target

DISCUSSION

The purpose of this study was to describe the pattern of harassment behavior in bonobos in light of two competing hypotheses (Exploratory Aggression and Rank Improvement) and to compare the results with those that have been reported for chimpanzees, a closely related species with both broad similarities in social system and key differences in dominance structure.

General Pattern of Harassment in Bonobos

Immature harassment of adults occurred frequently in this population of captive bonobos. The morphology of the behavior was similar to what was reported by Adang (1984) for chimpanzees, where individuals would aggressively pester an adult without being provoked and outside of the immediate temporal association of a conflict. The repertoire of harassment behaviors performed by immature bonobos was also similar to what was reported for chimpanzees (Adang 1984; Nishida 2003), varying from mild (eg. throwing leaves) to more physical (eg. kicking) types of aggression. Instances of harassment constituted roughly a third (36%) of all agonistic events recorded during the study period and represented the greater majority (84%) of those that occurred between immatures and adults. These events rarely escalated into a conflict but were a noticeable source of unrest within the group. Continued harassment of an individual responding agonistically, for example, would sometimes result in the group collectively moving to a new location within the enclosure or the separation of individuals into more diffuse spatial arrangements.

Adang (1984, 1985) reported that both male and female immature chimpanzees engaged in harassment behaviors in roughly equal frequency. Nishida (2003), however, observed that harassment was almost exclusively performed by immature male chimpanzees at Mahale and argued that harassment functioned primarily as a mechanism for immature males to gain dominance over adult females. More broadly, sex differences in the social interactions of immatures with adults (including aggressive interactions) has been documented in wild chimpanzees where male immatures interact more with adults than do female immatures and is in accordance with the documented sex differences in the social interactions of adults (Lonsdorf et al. 2014). We also found that while both the male and female immatures of our study population of bonobos harassed adults, immature males performed the behavior significantly more than did immature females. This result does, however, not agree with the observed interaction pattern of adult bonobos where adult females are known to interact frequently with both other adult females and adult males (White 1998; Hohmann et al. 1999). More detailed studies pooling all types of social interactions between immatures and adults and longitudinal studies following multiple immatures are needed in bonobos to fully understand this observation.

As discussed above, adult female bonobos can hold high rank positions (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016; this study) and it may be reasonable to expect that the offspring of high-ranking females would perform harassment significantly more than the offspring of low-ranking females because the threat of retaliation from the target is mitigated by the potential dominance asserted by their mother over the target. A somewhat similar effect is seen in species where female rank is inherited and matrilineal rank order is maintained through kin-based alliances (Chapais 1992; Chapais and Gauthier 2002) and there is evidence that the rank status of mothers can impact the relative rank status of their sons in bonobos (Surbeck et al. 2010). Surprisingly, we found that all immatures in this population frequently harassed adult group members, irrespective of their mother's rank, an effect that may be the result of the high levels of social tolerance that have been reported for bonobos (Hare et al. 2007; Hare and Kwetuenda 2010), although these findings on social tolerance have recently come into question (Bullinger et al. 2013; Cronin et al. 2015).

Support for the Exploratory Aggression Hypothesis

We found significant support for the Exploratory Aggression hypothesis (Adang 1984, 1985), which makes predictions about the generalized function of harassment behavior as a means of social exploration. At Arnhem, Adang (1984) found that immatures directed harassment primarily at group members other than their own mother and the adult females that provided some allo-maternal care, individuals with whom they presumably had fewer opportunities to engage socially. Adult female chimpanzees at some field sites form close spatio-temporal associations (Wakefield 2013) but there is only limited evidence that they engage in allo-maternal care (Nishida 1983; The Jane Goodall Institute 2010; Kishimoto et al. 2014). Harassment, however, may still function as a way for immatures to reduce uncertainty when forming social connections outside of those associated with their mothers. Although the immature bonobos in our study population were never observed harassing their own mother, we were unable to test whether or not bonobos exhibit a pattern similar to chimpanzees (Adang 1984) because no adult females engaged in allo-maternal care during the study period. However, female bonobos are known to form strong and lasting social connections and actively maintain close spatio-temporal association in the wild (White 1996, 1998). Studies on adult female association patterns, allo-care, and harassment by immatures are needed in to better examine this component of the proposed function.

The Exploratory Aggression hypothesis also makes predictions about the mechanistic properties of harassment and stipulates that the behavior will be most frequent when targets react in a way that reduces uncertainty by providing information about aggression and relationships between individuals (Adang 1985). We found that harassment would continue more frequently if the target reacted with an agonistic behavior than if they responded neutrally. These results support the hypothesis that agonistic responses are reinforcing in nature and are a mechanism through which immatures learn about the cause and effect of different agonistic behaviors and their relationship to the target (Adang 1984, 1985). Furthermore, when agonistic responses were separated into aggressive and submissive categories, both behaviors were correlated with frequency of harassment. This result is important because it demonstrates that immatures use harassment to explore both sides of agonistic behavior and not strictly as a tool of dominance or way to elicit submission from a target.

Adang (1985) also observed that the immature chimpanzees of Arnhem explored the differential effects of aggression across the dominance hierarchy by directing mild forms of harassment behavior at high-ranking individuals and more physical contact aggressive behaviors at low ranking individuals. He concluded that this behavioral pattern is less related to reducing uncertainty and is instead a reflection of immatures investigating the authority of high-ranking individuals and learning about the constituents of dominance as a behavior (Adang 1985). We found a similar pattern of behavior in this group of bonobos, where high-ranking targets more frequently received more mild aggression and low-ranking received more physical contact harassment behaviors. Moreover, high-ranking individuals across species generally exhibit a high degree of social power (Lewis 2002) that can be used to insert force into inter-individual interactions (Flack and de Waal 2004). For example, although the highest-ranking individual in this group of bonobos (Unga) was never observed to be harassed, when provoked by group members in other contexts, her response behaviors were often highly aggressive and frequently resulted in the wounding of the potential aggressor, including immatures (Boose, unpublished data). Directing mild forms of harassment behavior towards high-ranking individuals is a way for immatures to reduce the potential risk of retaliation by exploring authority and the parameters of dominance from a distance.

Support for the Rank Improvement Hypothesis

We found mixed support for the Rank Improvement hypothesis (Nishida 2003), which makes predictions based on harassment as a mechanism of rank acquisition in immatures. At Mahale, Nishida (2003) found that harassment was primarily performed by immature males and was directed almost exclusively at adult females. Although he was unable to document this transition of power during his study period, he predicted that immatures would not harass adults once dominance over them had been established (Nishida 2003). During the course of our study period, two adolescent bonobos (Bila-Isia and JoT) began to ascend the adult dominance hierarchy, measured as an ability to elicit submission from adults outside of the context of harassment. Both Bila-Isia and JoT received submission signals from the two lowest-ranking adults, Maiko and Toby. JoT also received submission from Susie, a mid-ranking adult female in the group, but was never observed receiving submission from Jimmy or Lady, the two individuals ranking directly below Susie. However, because Lady is the mother of JoT it is likely that there was no opportunity to observe dominance interactions between the two. Maiko, Toby, and Susie continued to be able to elicit submissive responses from Bila-Isia and JoT and dominance between these adolescents and adults was, therefore, considered to be incomplete. Furthermore, both Bila-Isia and JoT were observed continuing to harass Maiko, Toby, and Susie after they successfully received submission signals from them.

Although we were not able to confirm the assumption that immatures will not harass adults they already out-rank, we found some support for the hypothesis that harassment functions to facilitate rank acquisition. In our study population, harassment received was negatively associated with the dominance rank of targets and low-ranking targets were more likely to respond with agonistic behaviors. These results suggest that immatures are using harassment to ascend the dominance hierarchy and indicate that low-ranking individuals perceived harassment as a challenge to their rank status. In addition, adolescents were more likely to elicit agonistic responses from targets and infants and juveniles were more likely to receive neutral behaviors in response to harassment indicating that targets viewed harassment differently based on the age-class of the actor and their potential ability to establish dominance over them.

The Rank Improvement hypothesis also predicts that responding to harassment with aggression will lead to the continuation of harassment whereas submissive responses will result in the cessation of harassment because submission indicates dominance over the target. We did not find support for this prediction. As stated above, we found that both aggressive and submissive responses were followed by continued harassment behavior from the immature. Although it is possible and likely that immatures are using harassment to acquire rank, these results more closely support the assumption generated by the Exploratory Aggression hypothesis that a primary function of harassment is to reduce uncertainty by affording immatures the opportunity to both control (i.e., elicit submission) and predict (i.e., elicit aggression) agonistic interactions.

Further Considerations

While there are broad consistencies presented in this paper, the patterning of harassment behaviors should also be expected to reflect a species' dominance and social structures. For example, female chimpanzees rank lower than males and are targets of harassment more frequently than are males (Adang 1984, 1985; Nishida 2003). Accordingly, the patterning of harassment and response behaviors should be different in bonobos in groups where females hold higher rank positions than males and/or where males occupy the lowest rank positions, as was the case in this study. We found that adult male bonobos were targeted more frequently than were adult females and reacted more agonistically to being harassed than did females, suggesting that male bonobos, like female chimpanzees, viewed harassment as a challenge to their rank status. These results are consistent with the different dominance structures of bonobos and chimpanzees and support the proposed function of harassment as a tool of rank acquisition.

The results presented in this paper, however, show that targets may not perceive harassment solely as a rank challenge and that harassment may not function the same during the course of development. The infant and juvenile bonobos of our study group received mostly neutral responses to harassment whereas the adolescents received mostly agonistic responses. In addition, the observation that the alpha female, Unga, never received harassment demonstrates that immatures have some ability to assess the potential risk of different targets. Gathering information about and practicing aggression as an immature is important for later rank acquisition endeavors and to successfully function within a group. For example, in some species where rank is inherited, younger individuals use agonistic experiences with their peers to learn the fundamentals properties of rank acquisition as an adult (Holekamp and Smale 1991, Chapais and Gauthier 2002) as well as how to use allies to establish and stabilize the dominance hierarchy (Chapais 1988). Adang (1986) hypothesized that younger immatures may use harassment primarily as a mechanism to explore aggression whereas adolescents, who are engaged more in the testing and exploration of dominance, are using harassment primarily as a means to establish rank. Further studies tracking the development of immatures as they transition into the adult dominance hierarchy are needed to accurately test the prediction that the function of harassment changes as immatures age.

It is also worth noting here that, for five of the eight adults in this bonobo group, harassment constituted the majority (>50%) of aggression received during the study period. These five individuals were often observed responding in a manner consistent with the induction of a stress response (e.g., fleeing, screaming, fear grimacing). Although harassment of adults by immatures is a natural component of bonobo development, the effects of harassment are an important consideration for the management of stress in captive animals where it can be difficult for individuals to avoid each other or to remove themselves from the social situation.

Conclusion

In conclusion, harassment is a distinct type of agonistic behavior that functions both as a mechanism of exploratory aggression and in a manner that facilitates rank acquisition. Our results on harassment behavior in bonobos provide support for several of the predictions generated by the Exploratory Aggression hypothesis and offer mixed support for the predictions generated by the Rank Improvement hypothesis. The results presented here also demonstrate that there are general patterns and broad similarities to harassment of adults by immatures between bonobos and chimpanzees, and emphasizes the need to examine this behavior separately from other types of immature-adult interactions in all species. At the same time, the comparison of bonobo harassment behaviors with those seen in chimpanzees shows that there are distinct patterns in choice of targets and the adults' responses that reflect differences that are consistent with each species' social structure. Harassment is, therefore, an important part of the complex behavioral repertoire that immatures practice in order to become fully functioning and integrated members of their social group.

BRIDGE TO CHAPTER III

The objective of Chapter II was to examine the patterning of harassment behavior in bonobos and to test predictions generated by the Exploratory Aggression and Rank Improvement hypotheses. The results presented in this chapter demonstrated that harassment behavior functions as a mechanism through which immatures learn about aggression and the nature of dominance interactions. While Chapter II provides important insights into the often-overlooked sociality of immatures, particularly within agonistic-type interactions, the purpose of Chapter III is to examine a previously unstudied type of affiliative interaction known as *infant handling*. The study presented in Chapter III will detail the patterning of expression of infant handling in bonobos and will test the predictions generated by six functional hypotheses in order to better understand the contribution of infant sociality to the social and dominance structures in bonobos.

CHAPTER III

NON-MATERNAL INFANT HANDLING IN BONOBOS (*PAN PANISCUS*): OXYTOCIN AND SUPPORT FOR THE LEARNING-TO-MOTHER HYPOTHESIS

This chapter includes previously unpublished co-authored material, facilitated by a number of people, including Frances White, Josh Snodgrass, and Audra Meinelt. The author, Klaree Boose, was the principle investigator for this work, responsible for the study design, behavioral data collection, hormonal analyses, statistical analyses, and manuscript preparation. Frances White is the academic adviser for this dissertation and contributed to this work by participating in the development of study design and statistical analyses. Josh Snodgrass is the principle investigator of Global Health Biomarker Lab at the University of Oregon and was instrumental in providing laboratory space and equipment for the hormonal analyses conducted for this study. Audra Meinelt is an assistant curator at the Columbus Zoo and provided institutional support for data collection, storage, and shipment of samples.

INTRODUCTION

Group members in many species of primate exhibit a marked interest in infants, particularly newborn individuals (Small 1990; Silk 1999). This phenomenon is known as ‘natal attraction,’ and occurs when conspecifics approach, examine, touch, and smell the infants (Hrdy 2009). It has been hypothesized that this attraction is primarily a response to the infant being a novel object in the environment, where the sudden appearance of a new individual sparks an intense curiosity among group members (Small 1990; Silk 1999). Although care-giving is not always coupled with natal attraction, many species also exhibit allocare behaviors, where non-maternal individuals assist in the feeding, carrying, protecting, and indirect provisioning of immatures. This phenomenon is especially prevalent in birds and mammals (Emlen 1991; Gittleman 1985; Reidman 1982). While allocare behaviors represent examples of cooperative breeding or reciprocal altruism (Emlen 1991) in many species, the fitness benefit is not always apparent in others. Several different terms, therefore, have been used to describe these behaviors such as ‘communual care,’ ‘allomaternal care,’ ‘allomothering,’ ‘babysitting,’ and ‘kidnapping.’ While some of these terms imply specific functions, others are more vague and authors have most recently favored the term ‘infant handling’ (Wasser and Barash 1981; Paul and Kuester 1996; Maestripieri 1994). The term ‘infant handling’ is, therefore, used to describe all interactions between infants and non-maternal group members, including both aggressive and affiliative behaviors.

Infant handling occurs across a wide array of mammalian taxa (Hrdy 1976; Riedman 1982; Gittleman 1985; Kohda 1985; Lee, 1987; Emlen et al. 1991; Packer et al. 1992; Stanford 1992; Förster and Cords, 2005; Dugdale et al. 2010) and the patterning and frequency of expression of handling behaviors varies considerably across primate species (Isler and van Schaik 2012; Tecot and Baden 2015). For example, non-maternal carrying, grooming, and cradling are common behaviors, whereas non-maternal nursing and adoption of infants occurs much less frequently (Jay 1962; Poirier 1968; Ren et al.

2012). Marmosets and tamarins perform considerable amounts of non-maternal infant handling in the form of carrying, feeding, and protection (Goldizen 1987; Tardif et al. 1992; Porter and Garber 2009) and Hanuman langur (Hrdy 1977; McKenna 1981), capped langur (Stanford 1992), and squirrel monkey (Baldwin 1969) infants spend nearly equal amounts of time with non-mothers as they do their own mother during the first months after birth. In some species, such as langurs, infants are handled by group members while they are only hours old (Hrdy 1976; McKenna 1979; Dolhinow and Murphy 1982; Vogel 1984; Sommer 1989; Stanford 1991, 1992) whereas savanna baboon, rhesus macaque, and Japanese macaque infants spend less than 5% of their time with non-mothers (Nicolson 1987). In addition, not all infant handling behaviors can be categorized as affiliative. In several species of primates, aggressive interactions such as physical abuse and kidnapping have been observed (Quiatt 1979; Silk 1980; Wasser and Barash, 1981 Clarke et al. 1998).

Many factors contribute to this variability of expression of infant handling both within and between species, including the type and availability of social partners, infant age (Hrdy 1976, 2009; Brent et al. 2008; Silk 1999; Silk et al. 2003; MacKinnon 2011) and sex (Forster and Cords 2005), the dominance rank of the mother and handler (O'Brien and Robinson 1991, Silk 1999; Fruteau et al. 2011; Altmann 1980; Henzi and Barrett 2002), levels of agonism, relatedness between the handler, the infant, and the infant's mother (Hamilton 1964; O'Brien and Robinson 1991; Kapsalis 2004; Silk et al. 2003a,b), as well as the handler's age and parity (Nicolson 1987; Silk 1999; Eberle and Kappeler 2006; see Badescu et al. 2015 for review). Furthermore, although individuals in most primate species demonstrate a strong proclivity to handle infants, most non-maternal handlers do not delay their own reproduction (Hrdy 1976; McKenna 1987; Nicolson 1987; Maestripieri 1994; exception: callitrichids, see Goldizen and Terborgh 1989; Feistner and Price 1991). Numerous hypotheses, therefore, have been put forth to account for the heterogeneity observed both within and between species and to explain the adaptive value of infant handling in primates (see Maestripierei 1994 for review; Mitani and Watts 1997; Solomon and French 1997; Ross and MacLarnon 2000; Isler and van Schaik 2012).

Functional Hypotheses

Researchers have noted that the functional hypotheses on infant handling are often divided along two theoretically different lines (Hsu et al. 2015): 1) those where paternal care and cooperative breeding are obligate (e.g., callitrichids and pair bonded species: [Goldizen 1987; Solomon and French 1997; Quinlan and Quinlan 2008; Fernandez-Duque et al. 2009]) and 2) those where non-maternal care is not considered essential for infant survival (see Maestripieri 1994). Although these differing theoretical lines are not mutually exclusive, they are often considered separately in investigations on the function of infant handling in a species (Hsu et al. 2015) and this paper will focus on the latter framework by testing the following hypotheses.

The ***Kin Selection*** hypothesis suggests that infant handling increases the inclusive fitness of the handler, by aiding the survival of a related infant, shortening the inter-birth intervals (IBI's) of related females by reducing weaning times, and/or reducing the burden of infant care and thus providing mothers with more time to feed and groom (Hamilton 1964; Hrdy 2009). The ***Reproductive Competition*** hypothesis describes infant handling as a behavior through which females reduce the reproductive success of other females through excessive handling and potentially harmful aggressive handling behaviors (Hrdy 1976; Silk 1980; Wasser and Barash 1981; Wasser 1983; Gittleman 1985; Maestripieri 1994). Conversely, the ***By-Product*** hypothesis does not ascribe any adaptive value to infant handling and describes the behavior as a consequence of prosociality and selection for high responsiveness to infants (Quiatt 1979; Scollay and DeBold 1980).

Hypotheses generated from the ***Biological Market*** paradigm describe infant handling as a form of reciprocal altruism not dependant on relatedness (Noe and Hammerstein 1994, 1995), where individuals exchange handling behaviors for any social commodity such as grooming (Muroyama 1994; Henzi and Barrett 2002; Barrett and Henzi 2006; Ginther and Snowdon 2009; Tiddi et al. 2010; Fruteau et al. 2011) or potential future mating opportunities (Busse and Hamilton 1981; Lemasson et al. 2008; Huchard et al. 2010). Within this paradigm two functional hypotheses have been described: 1) the ***Reciprocity*** hypothesis suggests that handling behaviors are reciprocated between mothers, where the handler provides care-giving behaviors to a female who in turn provides care-giving behaviors to the handler some time in the future (Hrdy 1976; Stanford 1992); and 2) the ***Alliance Formation*** hypothesis suggests that handling behaviors strengthen the social bonds between the handlers and mothers' of infants and that individuals will perform handling behaviors in exchange for coalitionary support during conflicts at some time in the future (de Waal 1990; Manson 1999; Maestripieri 1994).

The ***Learning-to-Mother*** hypothesis suggests that infant handling is a selfish behavior that evolved to enhance the parenting skills of handlers by providing information on how to appropriately care for an infant (Lancaster 1971; Hrdy 1976; Riedman 1982; Fairbanks 1990; Meaney et al. 1990). There is considerable support for this hypothesis in species across numerous taxa, (scrub-jays: Woolfenden and Fitzpatrick 1984; pinnipeds: Riedman 1982; gerbils: Salo and French 1989; tamarins: Tardif et al. 1984; and vervets: Fairbanks 1990), where females often demonstrate the highest rates of infant handling (Clark 1978; Caine and Mitchell 1980; Hiraiwa 1981; Nicolson 1982, 1987; Small 1982; Paul and Kuester 1996). However, despite numerous studies connecting the hormone oxytocin to maternal behavior in mammals (see Pedersen 1997; Strathearn 2011; Feldman 2012; Kim et al. 2014), the relationship between oxytocin and infant handling as a mechanism of learning-to-mother is not known.

Oxytocin and Maternal Behavior

Oxytocin (OT), along with other neuropeptide hormones, functions as a modulator of complex social behavior and social cognition in mammals (Lim et al. 2006). Produced by the hypothalamus and stored and secreted by the pituitary gland, OT acts primarily as a neuromodulator in the brain where, once released, is not immediately reabsorbed or broken down into a metabolite and diffuses into the cerebrospinal fluid where it influences neurons in several areas of the brain. OT has long been recognized for its functions in several aspects of reproduction including parturition, lactation, and mating (Fuchs et al. 1982; Caldwell et al. 1986; Smith 1989; Witt and Insel 1991) and has also been associated with the regulation of social behaviors (see Benarroch 2013; Feldman 2012; Meyer-Lindenberg et al. 2011 for review) such as anxiety and affiliation (Insel 1992; Insel and Winslow 1991; Witt et al. 1992), interpersonal trust (Van IJzendoorn and Bakermans-Kranenburg 2012), recognition of emotions and empathy (Rodrigues et al. 2009; Hurlemann et al. 2010; Lischke et al. 2012; Perry et al 2013), pair bonding in monogamous species (Insel 1992; Insel and Hulihan 1995; Ross et al. 2009; Snowden et al. 2010; Schneiderman et al. 2012), and social bonding and food sharing in chimpanzees (Crockford et al. 2013; Wittig et al. 2014).

More recently, research has begun to focus on the role of OT as a key neuromodulator of caregiving, responsible for the facilitation and maintenance of maternal behaviors (Pedersen 1997; Strathearn 2011; Feldman 2012; Pedersen 2013; Kim et al. 2014) and studies on animal models have significantly advanced our understanding of the neuroendorine pathways of OT mediated maternal behaviors. For example, injection of OT stimulates the onset of species-specific maternal behaviors in rats (Pedersen and Prange 1979). In mice, variations in lactation-induced OT levels have been found to correspond to variations in maternal behaviors (Francis et al. 2000) and administration of OT has been found to suppress rates of infanticide and simultaneously increase care-giving behaviors (McCarthy et al. 1986; McCarthy 1990). In female sheep (ewes) central injection of OT has been found to rapidly stimulate species typical maternal responses (Kendrick et al. 1987), while the administration of peridural anesthesia, which blocks the normal rise in cerebrospinal fluid (CSF) concentrations of OT, was found to inhibit onset of maternal behaviors (Levy et al. 1992). In rhesus macaques, researchers have found that variations in maternal behaviors, such as time spent grooming and nursing, are associated with variations in circulating OT (Maestripieri et al. 2009). OT has also been implicated in the modulation of maternal behaviors in humans, particularly during pregnancy and the postpartum period. For example, peripheral OT levels rise and remain high in pregnant and parturient women (Feldman et al. 2007; Levine et al. 2007; Gordon et al. 2008, 2010) relative to non-pregnant women (Feldman et al. 2007; Gordon et al. 2008). Researchers have also found that OT levels during pregnancy are predictive of maternal behaviors such as infant gaze, vocalizations, positive affect, and affectionate touch during the postpartum period (Feldman et al. 2007) and mothers who exhibit a pattern of rising OT during pregnancy and the early postpartum period self-reported stronger attachment to offspring (Levine et al. 2007). In addition, higher OT levels have found to be associated with greater infant affect synchrony and social engagement (Feldman et al. 2010). The results of these studies indicate that OT may function in a state vs. trait manner, ready to influence the onset and facilitation of maternal behaviors when the context of providing care-giving behaviors to infants arises.

Objective

Although male-immature interactions have been studied in gorillas (Rosenbaum et al. 2011; Rosenbaum et al. 2015) and cases of adoption of orphans have been reported in some species of (Palthe and van Hooff 1975; Blersch and Schmidt 1992; Boesch et al. 2010; Hobaiter et al. 2014), little is known about the social and demographic factors that affect the expression or absence of infant handling in great apes. Infant handling, to our knowledge, has not yet been studied in bonobos and the purpose of this paper, therefore, is to describe the basic pattern of occurrence of infant handling in bonobos and to test the predictions generated by the proposed functional hypotheses, including examining the relationship between oxytocin and handling behaviors.

Bonobos are a male-philopatric species that exhibit a multi-male multi-female fission-fusion community structure (Nishida 1968; White 1988; Kano 1992) where females generally disperse during adolescence (Kano 1992; Gerloff et al. 1999; Eriksson et al. 2006; Stumpf 2011) and reach the age of first parturition around 13-15 years (Stumpf 2011). Female bonobos can occupy the highest rank positions within the group (Furuichi 1997; Stevens et al. 2007; Surbeck and Hohmann 2013; Goldstone et al. 2016) and are known to form female-female coalitions (White and Wood 2007; Tokuyama and Furuichi 2016) and strong bonds with both males and females (White 1998; Hohmann et al. 1999). We therefore expect that the patterning of infant handling behaviors will reflect these species-typical social and dominance structures.

Predictions

As discussed above, there are several distinct but not mutually exclusive hypotheses on the function of infant handling that have been reviewed and tested in many primate species. Each generates a different set of predictions (Table 3.1).

1. The ***Kin Selection*** hypothesis assumes that infant handling behaviors provide a net positive fitness benefit and therefore predicts that:
    a. positive handling behaviors will be occur significantly more frequently than negative behaviors
    b. individuals will handle related infants significantly more frequently than unrelated infants

2. The ***Reproductive Competition*** hypothesis assumes that infant handling negatively impacts infant survival and predicts that:
    a. negative handling behaviors will be occur significantly more frequently than positive behaviors
    b. individuals will direct handling behaviors towards unrelated infants significantly more frequently than related infants
    c. females will handle infants significantly more frequently than males;
    d. adult females will handle significantly more frequently than adolescent or juvenile females
    e. because lower ranking individuals have less social power than higher ranking individuals, infants of lower-ranking females will be handled significantly more frequently than higher-ranking female

3. The ***By-Product*** hypothesis assumes that natural selection will favor responsiveness to infants, particularly among females, and predicts that:
    a. females will handle significantly more frequently than males
    b. handling frequency will not differ significantly between parous females without infants and nulliparous females
    c. positive handling behaviors will be occur significantly more frequently than negative behaviors

4. The ***Biological Market*** model assumes that infant handling is a social commodity and predicts that handling behaviors will be performed in exchange for any social commodity. Within this paradigm, two hypotheses have been defined:
    a. The ***Reciprocity*** hypothesis predicts that
        i. positive handling behaviors will be occur significantly more frequently than negative behaviors
        ii. parous females will perform handling behaviors significantly more frequently than other age-sex categories and will exchange the service of handling each other's infants
        iii.
    b. The ***Alliance Formation*** hypothesis predicts that
        i. the infants of higher-ranking females will be handled significantly more frequently than lower-ranking females

        ii. handling behaviors will be positively correlated with agonistic support from mothers not related to the handler during conflicts involving the handler

5. The ***Learning-to-Mother*** hypothesis assumes that infant handling evolved as a mechanism through which nulliparous females learn about species appropriate maternal behavior and predicts that:
    a. immature and nulliparous females will perform handling behaviors significantly more frequently than other age-sex categories
    b. positive handling behaviors will be occur significantly more frequently than negative behaviors

   We further predict that if infant handling functions as a mechanism to learn maternal behavior and if OT functions as a facilitator of maternal behavior, then handling behaviors will:

    c. be positively correlated with OT in immature and nulliparous females
    d. not be correlated with OT in parous females because it is more likely OT would be correlated with interactions with their own infants
    e. not be correlated with OT in males because, although it is possible that OT facilitates infant handling as a type of social interaction in males, OT in males should not be correlated with infant handling alone

Table 3.1: Predictions and support for the functional hypotheses on infant handling

		Prediction supported?					Support for hypothesis?
HYPOTHESIS		**2011**	**2012**	**2013**	**2014**	**2015**	
Kin Selection							**mixed**
	positive > negative handling behaviors	y	y	y	y	y	
	related > unrelated infants	y	y	n	y	n	
Reproductive competition							**no**
	positive < negative handling behaviors	n	n	n	n	n	
	related < unrelated infants	n	n	n	n	n	
	female > male handlers	n	n	n	n	n	
	adult female > immature female handlers	n	n	n	n	n	
	infants of lower ranking females > higher ranking females	n	n	n	n	n	
By-Product							**no**
	positive > negative handling behaviors	y	y	y	y	y	
	female > male handlers	n	n	n	n	n	
	parous females without infants = nulliparous females	n	n	n	n	n	
Reciprocity							**no***
	positive > negative handling behaviors	y	y	y	y	y	
	parous females > other age-sex categories of handlers	n	n	n	n	n	
Alliance formation							**mixed**
	infants of lower ranking females < higher ranking females	n	n	n	n	n	
	handling behaviors + correlated with coalitionary support	y	y	y	y	y	
Learning-to-Mother							**yes**
	positive > negative handling behaviors	y	y	y	y	y	
	immature and nulliparous females > other age-sex categories of handlers	mostly	mostly	mostly	mostly	mostly	
	handling behaviors + correlated with oxytocin in immature and nulliparous females	y	y	y	y	y	
	handling behaviors not correlated with oxytocin in immature males	y	y	y	y	y	

*Note: *indicates small sample size*

METHODS

Subjects and Housing

All data were collected on the captive group of bonobos housed at the Columbus Zoo and Aquarium (CZA) in Columbus, Ohio, USA during the summer months of 2011 (June 23 – August 29), 2012 (May 20 – July 13), 2013 (April 14-June 16), 2014 (June 3-July 10), and 2015 (August 27-September 14). Daily observations usually began around 0730 hours and ended between 1300 – 1700 hours resulting in 1819 observation hours. Over the course of the study, CZA had 11 females and 8 males that were housed in a complex of areas consisting of two large indoor public viewing exhibits (54.8 m^2 each) with multiple climbing structures, two off-exhibit indoor enclosures (22.6 m^2 each), two off-exhibit outdoor enclosures (18.5 m^2 each) and a large naturalistic outdoor public viewing exhibit (57.9 m x 45.7m, 2647.7 m^2) with grass, mature trees, and an artificial stream and waterfall. The keepers at CZA managed the bonobos to simulate the species typical fission-fusion process of variable party composition where the bonobos were allowed access to each other each morning and parties were set based mostly on individual bonobo association preferences. This management process usually resulted in three parties that lasted for 2-3 days, rarely changed on a daily basis or exceeded 4 days, and where all immatures had abundant opportunity to interact with all individuals (see Boose et al. 2013 for description).

Age Classifications

The individuals of this study where classified according to the detailed descriptions of age-class characteristics of bonobos given by Thompson-Handler et al. (1984). For example, Thompson-Handler et al. (1984) described an infant as an individual that ‘keeps in frequent proximity to mother; commonly rides ventrally but also may ride dorsally during progression; nurses frequently’ and a juvenile as an individual ‘no more than half [the] size of [an] adult; generally independent but closely associated with [the] mother and occasionally seen to cling; [with] secondary sexual characteristics slight’ (p. 349). Individuals were therefore categorized according to the following: infant = 0-2 years; juvenile = 3-7 years; adolescent I = 8-9 years; adolescent II = 10-12 years; and adult ≥ 13 years. These age classes vary slightly from what was reported for a wild population of bonobos (Kano 1992) and reflect the accelerated development that can occur in captivity. Additionally, adolescents were split into two developmental categories: 1) adolescent II, where female ano-genital swellings are accompanied by menstruation and fertility, and where males undergo a significant growth spurt, including testicles that become larger, more pendulous, and are considered to be fully functioning; and 2) adolescent I, where individuals begin to display the physiological characteristics associated with the transition of puberty such as ano-genital swelling in females and expansion in testicle size in males, but where both sexes are generally still non-fertile (Marson et al. 1991; Stumpf 2011). Individuals referred to as ‘immatures’ include both juveniles and adolescents, and since all adult females in this group were parous, females referred to as ‘nulliparous’ are all adolescent females who have never given birth.

Over the course of the study, several immature individuals changed age categories. For example, during the 2011 season there were 2 infants (1 male, 1 female), 3 juveniles (1 male, 2 female), 2 adolescent I's (1 male, 1 female), and 1 adolescent II (male) and during the 2012 season two individuals changed age class where 1 juvenile female became an adolescent I and 1 adolescent I female became an adolescent II, etc. (see Table 2). Bonobos are a male-philopatric species and in order to further mimic the natural population dynamics of wild bonobos where females emigrate to new groups during adolescence (Nishida 1968; White 1988; Kano 1992), CZA transferred three adolescent females (JoT, Lola, Gilda) to different zoos and received one adolescent female (Sukari) during the course of the study (see Table 3.2).

Table 3.2. Group composition and rank and age class assignments of the CZA bonobo colony (2011-2015)

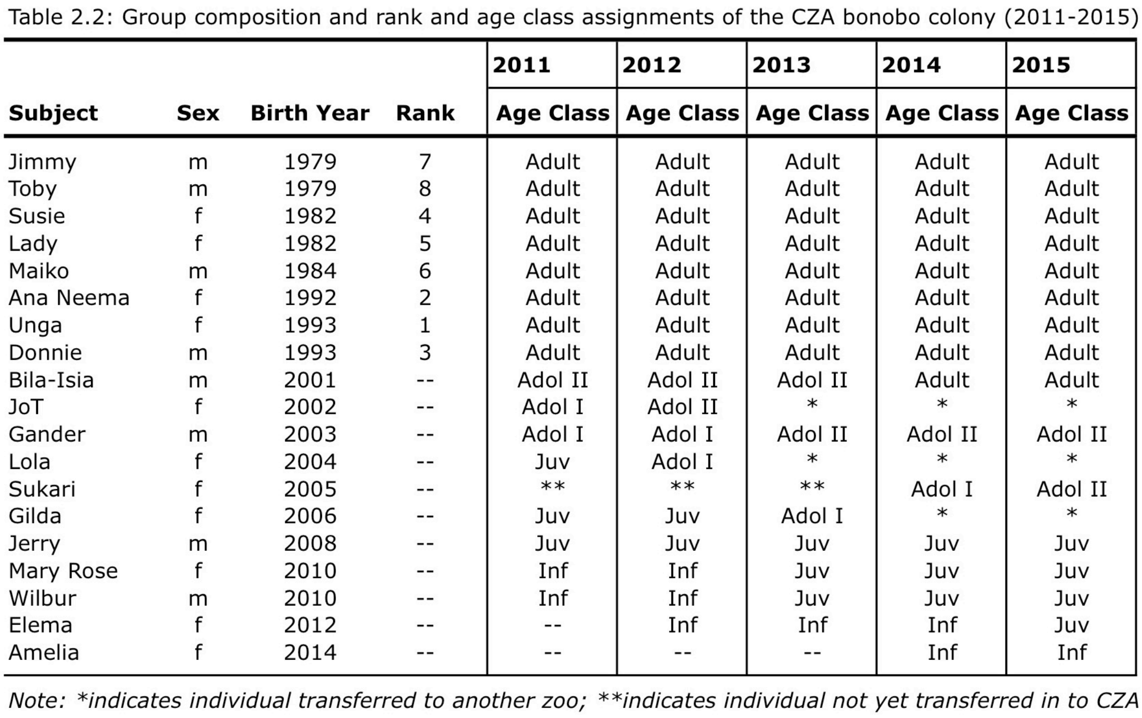


Table 2.2: Group composition and rank and age class assignments of the CZA bonobo colony (2011-2015)

				2011	**2012**	**2013**	**2014**	**2015**
Subject	**Sex**	**Birth Year**	**Rank**	**Age Class**	**Age Class**	**Age Class**	**Age Class**	**Age Class**
Jimmy	m	1979	7	Adult	Adult	Adult	Adult	Adult
Toby	m	1979	8	Adult	Adult	Adult	Adult	Adult
Susie	f	1982	4	Adult	Adult	Adult	Adult	Adult
Lady	f	1982	5	Adult	Adult	Adult	Adult	Adult
Maiko	m	1984	6	Adult	Adult	Adult	Adult	Adult
Ana Neema	f	1992	2	Adult	Adult	Adult	Adult	Adult
Unga	f	1993	1	Adult	Adult	Adult	Adult	Adult
Donnie	m	1993	3	Adult	Adult	Adult	Adult	Adult
Bila-Isia	m	2001	--	Adol II	Adol II	Adol II	Adult	Adult
JoT	f	2002	--	Adol I	Adol II	*	*	*
Gander	m	2003	--	Adol I	Adol I	Adol II	Adol II	Adol II
Lola	f	2004	--	Juv	Adol I	*	*	*
Sukari	f	2005	--	**	**	**	Adol I	Adol II
Gilda	f	2006	--	Juv	Juv	Adol I	*	*
Jerry	m	2008	--	Juv	Juv	Juv	Juv	Juv
Mary Rose	f	2010	--	Inf	Inf	Juv	Juv	Juv
Wilbur	m	2010	--	Inf	Inf	Juv	Juv	Juv
Elema	f	2012	--	--	Inf	Inf	Inf	Juv
Amelia	f	2014	--	--	--	--	Inf	Inf

*Note: *indicates individual transferred to another zoo; **indicates individual not yet transferred in to CZA*

Behavioral Observations

Data were collected using all occurrence sampling of infant handling and agonistic events (Altman 1974). Infant handling was defined as any affiliative or agonistic non-maternal interaction between a group member and an infant. Although infants are frequently part of different kinds of interactions while clinging to their mothers, handling specifically refers to the context of when the infant is not clinging to his or her mother. Furthermore, interactions occurring solely within the contexts of play and/or conflicts involving other group members were also excluded. Positive handling behaviors were those associated with affiliation (e.g., grooming, carrying, cradling) and negative handling behaviors were those associated with aggression (e.g., pulling, hitting, biting). A bout of infant handling was considered terminated when the handler ceased performing handling behaviors for 2 minutes.

Urine analyses

Urine collection and storage. Urine samples were collected in accordance with CZA's existing urine collection protocol using either a free catch method where individual subjects urinated through the mesh caging directly into a collection cup, or, where urine was pipetted directly off a clean floor surface immediately after a subject urinated into a plastic cryo tube. All subjects were previously trained to urinate on command (i.e., present genitals and urinate in exchange for a small food reward). Samples were then immediately frozen and stored at -20°C until they were packed on dry ice and shipped overnight to the Snodgrass Global Health Biomarker Lab at the University of Oregon in Eugene, OR where they were stored at -80°C until time of analyses.

Measurement of oxytocin. To avoid multiple freeze-thaw cycles, each sample was first brought to room temperature and 0.5 ml was aliquoted into several cryo tubes. Thawed samples were then diluted (1:4) in assay buffer supplied in the 96-well Oxytocin Enzyme Immunoassay Kit from Enzo Life Sciences™ (catalog no. 901-153A) and assayed according to the kit manufacturer's instructions. The manufacturer of this kit reported the detection limit for this assay as 15.0 pg/ml. To control for variation in the amount and concentration of voided urine, all samples were assayed for creatinine concentrations (Seltzer and Ziegler 2007) using the DetectX™ Creatinine Urinary Detection Kit from Arbor Assays. The manufacturer listed the detection limit for this assay as 0.037 mg/dL. Samples run for creatinine were diluted (1:20) and run according to the kit manufacturer's instructions. All plates were read using a BioTek™ microplate reader and analyzed with Gen5™ software version 2.0.

Test of parallelism. To validate the measurement of oxytocin in bonobo urine, tests of parallelism and accuracy were conducted using the instructions outlined by Brown et al. (2004) in the Smithsonian's Conservation and Research Center Endocrine Workbook (ppg. 21-24). 100 ul aliquots of urine from 10 samples were pooled and serially diluted two-fold in assay buffer. The serial dilutions of the pooled sample were then assayed according to the kit's instructions. The resulting value, expressed as percent bound (%B) over total binding (TB), for each of the pooled sample dilutions was plotted against a concentration of 1000 pg/ml for the neat sample and half the resulting concentration for each dilution (ex. 500 pg/ml for 1:2, 250 pg/ml for 1:4, etc.) (Brown et al. 2004, pg. 21). The displacement curve generated by these serial dilution concentrations was then compared to the standard curve by calculating the difference between the slopes of the lines produced by a linear regression of the serial dilution curve and the standard curve, respectively. No significant difference was found between the two slopes ($p=0.053$), indicating that the two curves are parallel and the analyte measured in bonobo urine demonstrates immunoactivity of the endogenous antigen similar to what was observed in the standards and is, therefore, immunologically similar to the oxytocin present in the standard solution provided by the kit manufacturer.

Test of accuracy. Because it is possible that there may be material present in bonobo urine that can interfere with the antigen-antibody binding process, an accuracy test was preformed to determine the degree to which the measured concentration reflects the true concentration of oxytocin in the sample. 100 ul aliquots of urine from 10 samples were pooled, diluted (1:4) in assay buffer, and divided into 7 aliquots. 6 of the aliquots were spiked with 100 ul of standards such that each aliqot of sample received one of the 6 concentrations of standard (1000, 500, 250, 125, 62.5, 31.2 pg/ml). One aliquot was left neat. Both the spiked and neat aliquots were then assayed according to kit instructions. The amounts observed (concentration value of aliquot from assay results) were then plotted against the expected amounts (concentration value of standard in respective aliquot) and a linear regression was performed. Slope values > or < 1 suggest there may be interfering substances present in the sample (Brown et al. 2004) and our results (slope = 1.079, $R^2 = 0.984$) indicate that bonobo urine likely does not contain any substances that interfere with detection of oxytocin in urine samples.

Data Analyses

Analyses of Variance and Frequency. *G* Tests of Goodness of Fit with Williams correction applied were used to compare frequency of type of handling behaviors and to compare frequency rates of handling across all infants. Assuming an equal likelihood of occurrence between frequencies of positive and negative handling behaviors, expected frequency ratios were entered as 1:1 (Sokal and Rohlf 2012). Because number of hours of observation differed between study years each of the four infants, total amount handled was divided by the number of observations hours for each infant and than assuming an equal liklihood of being handled, expected frequency rations were entered as 1:1:1:1 (Sokal and Rohlf 2012).

Because the composition of the group changed over the course of the study (for example, three adolescent females transferred to new zoos and a new adolescent female from another zoo was brought into the group), each year was considered separately in conducting analyses on the differences in frequencies of infant handling between age-sex categories. ANOVAs were used for all comparisons (Table 3) with the exception of the following: during the 2012 study year there were only two juveniles (one female, one male) and during the 2014 and 2015 study years there only two adolescents (one female, one male) (Table 2). Therefore, in order to compare differences in frequency of handling between the sexes within these age classes, *G* Tests of Goodness of Fit with Williams correction applied were used and expected frequency ratios were entered as 1:1 (Sokal and Rohlf 2012).

Rank analyses. Dominance rank among adults was determined from the direction and outcome (e.g., fleeing upon aggression) of a decided agonistic event and displacement matrix and analyzed using R (version 3.3.1). Linearity in the dominance rank of adults was found to be complete and significant (Landau's $h = 0.476$, $p < 0.01$) and adults were ordered into a linear dominance hierarchy and assigned a unique rank number where 1 represents the highest-ranking individual (Table 3.2). In order to test for the effect of mother's rank on frequencies of handling across all study years, the total amount each infant was handled was divided by the number of observations hours for each infant and then compared to each infant's mother's rank using Pearson correlations. Pearson correlations were also used to compare frequencies of handling of each handler to counts of coalitionary support received by each handler. Because bonobos are known to support kin during conflicts (Vervafcke et al. 2000; Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016) only counts of coalitionary support that were performed by females (with infants) unrelated to the handler were included in the analyses.

Oxytocin In order to investigate the potential connection between OT and infant handling among immature and nulliparous females, the mean OT value for each individual for each year was compared to the corresponding frequency of handling for that individual for that year. Because group composition changed over the course of the study (see above and Table 1), each handler's total amount of handling for a given year was divided by number of observation hours and number of available infants for that year. All analyses, with the exception of rank analyses, were run using BIOMstat (version 3.30t).

RESULTS

Type of Handling Behaviors

Over the course of the entire study, 1778 interactions classified as infant handling were recorded, where 1700 were cored as positive and 78 were scored as negative (Fig. 1). Observations of handling occurred at a rate of 0.68 per observational hour (1778/1819). The ***Kin Selection***, ***By-Product***, ***Reciprocity***, and ***Learning-to-Mother*** hypotheses all predict that positive handling behaviors will occur significantly more frequently than negative handling behaviors, while the ***Reproductive Competition*** hypothesis predicts that negative handling behaviors will occur more frequently. We found that positive handling behaviors, such as carrying, cradling, and grooming, occurred significantly more frequently than negative handling behaviors, such as pulling, hitting, and biting, for each year in the study period (2011: G=410.762, df=1, $p<0.001$; 2012: G=809.562, df=1, $p<0.001$; 2013 G=232.086, df=1, $p<0.001$; 2014: G=328.904, df=1, $p<0.001$; 2015: G=53.857, df=1, $p<0.001$).

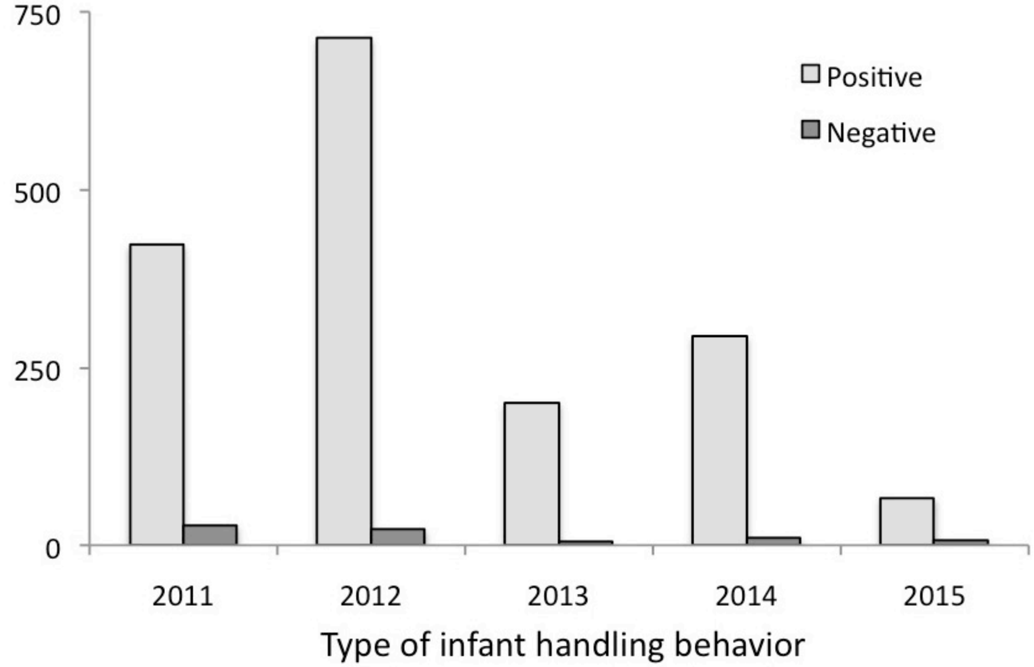


Fig. 3.1. Frequency distribution of type of infant handling behavior per study year

Kin Bias

Two infants were present at the beginning of the study period and two additional infants were born into the group during the 2012 and 2014 study years. The ***Kin Selection*** and ***Reproductive Competition*** hypotheses generate contrasting predictions regarding kin bias in handling frequency and frequency analyses were conducted to determine whether a preference for handling related infants existed among handlers. Because proportions of related and unrelated dyads changed from year to year over the course of the study, frequency analyses were conducted based on expected proportions of related and unrelated dyads involving infants and frequencies were analyzed for each study year. The ***Kin Selection*** hypothesis predicts that infant handling dyads between related individuals will occur significantly more frequently than between unrelated individuals and the ***Reproduction Competition*** hypothesis predicts that infant handling dyads between unrelated individuals will occur more frequently than between related individuals. For three of the study years infant handling dyads between related individuals occurred significantly more frequently than expected and less than expected between unrelated individuals (2011: G=19.72, df=1, p<0.01; 2012: G=222.54, df=1, p<0.01; 2014: G= 31.86, df=1, p<0.01) (Fig. 3.2). Infant handling dyads between unrelated individuals occurred significantly more frequently than expected, and infant handling dyads among related individuals occurred less frequently than expected, for the 2013 study period (G=15.38, df=1, p<0.01). There was no significant difference in expected frequencies of related and unrelated dyads for the 2015 study period (G=0.234, df=1, p=0.314) (Fig. 3.2).

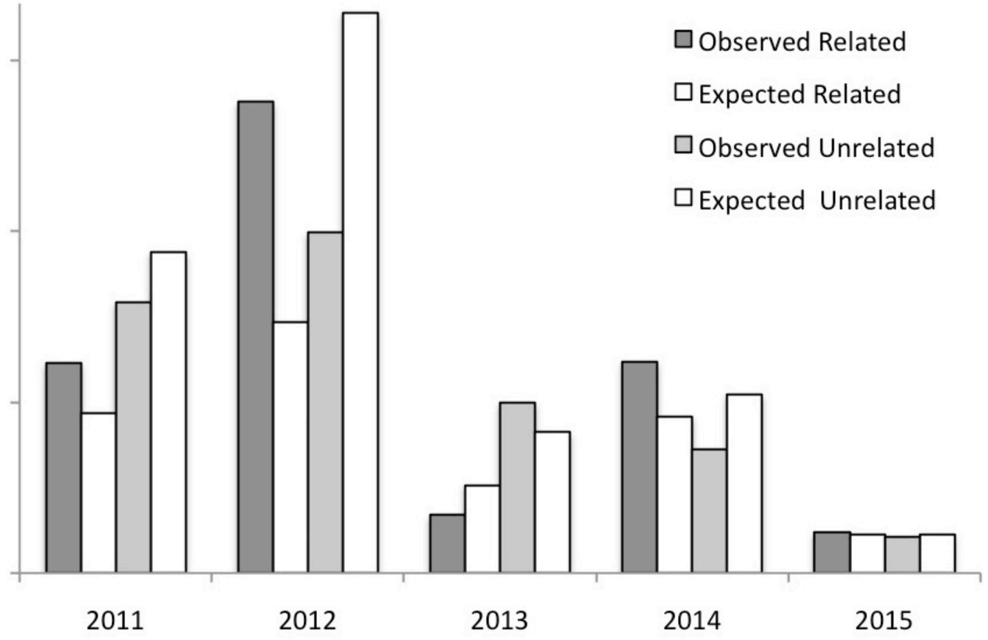


Fig. 3.2. Frequency distribution of expected and observed related and unrelated dyads per study year

Age-Sex Class Distribution Among Handlers

All non-infant individuals were observed handling infants over the course of the entire study. The ***Reproductive Competition*** and ***By-Product*** hypotheses predict that females will handle significantly more frequently than will males and we did not find a significant difference in frequency of handling between all males and all females for any of the study periods (2011: F=0.003, df=1,12, p=0.955; 2012: F=0.012, df=1,12, p=0.0911; 2013: F=0.707, df=1,11, p=0.418; 2014: F=0.020, df=1,12, p=0.891; 2015: F=0.554, df=1,11, p=0.472) (Table 3.3). The ***Reproductive Competition*** hypothesis also predicts that parous females will handle infants significantly more frequently than will immature and nulliparous females. We found that immature and nulliparous females handled infants significantly more frequently than parous females for all study periods, with the exception of the 2013 study year where no significant difference in handling frequency was found between parous females and immature and nulliparous females (see Table 3.3 for summary of statistics). The ***By-Product*** hypothesis also predicts that parous females without infants and nulliparous females will handle in equal frequencies. We did not find a significant difference in frequency of handling between parous females without infants and nulliparous females for three of the study periods (2012: F=2.985, df=1,2, p=0.226; 2013: F=0.716, df=1,1, p=0.553; 2015: F=8.900, df=1,2, p=0.096). We did find that nulliparous females handled infants significantly more frequently than parous females without infants for two the study periods (2011: F=20.021, df=1,2, p<0.05; 2014: F=2090.667, df=1,1, p<0.05) (Table 3.3).

Table 3.3. Summary of statistical analyses for differences in frequency distribution between age-sex categories

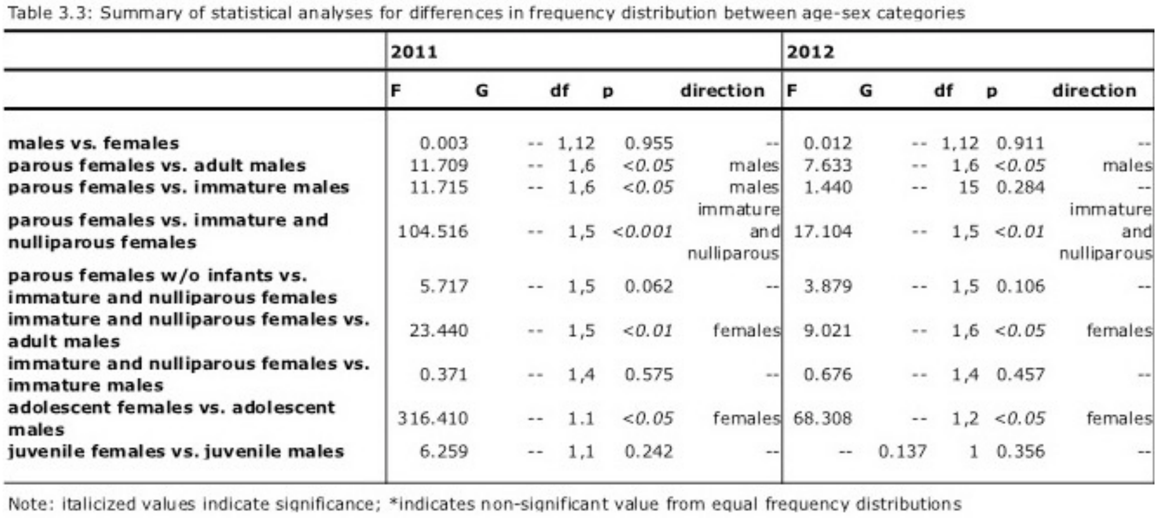
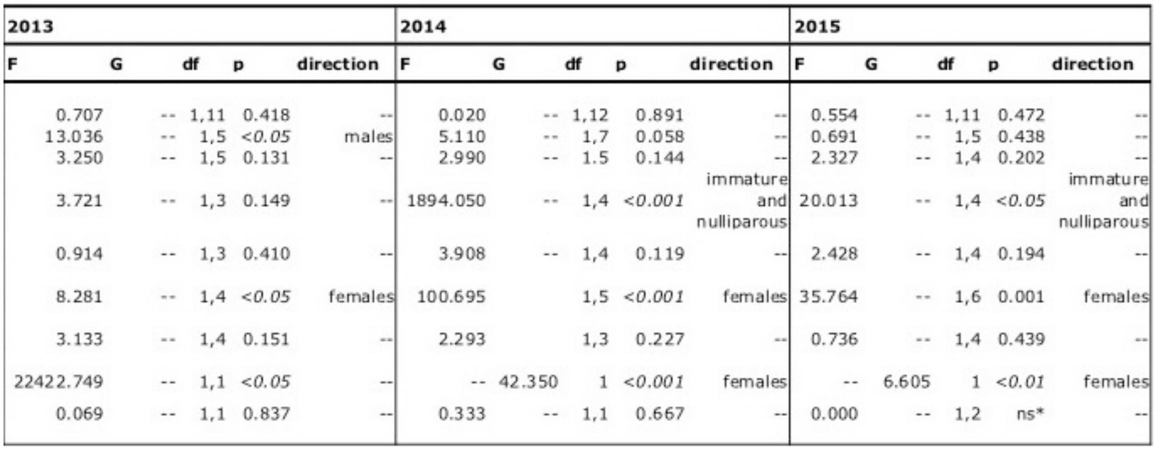


Table 3.3: Summary of statistical analyses for differences in frequency distribution between age-sex categories

	2011					2012				
	F	G	df	p	direction	F	G	df	p	direction
males vs. females	0.003	--	1,12	0.955	--	0.012	--	1,12	0.911	--
parous females vs. adult males	11.709	--	1,6	*<0.05*	males	7.633	--	1,6	*<0.05*	males
parous females vs. immature males	11.715	--	1,6	*<0.05*	males	1.440	--	15	0.284	--
parous females vs. immature and nulliparous females	104.516	--	1,5	*<0.001*	immature and nulliparous	17.104	--	1,5	*<0.01*	immature and nulliparous
parous females w/o infants vs. immature and nulliparous females	5.717	--	1,5	0.062	--	3.879	--	1,5	0.106	--
immature and nulliparous females vs. adult males	23.440	--	1,5	*<0.01*	females	9.021	--	1,6	*<0.05*	females
immature and nulliparous females vs. immature males	0.371	--	1,4	0.575	--	0.676	--	1,4	0.457	--
adolescent females vs. adolescent males	316.410	--	1.1	*<0.05*	females	68.308	--	1,2	*<0.05*	females
juvenile females vs. juvenile males	6.259	--	1,1	0.242	--	--	0.137	1	0.356	--

Note: italicized values indicate significance; *indicates non-significant value from equal frequency distributions



2013					2014					2015				
F	G	df	p	direction	F	G	df	p	direction	F	G	df	p	direction
0.707	--	1,11	0.418	--	0.020	--	1,12	0.891	--	0.554	--	1,11	0.472	--
13.036	--	1,5	*<0.05*	males	5.110	--	1,7	0.058	--	0.691	--	1,5	0.438	--
3.250	--	1,5	0.131	--	2.990	--	1.5	0.144	--	2.327	--	1,4	0.202	--
3.721	--	1,3	0.149	--	1894.050	--	1,4	*<0.001*	immature and nulliparous	20.013	--	1,4	*<0.05*	immature and nulliparous
0.914	--	1,3	0.410	--	3.908	--	1,4	0.119	--	2.428	--	1,4	0.194	--
8.281	--	1,4	*<0.05*	females	100.695		1,5	*<0.001*	females	35.764	--	1,6	0.001	females
3.133	--	1,4	0.151	--	2.293		1,3	0.227	--	0.736	--	1,4	0.439	--
22422.749	--	1,1	*<0.05*	--	--	42.350	1	*<0.001*	females	--	6.605	1	*<0.01*	females
0.069	--	1,1	0.837	--	0.333	--	1,1	0.667	--	0.000	--	1,2	ns*	--

The ***Reciprocity*** hypothesis predicts that parous females will handle infants significantly more frequently than other age-sex categories of handlers. There were no observations of reciprocal infant handling among parous females and parous females were never observed handling infants more frequently than any other age class (see Table 3.3 for summary of statistics). Conversely, we found that both immature and nulliparous females and adult males handled infants significantly more frequently across the study period, although the finding was not consistent across all study years (see Table 3.3 for summary of statistics). The ***Learning-to-Mother*** hypothesis predicts that immature and nulliparous females will handle significantly more frequently than other age-sex categories of handlers. We found that immature and nulliparous females handled infants significantly more frequently than any other age sex class across all study periods (see Table 3.3 for summary of statistics) except when compared to immature males. When immatures were separated into juvenile and adolescent age categories and then sex classes compared, we found that adolescent females handled significantly more frequently than did adolescent males for each of the study periods and that there was no difference in handling frequency between juvenile males and juvenile females (see Table 3.3 for summary of statistics).

Rank Effects and Coalitionary Support

All infants in this study were observed being handled and no significant difference in handling frequency per hours of observation for each infant was found among the infants (G=0.12, df=3, p=0.500). The ***Reproductive Competition*** and ***Alliance Formation*** hypotheses both generate predictions regarding the role of the mother's rank on handling frequency of infants. The ***Reproductive Competition*** hypothesis predicts that infants of lower ranking females will be handled significantly more frequently than the infants of higher ranking females and the ***Alliance Formation*** hypothesis predicts the opposite, where infants of higher ranking females will be handled significantly more frequently. We found no significant correlation between rank of the mother and number of handling interactions per hours of observations for each of the infants (p=0.0824, df=2, R^2=0.696; Fig. 3.3).

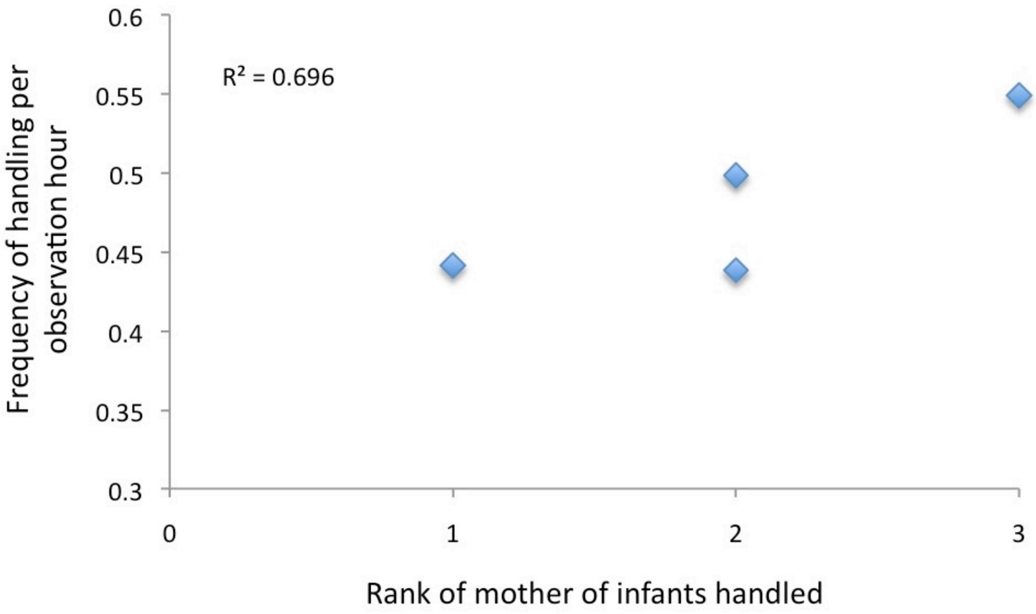


Fig. 3.3. Frequency distribution of handling behaviors received for each infant by rank of mother

The ***Alliance Formation*** hypothesis predicts that individuals will handle infants in exchange for coalitionary support during conflicts. We found a significant positive correlation between frequency of handling infants and agonistic support from mothers unrelated to the handler during conflicts with the handler over the course of the entire study period ($p<0.05$, df=26, $R^2=0.128$; Fig. 3.4).

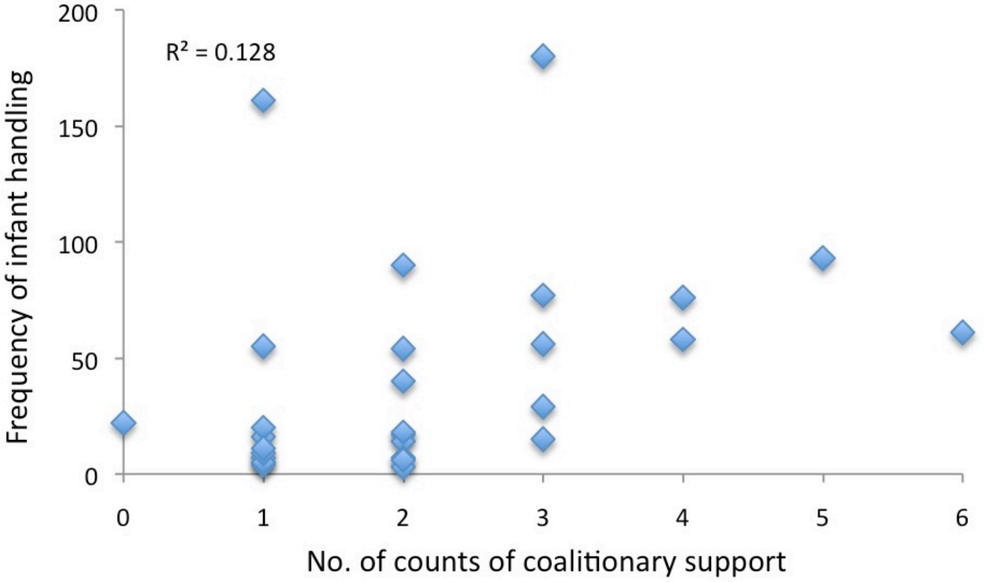


Fig. 3.4. Frequency distribution of handling behaviors performed by amount of coalitionary support received from unrelated mothers of infants

Oxytocin

We predicted that if the ***Learning-to-Mother*** hypothesis functions as a mechanism through which immature and nulliparous females learn species appropriate maternal behaviors, OT, a known facilitator of maternal behaviors, would be positively correlated with handling behaviors among immature and nulliparous females. We found a significant positive correlation between frequency of handling infants and mean OT, expressed as pg^{-1}creatinine, over the 2012 – 2015 study years (urine was not collected during the 2011 study year) ($p=0.001$, $df=8$, $R^2=0.733$; Fig. 3.5). Because other age-sex categories handled infants and there is evidence that OT also facilitates social bonding among group members in chimpanzees (Crockford et al. 2013; Wittig et al. 2014), we investigated the connection between mean OT and handling behaviors the other age sex categories. We did not find a significant correlation between mean OT, expressed as pg^{-1}creatinine, over the 2012 – 2015 study years, and infant handling behaviors among immature males ($p=0.060$, $df=11$, $R^2=0.205$; Fig. 3.6) or adult males ($p=0.403$, $df=16$, $R^2=0.003$; Fig. 3.7). There was, however, a significant negative correlation between mean OT expressed as pg^{-1}creatinine, over the 2012 – 2015 study years, and infant handling behaviors among adult females ($p<0.05$, $df=12$, $R^2=0.246$; Fig. 3.8).

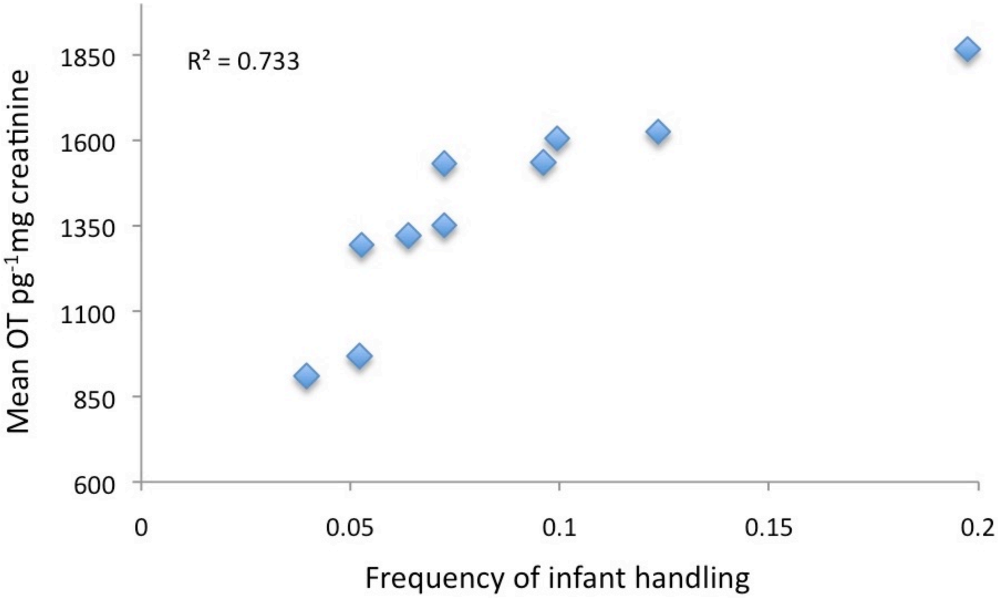


Fig. 3.5. Mean OT levels among immature and nulliparous females by frequency of handling behaviors per observation hour per infant

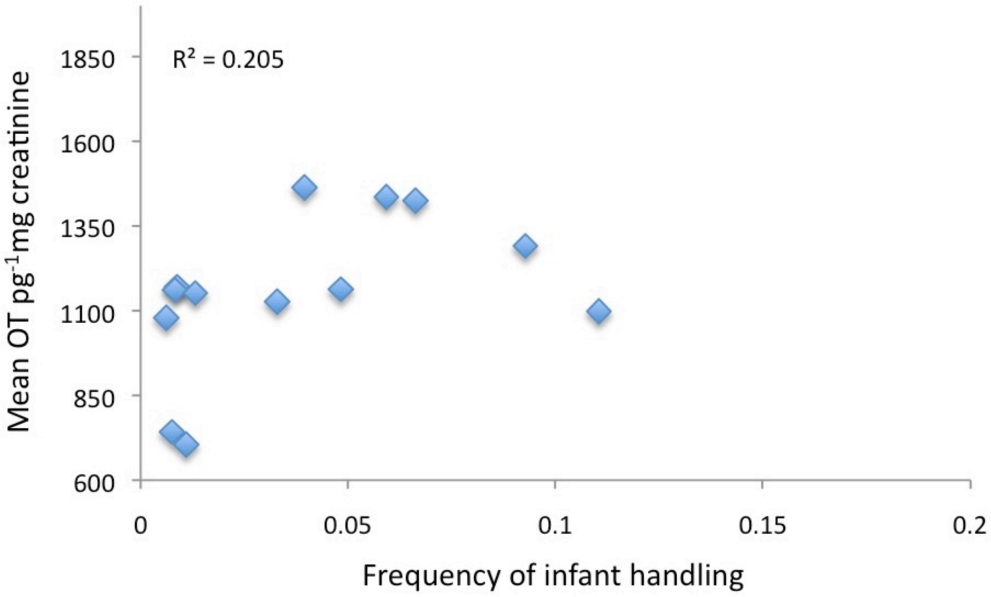


Fig. 3.6. Mean OT levels among immature males by frequency of handling behaviors per observation hour per infant

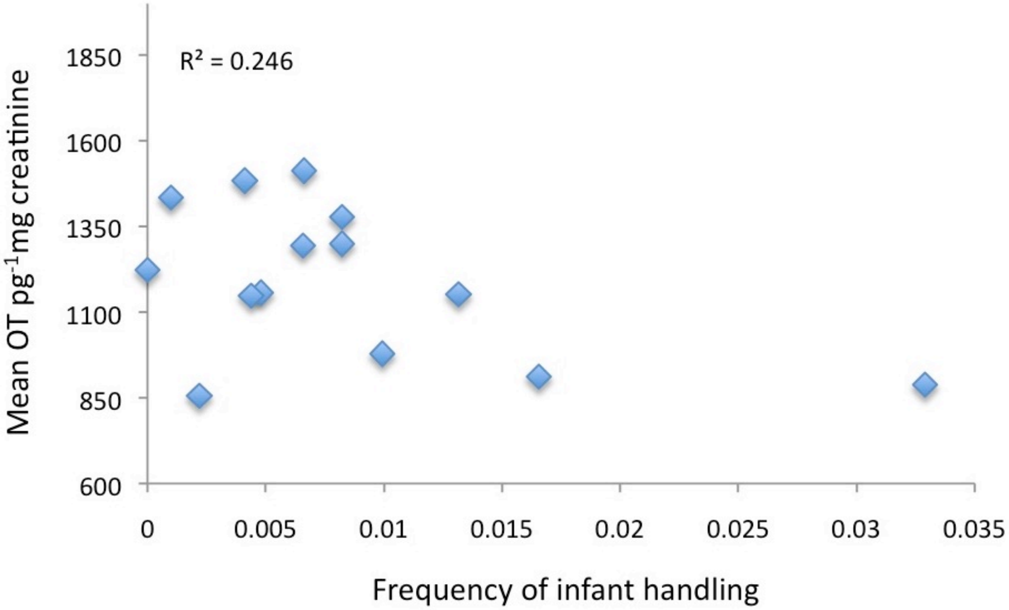


Fig. 3.7. Mean OT levels among parous females by frequency of handling behaviors per observation hour per infant

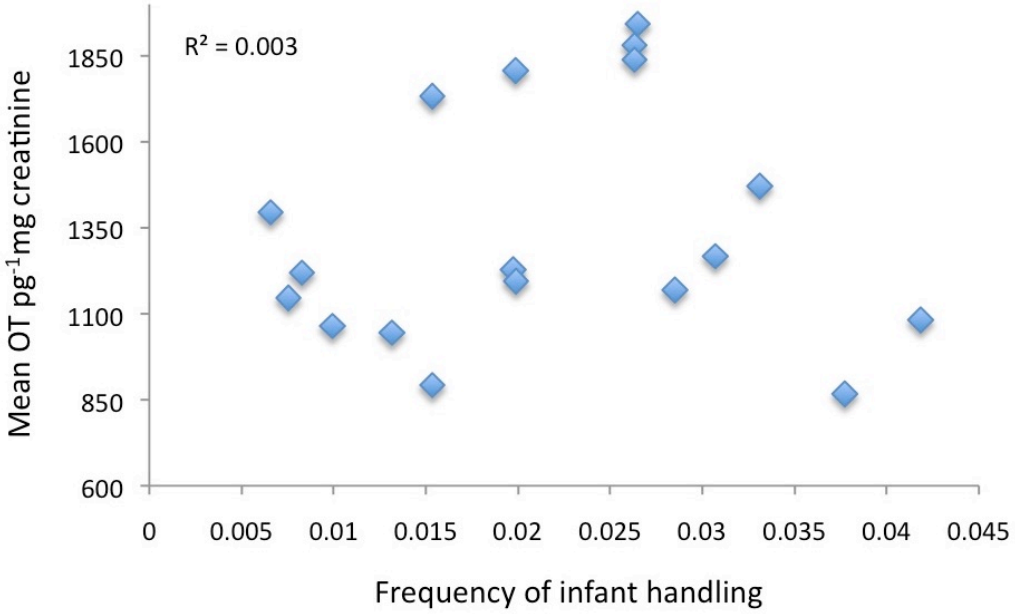


Fig. 3.8. Mean OT levels among adult males by frequency of handling behaviors per observation hour per infant

DISCUSSION

Although reports of infant handling in wild bonobos are scarce (Kano 1992; Mitani and Watts 1997), the handling of infants was a common phenomenon in this captive group. Over the course of five study years (2011-2015) we observed 1778 interactions between infants and non-maternal group members, occurring at a rate of about two every three hours. Even though all group members interacted regularly with all of the infants, individuals exhibited a significant bias toward handling related infants over unrelated infants during some of the study periods. While the ***Kin Selection*** hypothesis (Hamilton 1964; Hrdy 2009) suggests that handling provides direct and/or indirect fitness gains to the mother and/or handler and has primarily been invoked in species that practice cooperative or communal breeding (Emlen et al. 1991; Bourke and Franks 1995), there are few examples of kin bias in most cercopithecine species (Paul and Kuester 1996). There is, however, considerable evidence that humans practice extensive allocare and handling behaviors among kin (see Kramer 2010) and the degree to which infant handling may provide fitness gains in other great ape species is largely unknown. The results of our study support the predictions generated by the ***Kin Selection*** hypothesis and offer insight into a potential additional mechanism through which female IBI's are reduced. The IBI's of chimpanzees and bonobos differ slightly, where chimpanzee females give birth every 61.2-69.1 months on average and bonobo females give birth every 57.6 months on average (see Stumpf 2011 pg. 352). Although these differences have largely been attributed to the ecological constraints and seasonal influences on mating behavior and birth cycles in chimpanzees (see Stumpf 2011; Wallis 1995; Boesch and Boesch-Achermann 2000; Anderson et al. 2002; Emery Thompson and Wrangham 2008), it is possible that infant handling helps reduce the burden of care-giving for mothers in bonobos. Furthermore, social hazards, such as infanticide and lethal raiding, both of which occur in chimpanzees and have yet to be observed in bonobos, are powerful forces that may induce selection against non-maternal care (Silk 1999) and could be a contributing factor to why this behavior is absent in chimpanzees.

The ***Reproductive Competition*** hypothesis (Hrdy 1976; Silk 1980; Wasser and Barash 1981; Wasser 1983; Gittleman 1985; Maestripieri 1994) suggests that infant handling evolved as a mechanism of competition between females where adult females will aggressively handle, kidnap, or 'allomother to death' infants of unrelated females and the results of our study do not support any of the predictions generated by this hypothesis. While we found that the distribution of frequencies of interactions varied considerably between age-sex classes, immature and nulliparous females generally handled infants more frequently than any other age-sex category. We also found that aggressive behaviors directed toward infants in the context of handling were infrequent and usually mild (i.e., pulling on the infant). Silk (1999) has suggested that interactions categorized as negative handling behaviors may simply be the outcome of persistence by the handler when faced with maternal or infant resistance to being handled, particularly during times of potential danger. We found that two of the mothers (Susie, Ana Neema) in this study often resisted the handling of their infants by the youngest son (Jerry) of the alpha female (Unga). Jerry frequently directed aggression and harassment behaviors at Susie (Boose and White 2017) and Unga often responded to conflicts involving her offspring with highly aggressive behaviors, frequently resulting in the wounding of her opponent, including Susie and Ana Neema as well as individuals classed as immatures (Boose, unpublished data). It is probable that the mild negative handling behaviors observed in this group were the result of female reticence to allow her infant to be handled while in certain social contexts. The ***Reproductive Competition*** hypothesis also predicts that the infants of lower ranking females will be handled more frequently than the infants of higher ranking females. Although our results were not significant, there was the suggestion of a negative correlation between mother's rank and frequency of handling of each infant. We do not, however, believe this non-significant but suggestive result is the outcome of individuals targeting the infants of lower ranking females primarily for the reasons inherent to the ***Reproductive Competition*** hypothesis. Instead, we suggest this finding, coupled with the result that positive handling behaviors occurred significantly more frequently than negative behaviors, reflects both differences in maternal style and an avoidance of potential conflict with the alpha female (Unga). Researchers (Silk 1999) have noted that the motivations of mothers and handlers may represent a conflict of interest and individuals may, therefore, be more free to express handling behaviors toward infants of lower ranking females.

The ***Reciprocity*** hypothesis (Hrdy 1976; Stanford 1992) describes infant handling as a social commodity exchanged between parous females whose expression is dependent on social and demographic factors that influence opportunities for reciprocity. Our results supported the prediction that positive handling behaviors would occur more frequently than negative handling behaviors but we did not find support for the prediction that parous females would handle infants significantly more frequently than other age-sex categories. The only parous female without an infant (Lady) in our study group did not interact with infants more or less frequently than the other parous females, who were rarely observed interacting with others' infants. This result is interesting given the strong natal attraction and frequency of handling among the immature female bonobos in our study group. Furthermore, attempts to frame predictions on the function of infant handling around Socioecological factors suggest that in species with low or relaxed within-group contest competition (WGC), reciprocal exchange of handling between females should be less constrained than in species with high WGC because dominance relationships between females are more relaxed (Maestripieri 1994). Bonobo habitats are characterized by less seasonal variation in food availability as well as larger and more abundant fruiting trees and greater distribution of terrestrial herbaceous vegetation (THV) that may result in lower WGC, relative to chimpanzees (White and Wrangham 1988; Chapman et al. 1994; Malenky and Wrangham 1994; White 1996, 1998; White et al. 2015). Although bonobos form linear dominance hierarchies (Stevens et al. 2007), females exhibit intrasexual social tolerance within the context of feeding (Vervaecke et al. 2000) and further studies are needed to address whether these factors are related to infant handling in bonobos and whether they influence handling frequencies differently in parous vs. nulliparous females.

The ***Alliance Formation*** hypothesis also describes infant handling as a social commodity, namely a service that can be exchanged for coalitionary support during conflicts. Our results did not support the prediction that the infants of higher ranking females would be handled more frequently than the infants of lower ranking females. However, our results do support the prediction that handling would be positively correlated with coalitionary support from mothers during conflicts involving the handler. Female bonobos are known to form various types of coalitions both in captivity and the wild. For example, coalitions in captive females have been found to function as a mechanism to maintain female power over males, to acquire and maintain dominance rank, and to reduce tension and test the strengths of social bonds (Vervafcke et al. 2000) and in wild populations, female coalitions also function to maintain dominance over males (White and Wood 2007; Tokuyama and Furuichi 2016). However, coalitionary support from females is not always based on patterns of affiliation and older females support younger females more frequently than younger females support older females (Tokuyama and Furuichi 2016). The results presented in this paper may provide potential insight into these observations and further studies on coalitionary aggression, infant handling, and affiliative behavior are needed to understand the impact of infant handling on the patterning of coalitionary support in bonobos.

The ***By-Product*** hypothesis suggests that infant handling is the result of selection for infant responsiveness because females who respond promptly and frequently to infant signals should make good mothers (Quiatt 1979; Scollay and DeBold 1980). The predictions generated from this hypothesis overlap significantly with the predictions generated from the other hypotheses tested in this paper where our results supported the prediction that positive handling behaviors should occur more frequently than negative handling behaviors and did not support the prediction that females should handle infants more frequently than males. Furthermore, the ***By-Product*** hypothesis predicted that parous females without infants would still be attracted to and motivated to handle infants as much as nulliparous females are. Although our data did not support this prediction, this result may not accurately reflect the frequency distribution of handling between parous females without infants and nulliparous females because, over the course of the entire study period, there was only one parous female without an infant. Further studies on handling behaviors among parous females without infants and those who have recently lost an infant are needed to more accurately test this assumption.

We found significant support for the ***Learning-to-Mother*** hypothesis, which describes infant handling as a mechanism through which immature and nulliparous females learn about species appropriate maternal behaviors. Our results supported the predictions that positive handling behaviors would occur significantly more frequently than negative handling behaviors and gave mixed support for the prediction that immature and nulliparous females would handle more frequently than any other age-sex category where immature males were also frequently observed handling infants. Primate infants, particularly among the great ape species, take a long time to develop and reach maturity (see Leigh and Blomquist 2011 and Stumpf 2011). Offspring represent a costly investment to females and selection should favor mechanisms that afford immatures opportunities to learn species-typical behaviors, particularly those with a high cost-benefit ratio (Trivers 1972). As discussed above, natal attraction and infant handling are deeply rooted across primate taxa and there is considerable support for the ***Learning-to-Mother*** hypothesis. It is, therefore, not surprising that, under conditions of captivity where food is abundant and environmental hazards such as predation and infanticide are low, immature female bonobos are willing to provide some of the costly care normally attributed to mothers and that these adult females will take advantage of the opportunity to reduce their maternal burdens.

Finally, one of the objectives of this study was to investigate the connection between OT, a hormone known to modulate social bonding and maternal behaviors in mammals, and infant handling behaviors in bonobos. Our results supported our prediction that, if OT functions as a facilitator of maternal behavior, then OT levels would only be correlated with infant handling in immature and nulliparous females and not in parous females because parous females should only show correlation with interactions with their own infants. Our results also supported the prediction that, although it is possible that OT facilitates infant handling as a type of social interaction in males, OT in males should not be correlated with infant handling alone. OT is known to modulate social tolerance and care-giving behaviors in callitrichid (Saito and Nakamura 2011; Finkenwirth et al. 2016) and human males (Gordon et al. 2010b; Feldman et al. 201, 2011), both species where allocare is necessary to ensure infant survival. While it is interesting to consider the role of OT in the facilitation of care-giving behaviors in male bonobos, allocare is not essential to infant survival and any correlation between OT and infant handling behaviors should be considered as part of the larger context of affiliation and social bonding in this species. Additional studies on the relationship between affiliative interactions and OT across social contexts and age-sex categories are needed to fully understand the role OT plays in the facilitation of social bonding in bonobos. These results demonstrate the utility of incorporating data on hormones known to modulate behavior into behavioral studies. Our data presented here suggest that infant handling may function as a mechanism of learning-to-mother and that OT may facilitate the onset of care-giving and maintenance of maternal behaviors in young female bonobos.

Conclusion

In conclusion, infant handling is a distinct type of affiliative behavior that functions both as a mechanism of learning species typical maternal behaviors in young female bonobos and in a manner that may facilitate coalition formation between handlers and mothers of infants. The results presented here show that while juvenile males and females associate frequently with infants, adolescent females perform handling behaviors significantly more than do adolescent males. Furthermore, mean OT levels were correlated with handling behaviors in juvenile and adolescent females, but not in any other age-sex category. Although study design did not permit the testing of the long term consequences of associating with an infant in exchange for coalitionary support from that infant when they reach adulthood, the results presented show a positive connection between handling behaviors and coalitionary support of the handler by the mother of the infant handled. Results also showed that, during some of the study periods, handlers demonstrated a significant bias in handling related infants. Together these results on infant handling behavior in bonobos provide strong support for the ***Learning-to-Mother*** hypothesis, mixed support for the ***Alliance Formation*** and ***Kin Selection*** hypotheses, and potentially demonstrate evidence for a mechanism that contributes to the observed lower inter-birth intervals of bonobos relative to chimpanzees.

BRIDGE TO CHAPTER IV

The objective of Chapter III was to examine the patterning of infant handling behavior in bonobos and to test predictions generated by six functional hypotheses. The results presented in this chapter demonstrated that infant handling functions as a mechanism through which young females learn species typical maternal behaviors and as a potential mechanism of alliance formation and the reduction of inter-birth intervals.

While Chapter III provides important insights into the influence of social interactions with infants on development in bonobos and highlights the importance of these interactions on the social strategies of individuals across age-sex categories, the purpose of Chapter IV is to examine in detail the social strategies of males in females within the context of mating and the resulting influence of these inter-individual interactions on the social and mating strategies of other group members. The study presented in Chapter IV will detail the pattering of proceptive and receptive sexual behavior among females and will examine the potential influence of male directed aggression on the expression of female choice in mating partners.

CHAPTER IV

FEMALE CHOICE IN BONOBOS (*PAN PANISCUS*): EVIDENCE OF MALE CONSTRAINT AND COALITIONARY SEXUAL COERCION

This chapter includes previously unpublished co-authored material, facilitated by a number of people, including Frances White, Josh Snodgrass, and Audra Meinelt. The author, Klaree Boose, was the principle investigator for this work, responsible for the study design, behavioral data collection, hormonal analyses, statistical analyses, and manuscript preparation. Frances White is the academic adviser for this dissertation and contributed to this work by participating in the development of study design and statistical analyses. Josh Snodgrass is the principle investigator of Global Health Biomarker Lab at the University of Oregon and was instrumental in providing laboratory space and equipment for the hormonal analyses conducted for this study. Audra Meinelt is an assistant curator at the Columbus Zoo and provided institutional support for data collection, storage, and shipment of samples.

INTRODUCTION

Since its initial description, sexual selection theory (Darwin 1871) has been studied across a wide array of taxa, culminating in the identification of three primary mechanisms: intersexual selection, intersexual conflict, and intrasexual selection (Parker 1979; Smuts and Smuts 1993; Andersson 1994; Clutton-Brock and Parker 1995). These mechanisms are hypothesized to be the driving force behind the evolution of traits that influence reproductive success, but may or may not be related to individual survival (for reviews in primates see Manson 2003 and Kappeler and van Schaik 2004). Intersexual selection, or mate choice, involves the evolution of traits that increase an individual's attractivity to the opposite sex, such as signals of genetic quality, dominance rank, ability to secure resources and/or to provide infant care (see Manson 2011). Due to the inherent asymmetries in parental investment, intersexual conflict arises when male and female mating interests do not align and involves strategies employed by individuals to override mate choice in the opposite sex (Parker 1979; Smuts and Smuts 1993; Clutton-Brock and Parker 1995; Wigby and Chapman 2004; Chapman 2006). Competition for mates, or intrasexual selection, can result in traits such as armaments and sexually dimorphic musculature that increase a male's ability to access females, especially in species where there is little or no direct paternal care (Anderson 1994; Kappeler and van Schaik 2004). In turn, these traits can facilitate male strategies during intersexual conflict, whereby males use aggression and the threat of force against females to constrain female choice in mating partners (Smuts and Smuts 1993; Clutton-Brock and Parker 1995; Muller and Wrangham 2009; Muller et al. 2011).

Under such circumstances, where male and female mating interests do not align, male constraint of female choice can operate through a variety of mechanisms, collectively referred to as sexual coercion, that include harassment, mate guarding, interventions into copulations, intimidation, and infanticide (Hrdy, 1979; Smuts and Smuts 1993; Clutton-Brock and Parker 1995; van Schaik and Janson 2000; van Schaik et al. 2004; Clarke et al. 2009; Muller et al. 2009; Watson-Capps 2009; Stumpf et al. 2011;

Muller et al. 2011). Sexual coercion in general, as defined by Smuts and Smuts (1993, ppg. 2-3), is the ‘use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female.’ Clutton-Brock and Parker (1995) identify three distinct forms of direct sexual coercion, *forced copulation*, *intimidation*, and *harassment*, which function to overcome female resistance to mating and differ mainly in their temporal association between aggression and mating. *Forced copulations* do occur in primates (e.g., orangutans: Galdikas 1981), albeit relatively infrequently (e.g., chimpanzees: Goodall 1986; Muller and Wrangham 2009), and refer to the context in which the temporal association between aggression and mating is indistinguishable. *Harassment* refers to ‘repeated attempts to mate that impose costs on females, inducing eventual female submission’ whereas *intimidation* ‘involves physical retribution against female refusals to mate, increasing the likelihood of submission to future advances’ (Muller and Wrangham 2009, pg. 10). Muller and Wrangham (2009, p. 10) identify three forms of indirect sexual coercion they collectively categorize as ‘coercive mate guarding’: *punishment*, *herding*, and *sequestration*, which function to influence a female’s ability to mate with other males. These mechanisms vary mainly in the timing of aggression and female spatial proximity to rival males where *punishment* refers to male directed aggression at females in response to association or copulation with other males, and *herding* and *sequestration* involve spatially separating females from rival males (Clutton-Brock and Parker 1995; Clarke et al. 2009; Muller and Wrangham 2009; Muller et al. 2011).

Male sexual strategies, however, do not operate in the absence of female attempts to exercise choice. As Stumpf et al. (2006) have noted, female counter strategies have been shown to enhance female mating and reproductive success across several species (Partridge 1980; Dunbar 1984; Wallen and Winston 1984; Keddy 1986; Boinski 1987; Bercovitch 1991; Manson 1992; Perloe 1992; Soltis et al. 1997; Buck 1998; Reynolds and Gross 1992; Norris 1993; Petrie 1994, Eberhard 1996; Promislow et al. 1998; Cunningham and Russell 2000; Kolm 2001; Drickamer et al. 2000, 2003; Adair-Gowaty et al. 2002; Hine et al. 2002). For example, exaggerated sexual swellings and polyandrous (i.e., promiscuous) mating are designed to concentrate paternity towards the alpha male while simultaneously spreading copulations across other males in order to confuse paternity and reduce the risk of infanticide (Nunn 1999). Other mechanisms, such as proceptivity (i.e., female approaches or solicitations for copulation) and resistance to copulations, also have the potential to influence paternity and should therefore be under strong selective pressure to evolve (Stumpf et al. 2006).

The expression and efficacy of these mechanisms, however, are dependent on mating system and can vary according to the degree of male dominance and intersexual conflict characteristic of a species. For example, in chimpanzees, a species with promiscuous mating, no direct paternal care, relatively frequent infanticide, and a high degree of male dominance (Goodall 1986), researchers from the Tai National Park (Stumpf et al. 2005) have found that females increase resistance rates and decrease proceptivity rates during the periovulatory period (POP), when conception is most likely to occur (Emery-Thompson 2005), suggesting that females alter their sexual strategies across their cycles to exercise choice. Furthermore, Stumpf et al. (2006) found that resistance rates were inversely related to male mating success during POP and concluded that females were likely effective at influencing paternity. Muller et al. (2009, 2011), however, have argued that the apparent choice of female chimpanzees described by Stumpf et al. (2005, 2006) is being driven by the aggression females receive from males across all contexts. In their study group, female proceptivity was correlated with rates of aggression received throughout their cycles (Muller et al. 2011) and conclude that this continuous aggression is representative of the intersexual conflict over mating exclusivity. They argue the primary sexual strategy of females is infanticide prevention via promiscuous mating and that male aggression against females functions as a long-term coercive strategy to constrain this effort (Muller et al. 2011). More recently, results of studies conducted at the Gombe chimpanzee field site have shown that while male directed aggression and copulation frequency were correlated during the maximum swelling phase (MSP) of the ovulatory cycle, paternity was correlated with aggression during the non-swollen phase and support the hypothesis that male sexual coercion is a reproductive strategy that develops over time (Feldblum et al. 2014).

The purpose of this paper is to explore the patterning of sexual behavior, male directed aggression, and female mate choice in bonobos (*Pan paniscus*) who like chimpanzees, exhibit a promiscuous mating system with no direct paternal care (Kano 1992; Furuichi 1992), but differ drastically in their dominance structure, where females form coalitions against males (Parish 1996; Paoli et al. 2009; Tokuyama and Furuichi 2016) and often attain the highest rank positions (Furuichi 1997; Stevens et al. 2007;

Surbeck and Hohmann 2013; Goldstone et al. 2016), and where there is an inferred low risk of infanticide (Kano 1992; Stanford 1998). Researchers have long suggested that the relatively high dominance rank of females allows for active female choice (Furuichi 1992; Kano 1996; Fruth et al. 1999) that is facilitated by prolonged and frequent estrous (swellings) during which time they are continuously receptive and attractive to males (Takahata et al. 1996; Furuichi and Hashimoto 2004; Paoli et al. 2006). The reports of prolonged estrous and continuous receptivity have in turn been interpreted as lower sexual competition among bonobo males relative to chimpanzee males (Kano 1989; Furuichi and Hashimoto 2004) and predict, therefore, an absence of sexual coercion and low mating and reproductive skew in bonobos relative to chimpanzees (Smuts and Smuts 1992; Wrangham 1993). Support for this hypothesis has been mixed. Some studies reporting on copulation frequency across males have shown no concentration of copulations towards one male (Gerloff et al. 1999; Furuichi and Hashimoto 2004) while others have shown that copulations can be skewed toward a male, who may or may not be the highest rank male (Kano 1996; Marvan et al. 2006; Paoli and Palagi 2008; Boose et al. 2012). Furthermore, a recent study has shown that paternity is more highly skewed in bonobos than in chimpanzees and that high ranking males are successfully able to monopolize reproduction, accounting for the majority of the offspring sired (Surbeck et al. 2017).

In light of this data, the question becomes: are observations of mating and reproductive skew the result of unfettered female choice or is male constraint operating on some level? To properly investigate this question, it is important to consider the effects of male aggression on female mating behavior across all contexts (Muller et al. 2009; Feldblum et al. 2014). Few studies have reported on rates of male directed aggression and mating in bonobos and, among those that have, the results are mixed. Hohmann and Fruth (2003) found that estrous females were the targets of male aggression more often than expected by chance, but Surbeck and Hohmann (2013) found that males did not aggress females displaying MSP and Paoli et al. (2009) found lower rates of aggression during MSP and no correlation between male directed aggression and mating. This study will address the gap in our understanding of the relationship between male directed aggression and female mate choice in bonobos to more fully understand the proximate mechanisms that produce mating and reproductive skew in this species.

HYPOTHESES AND PREDICTIONS

Hypothesis 1: Female bonobos exhibit continuous receptivity to confuse paternity and maintain low levels of male-male competition and intersexual conflict

Predictions 1: If females exhibit continuous receptivity, then we expect:

a) rates of receptivity among females will not vary across males
b) mating skew among males will be low, frequency of copulations will be evenly distributed across males

Hypothesis 2: Patterns of female mating behavior are the expression of unfettered choice in order to concentrate paternity towards a preferred male

Predictions 1: If female proceptive behavior is an expression of female choice in the absence of male sexual coercion, then we expect:

a) females will solicit copulations from and mate more frequently with the preferred male(s) over other males
b) female solicitations will not be correlated with aggression received

Prediction 2: If female receptive behavior also operates in the absence of male sexual coercion, then we expect:

c) female receptivity will not be correlated with aggression received
d) females will deny solicitations for copulations from non-preferred males and success rate of denials for solicitations will not be correlated with female dominance rank

Hypothesis 3: Patterns of female mating behavior reflect male counter strategies to constrain female choice

Prediction 1: If female proceptive behavior is the result of male sexual coercion, then we expect:

a) female solicitations will be correlated with aggression received

Prediction 2: If female receptive behavior is the result of male sexual coercion, then we expect:

b) female receptivity will be correlated with aggression received
c) female denial of solicitation for copulations will be correlated with female dominance rank

Hypothesis 4: High mating skew across males, whether the result of active female choice or male constraint of choice, should result in the expression of alternate male mating strategies

Prediction 1: If there is variation in female receptivity across males and aggression is correlated with mating success, then we expect

a) males to engage in direct sexual coercion, under conditions of low likelihood of retaliation in the form of coalitionary aggression

Hypothesis 5: Muller and Wrangham (2009) have argued that for a behavior to be considered direct sexual coercion it must impose a fitness cost on the target. Exposure to environmental stressors, such as conflict with group members, is known to increase cortisol values in many species of group living primates (e.g., bonobos: Surbeck et al. 2012; chimpanzees: Muller and Wrangham 2004). Furthermore, chronically elevated cortisol levels can disrupt the natural circadian rhythm and function of cortisol in the body (Karlamangla et al. 2013; Novak et al. 2013) and can have a long-term negative impact on survival (see for review Lupien et al. 2009; Novak et al. 2013). Female targets of direct sexual coercion are, by definition, receiving aggression for resisting the copulatory efforts of non-preferred males and should, therefore exhibit a stress response.

Predication 1: If sexual coercion induces a stress response, then we expect

a) cortisol values in females who receive aggression from males will be correlated with frequency of aggression received

b) on days when direct sexual coercion takes place, cortisol values in targets will be significantly higher than mean cortisol values determined for that individual

METHODS

Subjects and Housing

All data were collected on the captive group of bonobos housed at the Columbus Zoo and Aquarium (CZA) in Columbus, Ohio, USA during the summer months of 2012 (May 20 – July 13), 2013 (April 14-June 16), 2014 (June 3-July 10), and 2015 (August 27-September 14). Daily observations usually began around 0730 hours and ended between 1300 – 1700 hours resulting in 1396 observation hours. Over the course of the study, CZA had a total of 11 females (4 adult and 4 adolescent) and 8 males (5 adult and 1 adolescent) (Table 1) that were housed in a complex of areas consisting of two large indoor public viewing exhibits (54.8 m2 each) with multiple climbing structures, two off-exhibit indoor enclosures (22.6 m2 each), two off-exhibit outdoor enclosures (18.5 m2 each) and a large naturalistic outdoor public viewing exhibit (57.9 m x 45.7m, 2647.7 m2) with grass, mature trees, and an artificial stream and waterfall. The keepers at CZA managed the bonobos to simulate the species typical fission-fusion process of variable party composition where the bonobos were allowed access to each other each morning and parties were set based mostly on individual bonobo association preferences. This management process usually resulted in three parties that lasted for 2-3 days, rarely changed on a daily basis or exceeded 4 days, and where all immatures had abundant opportunity to interact with all individuals (see Boose et al. 2013 for description).

Age Classifications

The individuals of this study were classified according to the detailed descriptions of age-class characteristics of bonobos given by Thompson-Handler et al. (1984). For example, Thompson-Handler et al. (1984) described an adult male as an individual that is 'full size, scrotum fully pendant' and an adolescent male as an individual that is 'smaller and more gracile than adult (approximately three-quarters size), scrotum not fully pendant' (p. 349). Individuals were therefore categorized according to the following: adolescent I = 8-9 years; adolescent II = 10-12 years; and adult ≥ 13 years (see Boose and White 2017 for full description). These age classes vary slightly from what was reported for a wild population of bonobos (Kano 1992) and reflect the accelerated development that can occur in captivity. In the wild, females younger than 10 years are generally assumed to exhibit adolescent sterility and are therefore considered to be non-fertile (Marson et al. 1991; Stumpf 2011). In captivity, however, females can reach menarche as early as 9 years (Boose, unpublished data) and can give birth during adolescence (Boose, unpublished data). Furthermore, adolescent males have been observed copulating with ejaculation (Boose, unpublished data). Since it is possible that these adolescent males and females are contributing to the distribution of reproductive success within the group, they have been included in the dataset for this study.

Reproductive Status of Females

All of the adult females of this group were multiparous and three of these females either gave birth, were pregnant, or were currently breastfeeding an infant ≤ 2 years of age, and were considered to be under lactational amenorrhea. These three females were not included in the data set for the study periods where they fit one of the above conditions. For example, Lady was pregnant during the 2015 study period and her behaviors and cortisol values were not included in the 2015 study period dataset (Table 4.1). Female bonobos can sometimes give birth after a relatively short interval and have been known to carry two dependent offspring at the same time (Furuichi and Hashimoto 2002). Furthermore, females are known to resume cycling with maximum swelling in ≤ 15 months (Furuichi and Hashimoto 2002) and, therefore, females with infants >2 years were included in the data set.

Additionally, because sexual swellings in many species of primate function to reduce the risk of infanticide by facilitating polyandrous mating and thus confusing paternity (Hrdy 1979), it can be important to determine the relative change in female sexual behavior across the ovulatory cycle (e.g., see above description in chimpanzees; Stumpf et al. 2005, 2006; Muller et al. 2011). The sexual swellings of female bonobos, however, have been shown to be poor determinants of the timing of ovulation relative to the onset of the MSP (Reichert et al. 2002; Douglas et al. 2016) and should not be considered reliable indicators of POP. For these reasons, we do not distinguish between periods of non-swelling and the MSP and female sexual behavior across the entire ovulatory cycle is included in the data.

Table 4.1: Group composition, rank and age class assignments, and female reproductive status of the CZA bonobo colony (2012-2015)

			2012			2013			2014			2015		
Subject	**Sex**	**Related Individuals**	**Age Class**	**Sex Rank**	**Reproductive Status (females)**	**Age Class**	**Sex Rank**	**Reproductive Status (females)**	**Age Class**	**Sex Rank**	**Reproductive Status (females)**	**Age Class**	**Sex Rank**	**Reproductive Status (females)**
Unga	f	*Gander*	Adult	1	lactating	Adult	1	lactating	Adult	1	parous	Adult	1	parous
Ana Neema	f	*Bila-Isia, Gilda*	Adult	2	parous	Adult	2	parous	Adult	2	pregnant	Adult	2	lactating
JoT	f	*Lady*	Adol II	3	nulliparous	*	*	*	*	*	*	*	*	*
Susie	f	*Donnie, Lola*	Adult	4	parous	Adult	3	parous	Adult	3	parous	Adult	3	parous
Lady	f	*JoT*	Adult	5	parous	Adult	4	parous	Adult	4	parous	Adult	4	pregnant
Lola	f	*Donnie, Susie, Toby*	Adol I	6	nulliparous	*	*	*	*	*	*	*	*	*
Gilda	f	*Bila-Isia, Ana Neema*	Juv	--	--	Adol I	5	nulliparous	*	*	*	*	*	*
Sukari	f		**	**	**	**	**	**	Adol I	5	nulliparous	Adol II	5	nulliparous
Donnie	m	*Susie, Lola*	Adult	1		Adult	2		Adult	2		Adult	2	
Bila-Isia	m	*Ana Neema, Gilda*	Adol II	2		Adol II	1		Adult	1		Adult	1	
Jimmy	m		Adult	3		Adult	3		Adult	3		Adult	4	
Maiko	m		Adult	4		Adult	4		Adult	5		Adult	5	
Toby	m	*Lola*	Adult	5		Adult	6		Adult	6		Adult	6	
Gander	m	*Unga*	Adol I	6		Adol II	5		Adol II	4		Adol II	3	

*Note: *indicates individual transferred to another zoo; **indicates individual not yet transferred in to CZA*

Behavioral Observations

Data were collected using all occurrence sampling of copulations, solicitations for copulations, and agonistic events (Altman 1974). Because bonobos engage in a variety of sexual behaviors involving all age and sex categories, it is necessary to define copulation for the purpose of this paper. *Copulation* was defined as penile intromission into the vagina accompanied by thrusting movements from the male. Although it was not always apparent that the male achieved ejaculation, the presence of semen on the tip of the male penis was observed after most copulations. Furthermore, these interactions were scored as copulations for dyads of males (adult or adolescent) and females (adult or adolescent) only. Definitions for solicitations of copulations are based on those described by Furuichi and Hashimoto (2004) and expanded to include behaviors present in this group of bonobos. *Solicitation for copulation by males* was defined as presentation of erect penis accompanied by pushing the pelvic area forward in view of a female in proximity (within 2 m) and/or gesturing toward a female in proximity. Several males also accompanied these solicitation behaviors with bared-teeth and/or head nodding. *Solicitation for copulation by females* was defined as presentation of rump accompanied by crouching behavior in proximity of a male. Several females also exhibited bared-teeth and/or head nodding behavior either before or after solicitation. A solicitation bout was considered terminated after either 1) observation of male-female copulation, 2) if the actor ceased solicitation behaviors for 2 minutes, or 3) if the target moved out of proximity of the actor without the actor following the target. *Denial of a solicitation attempt* was defined as when a male presented for copulation within view and proximity of a female and where the female either ignored the male, or left proximity of the male without copulating with him and, for the purpose of this study, serves as a proxy for the evaluation of female resistance to male attempts to copulate.

Also for the purpose of this study, *direct sexual coercion* was defined as a behavioral sequence whereby a male solicits a female, the female attempts a denial of solicitation that is immediately followed by the male repeatedly soliciting the female and directing aggressive or threatening behaviors (hitting, kicking, biting, charging, chasing, etc.) toward the female who then copulates with the male within 30 seconds of the male ceasing aggressive behaviors. A *direct sexual coercion attempt* was defined as the sequence of behaviors described above without the female copulating with the male. Bouts of *direct sexual coercion* and *direct sexual coercion attempts* are considered terminated when the female either copulates with the male or the male ceases aggressing the female for 2 minutes. *Coalitionary coercion* was defined as any other group member supporting the male aggressor with aggressive behaviors directed toward the female target during bouts of direct sexual coercion and direct sexual coercion attempts.

Urine analyses

Urine collection and storage. Urine samples were collected in accordance with CZA’s existing urine collection protocol using either a free catch method where individual subjects urinated through the mesh caging directly into a collection cup, or, where urine was pipetted directly off a clean floor surface immediately after a subject urinated into a plastic cryo tube. All subjects were previously trained to urinate on command (i.e., present genitals and urinate in exchange for a small food reward). Samples were then immediately frozen and stored at -20°C until they were packed on dry ice and shipped overnight to the Snodgrass Global Health Biomarker Lab at the University of Oregon in Eugene, OR where they were stored at -80°C until time of analyses.

Measurement of cortisol. To avoid multiple freeze-thaw cycles, each sample was first brought to room temperature and 0.5 ml was aliquoted into several cryo tubes. Thawed samples were then diluted (1:20) in assay buffer supplied in the 96-well Detect X Cortisol Enzyme Immunoassay Kit from Arbor Assays™ (catalog no. K003-H5) and assayed according to the kit manufacturer's instructions. The manufacturer of this kit reported the detection limit for this assay as 45.4 pg/ml. To control for variation in the amount and concentration of voided urine, all samples were assayed for creatinine concentrations (Seltzer and Ziegler 2007) using the DetectX™ Creatinine Urinary Detection Kit from Arbor Assays. The manufacturer listed the detection limit for this assay as 0.037 mg/dL. Samples run for creatinine were diluted (1:20) and run according to the kit manufacturer's instructions. All plates were read using a BioTek™ microplate reader and analyzed with Gen5™ software version 2.0.

Kit validation. Tests of parallelism and accuracy were conducted according to the instructions outlined by Brown et al. (2004) to determine if the analyte measured in bonobo urine demonstrated similar immunoactivity of the endogeous antigen similar to what was observed in the standards and to rule out the possibility that there may be material present in bonobo urine that can interfere with the antigen-antibody binding process. Results of these tests demonstrated that the analyte in bonobo urine is immunologically similar to the cortisol present in the standard solution provided by the kit manufacturer and that bonobo urine likely does not contain any substances that interfere with detection of cortisol in the urine samples (see Squires 2016 for detailed description of the validation tests performed).

Data Analyses

Because hours of observation, group composition, and female reproductive status varied across study periods, rates of the behaviors investigated (proceptivity, receptivity, solicitation attempts, direct sexual coercion, and aggression given and received) were calculated for each subject for each study period by dividing the count of the behavior ($N_{\text{behav obs.}}$) by total hours of observation (H) and by number of non-kin mates available ($M_{\text{non-kin}}$), where appropriate.

$$r = (N_{\text{behav obs.}} / H) / M_{\text{non-kin}}$$

Female proceptivity and male status. Each female's average rate of proceptivity across all males was calculated using the equation above. In order to determine whether a female demonstrated mating preference for a particular male, we followed the formula given by Muller et al. (2011) where each female's rate of proceptivity was calculated for each male and then compared to that female's mean rate of proceptivity across all males. If the rate of proceptivity for a particular male was >25% above her mean rate of proceptivity, the male was categorized as a *preferred* male. If the rate of proceptivity for a particular male was <25% below her mean rate of proceptivity, the male was categorized as a *non-preferred* male. If the rate of proceptivity for a particular male was <25% above her mean rate and >25% below her mean rate, the male was categorized as a *neutral* male. To determine if one male was categorized as *preferred* significantly more frequently than other males, the frequency of solicitations by females was compared across males using a Goodness of Fit G test with Williams correction applied (Sokal and Rohlf 2012). To test for the effect of male rank on female proceptivity rates, the number of females for whom each male was categorized as *preferred* was compared to rank order among males. Because not all males had equal numbers of available female mating partners (i.e., some of the males had mothers in the group), the number of females for whom the male was categorized as *preferred* ($F_{\text{preferred}}$) was divided by the total number of non-kin females ($F_{\text{non-kin}}$) available to obtain the percentage of total females available for whom a male is categorized as *preferred*.

$$[(F_{\text{preferred}}) / (F_{\text{non-kin}})] \times 100$$

These percentages were then compared to each male's corresponding average rank number using a Pearson correlation. Because it is possible that male aggression toward females is driving female proceptivity, rate of aggression received from each male was compared to rate of proceptivity for that male for all female – *preferred* male dyads using a Spearman's rank order correlation.

Female receptivity and denial of solicitations. To test whether rates of female receptivity varied across males, we calculated the rate of female receptivity for each male and compared the mean value (total rate of female receptivity divided by number of available females for each male) across males using a Goodness of Fit G test with Williams correction applied (Sokal and Rohlf 2012). In order to examine the effect of female rank on rate of receptivity, we compared female rates of receptivity to their corresponding rank number using a Spearman's rank order correlation. To test whether successful denial of solicitations for copulations from *non-preferred* males varied across females according to rank, we calculated each female's percentage of successful denials across *non-preferred* males by totaling the number of times that a male solicited a female ($t_{solicitations}$), subtracting the total number of times that female was receptive to that male's solicitations ($R_{success}$), and dividing this number by ($t_{solicitations}$):

$$[(t_{solicitations} - R_{success}) / t_{solicitations}] \times 100$$

and then comparing the percentage to the corresponding female's average rank number across the study periods using a Spearman's rank order correlation. Because it is possible that male aggression toward females is driving female receptivity, rate of aggression received from each male was compared to rate of receptivity for that male for all female – *non-preferred* male dyads using a Spearman's rank order correlation.

Coalitionary and direct sexual coercion. In order to determine if there was a relationship between target rank and rate of direct sexual coercion received, rates of coercion received were compared to female rank for each study period. To examine whether performance of direct sexual coercion was evenly distributed or skewed across males, frequency of performance of direct sexual coercion events was compared across males using a Goodness of Fit G test with Williams correction applied (Sokal and Rohlf 2012). To test whether or not performing direct sexual coercion was dependent on presence of the actor's mother, frequency of performance of direct sexual coercion without the mother of the actor present was compared to frequency of performance of direct sexual coercion with the actor's mother present using a Goodness of Fit G test of independence (Sokal and Rohlf 2012). Finally, to test whether or not direct sexual coercion success was dependent on coalitionary support, frequency of success with and without coalitionary support was also compared using a Goodness of Fit G test of independence (Sokal and Rohlf 2012).

Cortisol and coercion. To test the potential stress effects of receiving aggression and direct sexual coercion from males, urinary cortisol values were measured several times during each study period for each female and mean values were compared to rates of aggression and direct sexual coercion received from males. Like humans, circulating cortisol values in bonobos exhibit a pattern of diurnal fluctuation, where, on average, values are highest in the morning (AM) and fall steadily throughout the day into the afternoon and evening (PM) (see Squires 2016). Chronically elevated PM values are thought to reflect frequent exposure to environmental stressors (Dickerson et al. 2004) and therefore rates of aggression and direct sexual coercion received were also compared to the difference between mean AM (0600-1159 hours) and mean PM (1200-2200 hours) values for each female for each study period using a Pearson rank correlation. Furthermore, to test the short-term effects of exposure to direct sexual coercion on cortisol values, PM urinary cortisol was measured, where possible, for females targets on days they received direct sexual coercion and compared to mean PM values for that female for that study period using a paired *t*-test (Sokal and Rohlf 2012).

RESULTS

Female Proceptivity

There were 437 sexual interactions classified as copulations during the course of this study and, on average, females initiated 46.5% of copulations across all males. Rates of proceptivity varied across females with an average rate of 0.0446 times per observational hour (range: 0.0037-0.1590; SD=0.0524). Patterns of female proceptivity are summarized in Table 2 and show that rates of female proceptivity varied across males.

Table 4.2. Rates of female proceptivity and male status per female, P=*preferred*, NP=*non-preferred*, and N=*neutral*; and rates of female receptivity across males

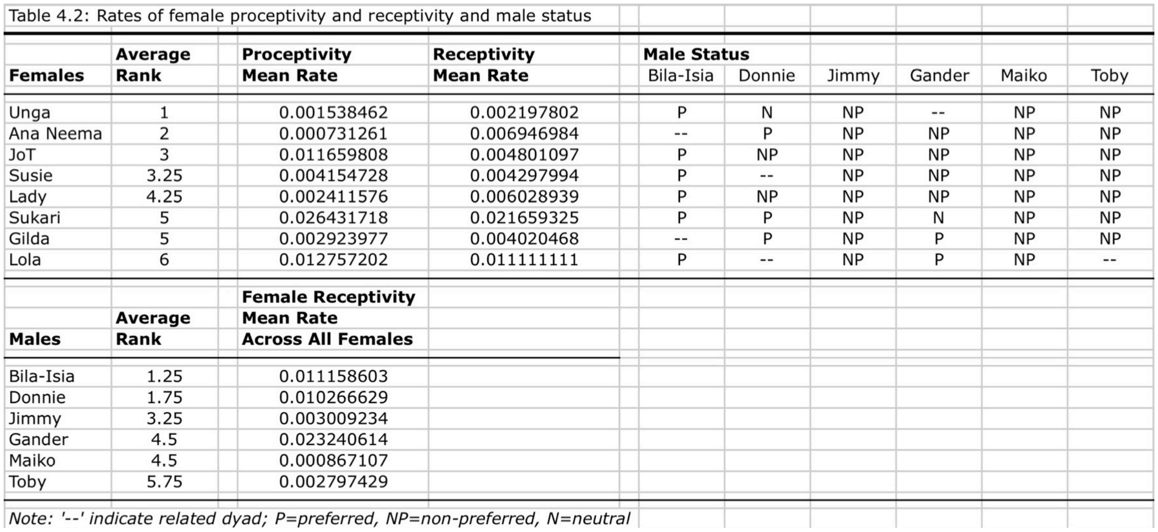


Table 4.2: Rates of female proceptivity and receptivity and male status

Females	**Average Rank**	**Proceptivity Mean Rate**	**Receptivity Mean Rate**	**Male Status** Bila-Isia	Donnie	Jimmy	Gander	Maiko	Toby
Unga	1	0.001538462	0.002197802	P	N	NP	--	NP	NP
Ana Neema	2	0.000731261	0.006946984	--	P	NP	NP	NP	NP
JoT	3	0.011659808	0.004801097	P	NP	NP	NP	NP	NP
Susie	3.25	0.004154728	0.004297994	P	--	NP	NP	NP	NP
Lady	4.25	0.002411576	0.006028939	P	NP	NP	NP	NP	NP
Sukari	5	0.026431718	0.021659325	P	P	NP	N	NP	NP
Gilda	5	0.002923977	0.004020468	--	P	NP	P	NP	NP
Lola	6	0.012757202	0.011111111	P	--	NP	P	NP	--

Males	**Average Rank**	**Female Receptivity Mean Rate Across All Females**
Bila-Isia	1.25	0.011158603
Donnie	1.75	0.010266629
Jimmy	3.25	0.003009234
Gander	4.5	0.023240614
Maiko	4.5	0.000867107
Toby	5.75	0.002797429

Note: '--' indicate related dyad; P=preferred, NP=non-preferred, N=neutral

The alpha male received solicitations from females significantly more frequently than expected, whereas all other males received solicitations from females significantly less frequently than expected (G=27.4207, df=10, p<0.01; Table 4.2). Furthermore, the alpha male was categorized as a *preferred* male for all females (Table 4.2, Fig. 4.1a) and the number of females for whom each male was categorized as a *preferred* male was significantly positively correlated with average male rank (Pearson: $R^2=0.661$, df=4, $p<0.05$). Rates of proceptivity among females were compared to rates of aggression from males for each male-female dyad where the male was categorized as a *preferred* male for that female (N=11). There was no significant correlation between rates of proceptivity and aggression received across all possible dyads (Spearman: $R^2=0.7904$, df=10, $p=0.7966$, Fig. 4.2).

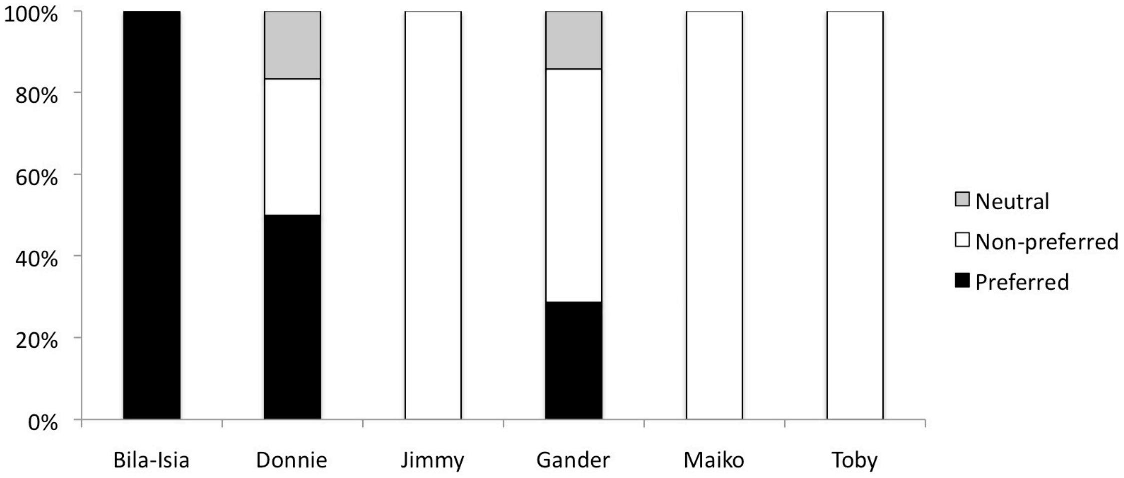


Fig. 4.1. Percentage of available females for whom the male was categorized as preferred, non-preferred, and neutral across males; males are arranged according to average rank with highest to the left and lowest to the right

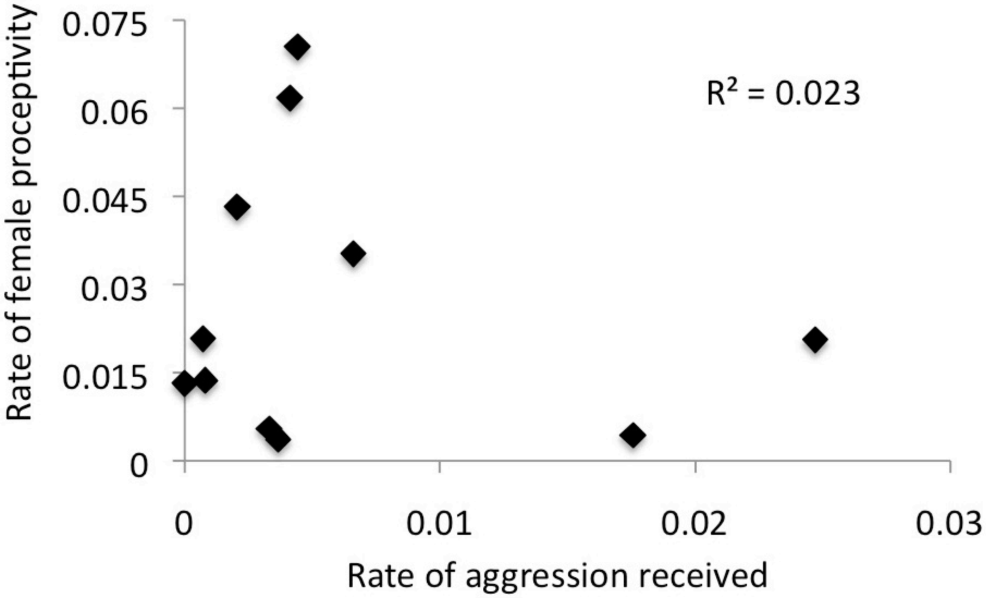


Fig. 4.2. Rate of female proceptivity by rate of aggression received from males; each point represents a dyad of a female and a male categorized as *preferred* for that female and the corresponding rates of female proceptivity and aggression received from that male

Female Receptivity

Males, on average, initiated 53.7% of copulations across all females. Rates of receptivity varied across females with an average rate of 0.4273 times per observational hour (range: 0.0110-0.1300; SD=0.0376) and were not significantly correlated with mean female rank (Spearman: R^2=0.023, df=6, p=0.3069, Fig. 4.3). Patterns of female receptivity are summarized in Table 2 and show that rates of female receptivity varied across males. Females, on average, were receptive to the son of the alpha female significantly more frequently than expected, whereas mean frequency of receptivity across females was lower than expected for all other males (G=25.461, df=5, p<0.01; Table 4.2). Females were not always receptive to solicitations from males and we found that percentage of solicitations denied across males categorized as *non-preferred* for each female was significantly positively correlated with female rank (Spearman: R^2=0.745, df=6, p<0.01, Fig. 4.4). Rates of receptivity among females were compared to rates of aggression from males for all possible male-female dyads where female receptivity or male aggression was observed (N=38). A significant positive correlation between rates of receptivity and aggression received from males was found across these dyads (Spearman: R^2=0.233, df=37, p<0.001, Fig.'s 4.5a and 4.5b).

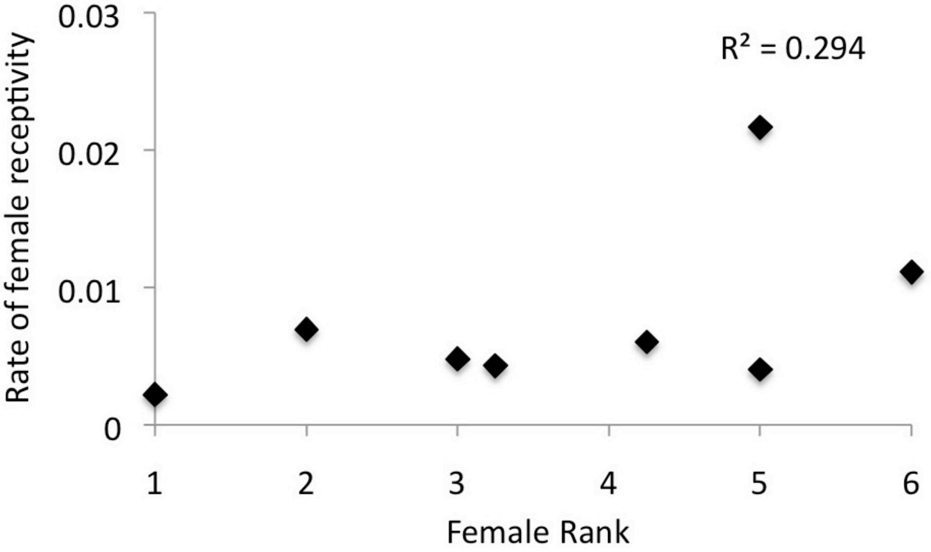


Fig. 4.3. Rate of female receptivity by average female rank

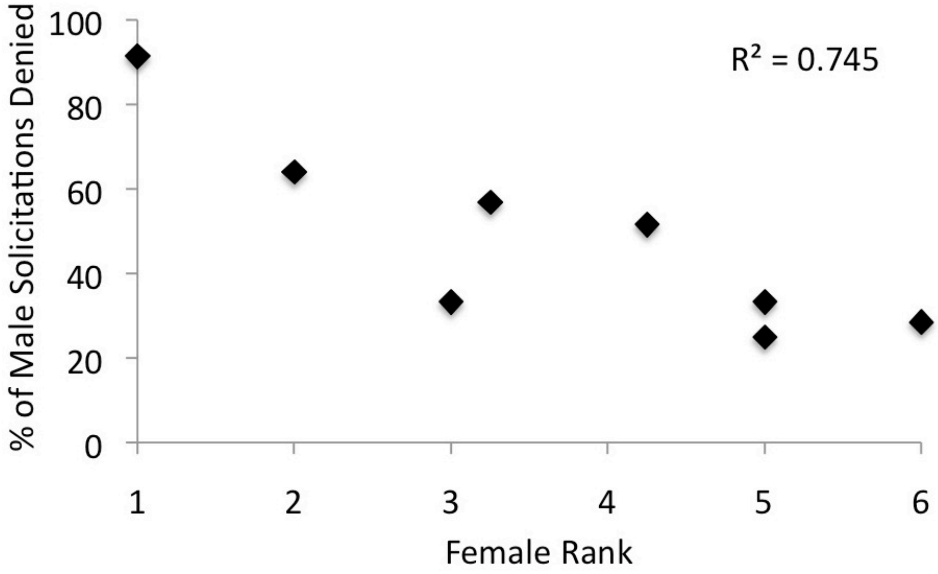


Fig. 4.4. Percentage of solicitations from *non-preferred* males denied by average female rank

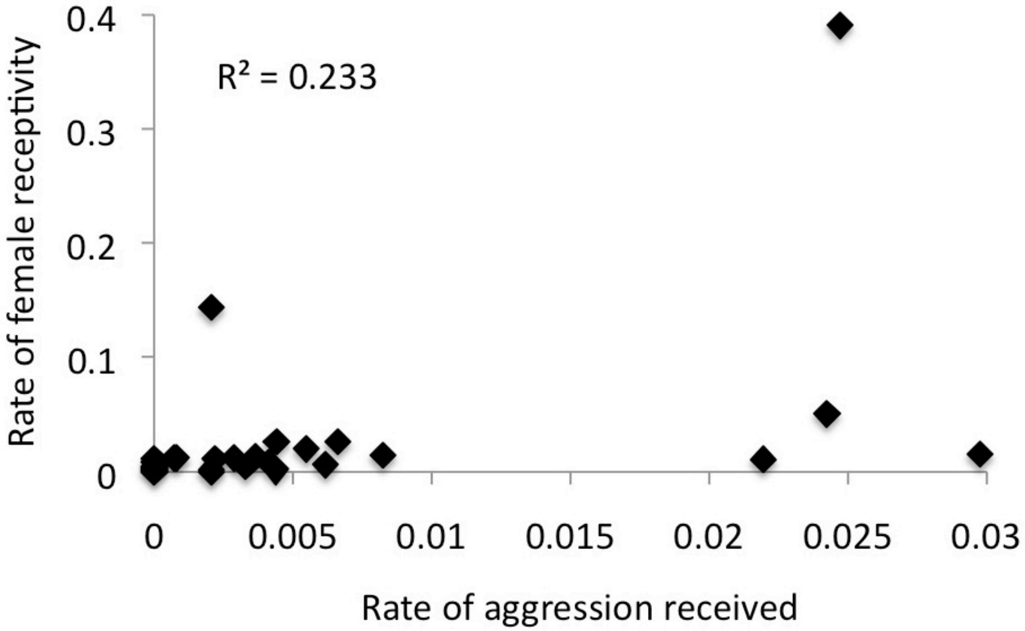


Fig. 4.5a. Rate of female receptivity by rate of aggression received from males; each point represents a male-female dyad and the corresponding rates of female receptivity and aggression received from that male

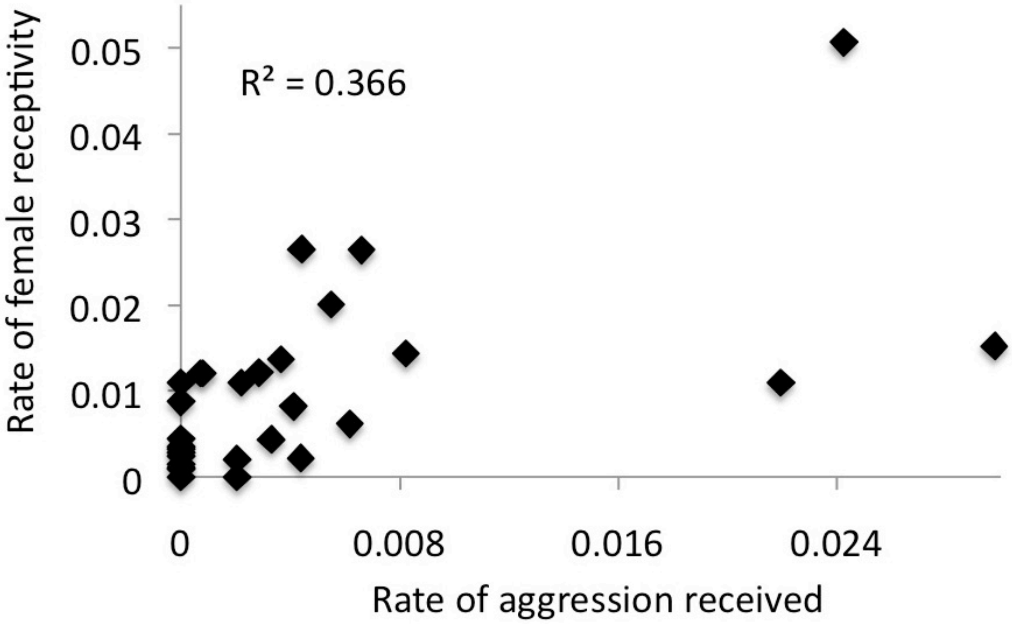


Fig 4.5b. Rate of female receptivity by rate of aggression received from males with outliers removed; each point represents a male-female dyad and the corresponding rates of female receptivity and aggression received from that male

Sexual Coercion Events

During the course of the study 56 bouts of direct sexual coercion were observed. The majority of these bouts ended in copulation between the aggressor and target (N=40). Rates of direct sexual coercion received varied across females but there was no significant correlation between direct sexual coercion received and female rank (Spearman: R^2=0.166, df=14, p=0.1349, Fig. 4.6). Two females were never observed to be targets of direct male sexual coercion, the alpha female (Unga) and a mid-ranked female (Susie), whose son (Donnie) was the alpha male during the first year of the study and maintained high status throughout the remaining study periods.

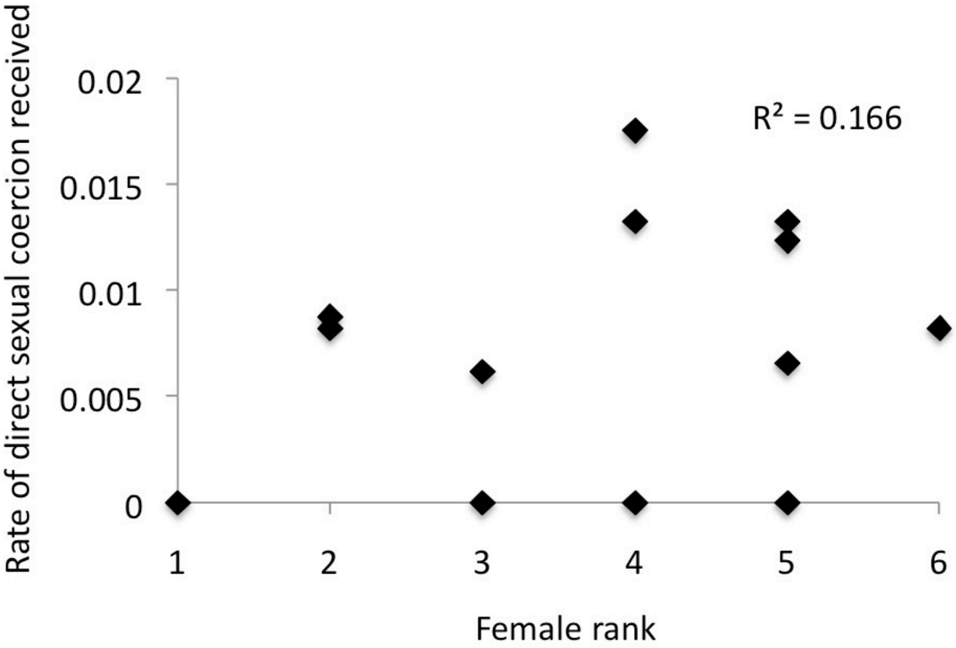


Fig. 4.6. Rate of direct sexual coercion received by average female rank

Distribution of frequency of participation in direct sexual coercion also varied across males where only two of the males were observed performing direct sexual coercion. Assuming equal likelihood of participation, the son of the alpha female was found to engage in direct sexual coercion significantly more frequently than expected, whereas all other males engaged in direct sexual coercion significantly less frequently than expected. (G=118.572, df=5, p<0.001; Fig. 4.7). The likelihood of a direct sexual coercion event taking place was found to be dependent on group composition where direct sexual coercion occurred significantly more frequently when the mother of the male aggressor was present in the group than when the mother was absent (G=3.973, df=1, p<0.05; Fig. 4.8). We also observed several instances of the alpha female (Unga) providing coalitionary support to her son (Gander) during his direct coercive attempts to copulate with females (N=11). Furthermore, the direct sexual coercion attempts (N=42) by this male were more likely to be successful if his mother provided coalitionary support (N=11) during the events than when she did not (G=10.490, df=1, p<0.01; Fig. 4.9).

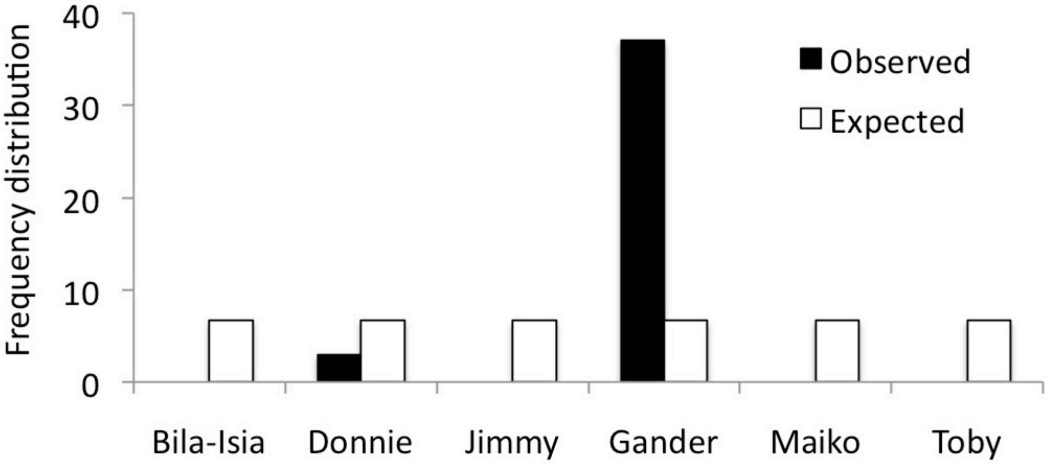


Fig. 4.7. Observed and expected values of direct sexual coercion performance across males; males ordered according to average rank with highest to the left and lowest to the right

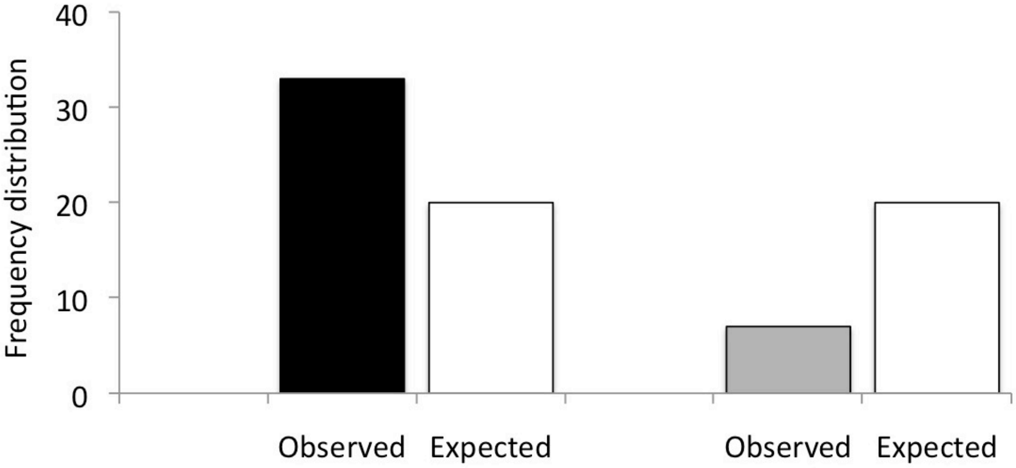


Fig. 4.8. Observed and expected values of direct sexual coercion performance by males when the mother was present vs. absent

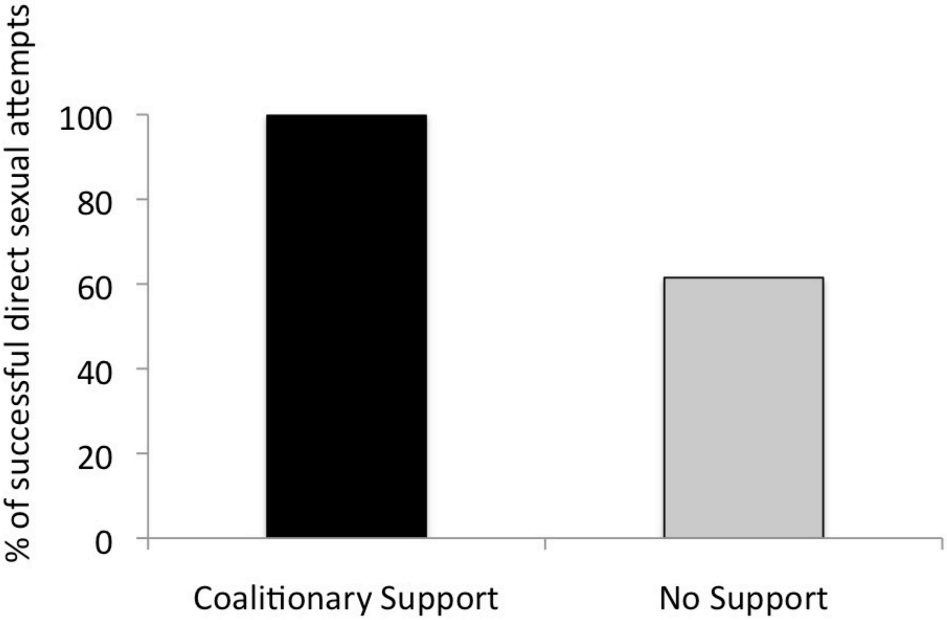


Fig. 4.9. Success rate of direct sexual coercion attempts for Gander with and without coalitionary support from his mother (Unga)

Female Stress Response to Sexual Coercion and Aggression from Males

Mean urinary cortisol values were compared to rates of aggression received from males and rates of direct sexual coercion events experienced for each female for each study period. Rates of aggression received from males were not correlated with either mean urinary cortisol values (Spearman: $R^2=0.020$, df=14, p=0.3046; Fig. 4.10a) or with mean AM-PM difference in urinary cortisol values (Spearman: $R^2=0.042$, df=14, p=3675; Fig. 4.10b). Rates of direct sexual coercion events experienced were also not correlated with mean urinary cortisol values (Spearman: $R^2=0.046$, df=7, p=0.100; Fig. 4.11a) but there was a significant negative correlation between direct sexual coercion events experienced and mean AM-PM difference in mean urinary cortisol values (Pearson: $R^2=0.363$, df=7, $p<0.05$, Fig. 4.11b). We also measured, where available, PM urinary cortisol of target females on the day of the event (after the event took place) and compared this value to each target female's mean PM urinary cortisol value for that study period. We found that, on average, individual PM urinary cortisol values on direct sexual coercion days were significantly higher than the mean PM urinary cortisol values for the corresponding study period across females (Mean difference: 53.0704, N=28, t=5.9505, df=27, $p<0.001$, Fig. 4.12).

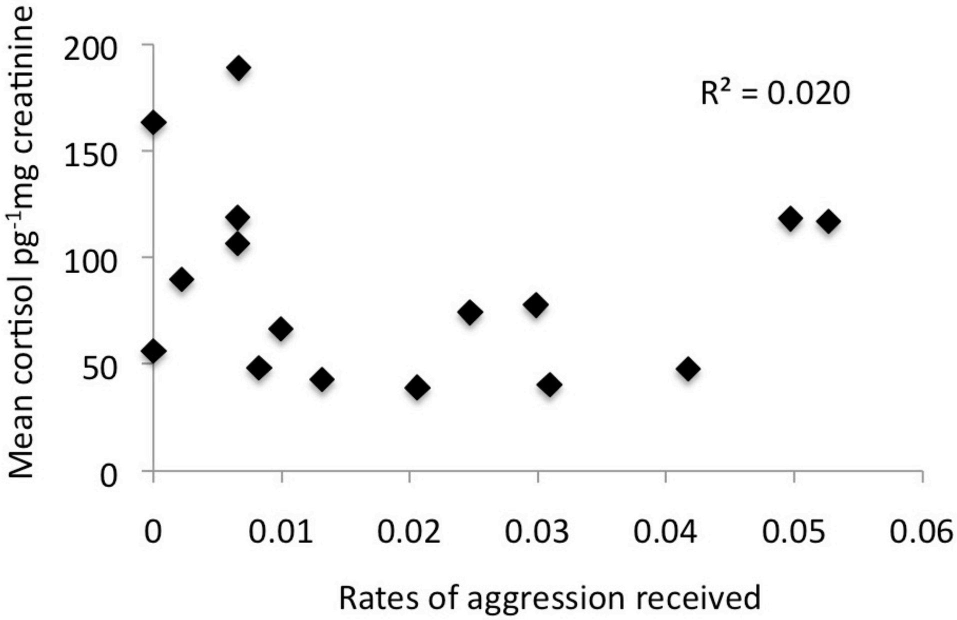


Fig. 4.10a. Mean urinary cortisol values and aggression received from males for each female for each study period

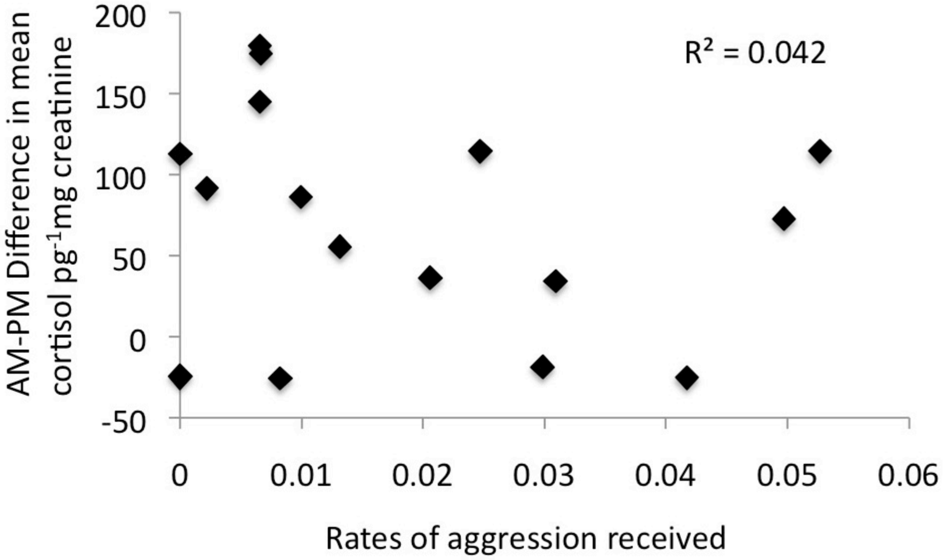


Fig. 4.10b. Mean AM-PM difference in urinary cortisol values and aggression received from males for each female for each study period

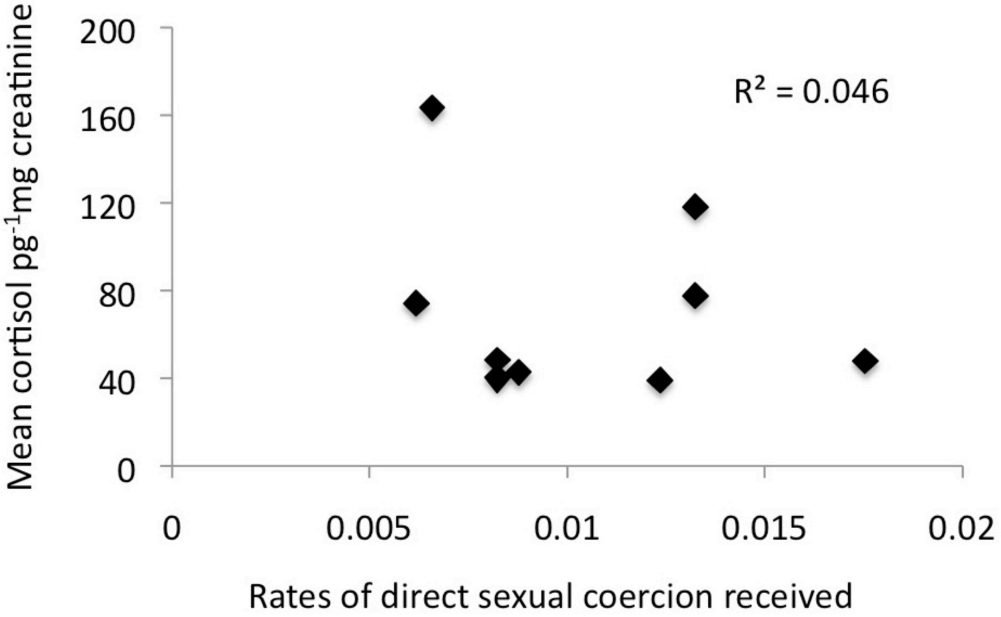


Fig. 4.11a. Mean urinary cortisol values and direct sexual coercion received for each female for each study period

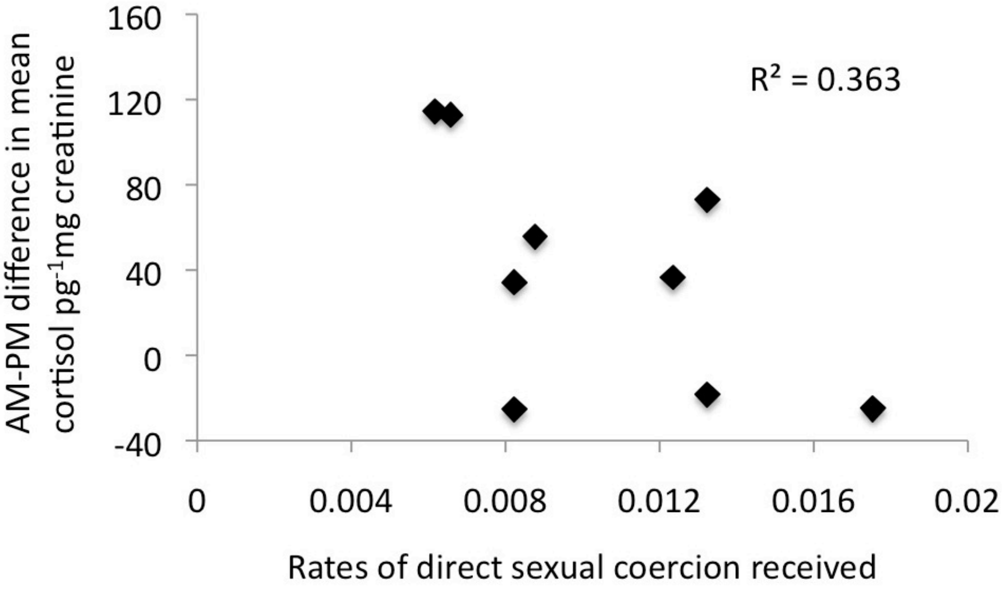


Fig. 4.11b. Mean AM-PM difference in urinary cortisol values and direct sexual coercion received for each female for each study period

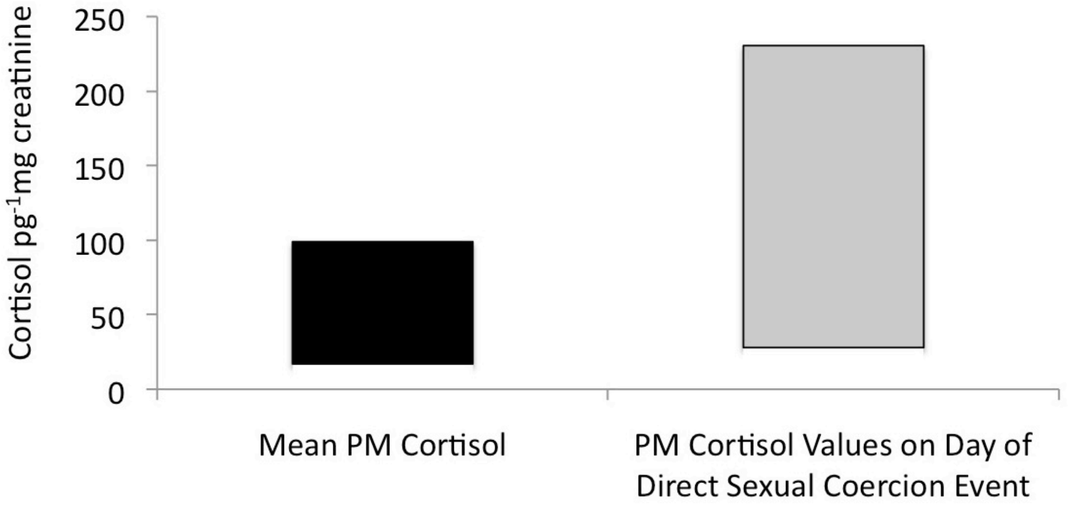


Fig. 4.12. Range of PM urinary cortisol values on direct sexual coercion days and range of mean PM urinary cortisol values across females

DISCUSSION

The purpose of this study was to investigate female sexual behavior and male aggression in light of the conflict between the hypothesis that female bonobos exhibit continuous receptivity, in order to confuse paternity and reduce male competition and intersexual conflict, and the evidence that mating and reproductive skew are high among males. We summarized and proposed several conflicting but not mutually exclusive hypotheses to explain the patterning of female mating behavior and male directed aggression. Our results indicate that, while female bonobos exercise mate choice through proceptive behaviors, resulting in a high degree of skew in mating success across males, alternate male mating strategies include the use of aggressive behaviors that functionally constrain choice by influencing female receptivity and the outcome of solicitations for copulation.

We found that females were not equally receptive to all males and that mating frequency among males was not evenly distributed and do not support the hypothesis that promiscuous mating in bonobos equates to continuous receptivity. Because of the asymmetry in parental investment, females are expected to be more selective of their mates in order to maximize reproductive success than are males (Darwin 1871, Trivers 1972). Recent paternity data from the wild indicate that there is high reproductive skew among male bonobos, where the highest rank male sired the most offspring (Surbeck et al. 2017), and we found the alpha male was solicited for copulations from females significantly more than other males, in line with other studies on copulation frequency in bonobos (Kano 1996). Each female in our study group, with the exception of the mother (Ana Neema) of the alpha male (Bila-Isia), demonstrated proceptivity rates toward the alpha male that were significantly higher than their average rate of proceptivity. This data support the hypothesis that females prefer to mate with the highest rank male in order to gain ‘good genes’ (Halliday 1983; Neff and Pitcher 2005; but see Qvarnstrom and Forsgren 1998). The alpha male of this group, however, was not the only male to have preferred status among females. Two other males (Donnie and Gander) were categorized as preferred by some, but not all, females. Some of this distribution can be attributed to in-breeding avoidance (see Feldman and Christiansen 1984). Both individuals (Ana Neema and Gilda) related to the alpha male, as well as an unrelated nulliparous female (Sukari), preferred to mate with the male who was the previous alpha (Donnie). We also found that the son (Gander) of the alpha female (Unga) was categorized as a preferred male for two nulliparous females (Lola and Sukari). The nulliparous females in this group copulated more frequently and had a greater number of males categorized as preferred than did parous females. Nulliparous females are known to copulate more frequently than parous females, which may function as a mechanism to establish social bonds when immigrating into a new group (Furuichi 1989; Idani 1991; Kano 1992; Furuichi and Hashimoto 2002) and could partially explain this trend in our data.

As discussed in the introduction, using female proceptivity alone as a proxy for female choice can be problematic (Muller and Wrangham 2009; Muller et al. 2011). Muller and colleagues (2009; 2011) have stressed the importance of considering the role of aggression in influencing female sexual behavior, having shown that female proceptive behavior is correlated with male directed aggression in chimpanzees, and hypothesize that male directed aggression functions to constrain female promiscuity and enhance mating exclusivity. We tested this hypothesis and found that rates of proceptivity across females were not correlated with aggression received from preferred males. Our data suggest that, in bonobos, this component of female mating behavior is not driven by male aggression and functions, therefore, as a mechanism through which females actively choose mates. However, we also predicted that if female mate choice operates unfettered in bonobos, female receptivity should vary across males and should not be correlated with aggression received from males and that females should be able to successfully deny solicitations for copulations from non-preferred males. We found that, although female receptivity varied across males, rates of receptivity were correlated with aggression received from males. Furthermore, we found that females were not always successful at denying solicitations from males and that successful resistance to solicitations from non-preferred males was correlated with female rank. Attempts to deny solicitations, however, may be a way in which females assess mate quality (Muller and Wrangham 2009). Muller and Wrangham (2009) argue that in order to function as a mechanism of indirect female choice, rates of resistance should be evenly distributed across all males and that deviation from equal distribution represents intersexual conflict in the form of direct sexual coercion (e.g., orangutans: Knott and Kahlenberg 2007; Knott 2009). Our data indicate that males use aggression against females to influence the outcome of copulation attempts and that female ability to resist these attempts is, at least in part, dependent on female dominance rank. These data partially support the hypothesis that low frequency of sexual coercion in this species is the result of the high social status of females (Furuichi 1992; Kano 1996; Fruth et al. 1999; Paoli et al. 2009; Stumpf et al. 2011; Emery-Thompson 2014).

Individual male opportunities to fertilize a female, however, represent a zero-sum game and under conditions of high reproductive skew and dominance rank correlated with mating success, lower ranking males are expected to express alternate mating strategies such as direct sexual coercion (Trivers 1972; Dunbar 1982). As discussed above, reports of mating and reproductive skew among male bonobos vary (Kano 1996; Gerloff et al. 1999; Furuichi and Hashimoto 2004; Marvan et al. 2006; Paoli and Palagi 2008; Boose et al. 2012; Surbeck et al. 2017), but researchers have long hypothesized that the low or absent levels of male sexual coercion in bonobos are the result of female-

female coalitionary aggression against males (e.g., Wrangham 1993, Parish 1996, and Paoli et al. 2009). Surbeck et al. (2013) report that only 2% of male aggression towards females was followed by female coalitionary aggression against that male. Tokuyama and Furuichi (2016) have shown that while female-female coalitions were used primarily to retaliate against males who direct aggression at females, only 1.4% were formed towards a 'male who was persistently soliciting copulation' and conclude that female coalitions evolved as a mutual benefit that females receive from keeping male aggression in check. It is, of course, difficult to demonstrate causation of the absence of a behavior, but the limited data provided on female coalitionary aggression against males in the context of mating do not represent rigorous testing of this hypothesis and are, therefore, speculative at best. Furthermore, the observation of additional alternate male strategies thought to facilitate male mating success, such as affiliation with females and proximity to mothers and their social network of females (Furuichi, 1989; Hare et al. 2012; Kano, 1992, 1996; Surbeck et al., 2011), should not preclude the use of direct sexual coercion among males when the costs are low and likelihood of success is high.

We predicted that under conditions of high mating skew, variation in female receptivity, and aggression correlated with mating success, males will engage in the alternate mating strategy of direct sexual coercion during times of low likelihood of retaliation in the form of coalitionary aggression. We observed 56 attempts of direct sexual coercion performed by two males with a combined success rate of 71.4%. Of the two males who engaged in direct sexual coercion behaviors, the son of the alpha female (Gander) participated in direct sexual coercion events significantly more than any other male. We also observed that all but two females were targets of direct sexual coercion, where only the alpha female and mother to Gander (Unga) and mother (Susie) of the previous alpha male (Donnie) did not receive any direct sexual coercion. Donnie was a high ranked male throughout the study and was often observed aggressing Gander and it is possible that Gander was reticent to direct aggression at Susie in the context of mating because of potential retaliation from Donnie. However, interestingly, Gander showed very little interest in mating in general with Susie, an older, multiparous female. Gander was instead primarily interested in mating with Lady, a low ranking multiparous female who, at the time of the study, did not have any offspring present in the group and would frequently and actively resist the mating efforts of this male.

Although this male's individual rank status among males rose over the course of the study, he never attained high dominance rank, remaining at a relatively moderate status and was often observed deferring to other males. However, conflicts in which he was involved were almost always met with coalitionary aggressive support from his mother, the alpha female, who was frequently observed to engage in intense forms of retaliatory aggression including physical contact that would often result in the wounding of targets (unpublished data). All individuals in this group were highly deferent to the alpha female, and she received the least amount of aggression from males during the course of this study. Furthermore, females were found to be most receptive to her son's solicitations for copulations. Evidence that mothers impact the relative dominance rank and subsequent mating success of their sons has been demonstrated in a wild population of bonobos (Surbeck et al. 2011). It is likely that this male's relative dominance rank was effectively as high as his mother's when she was present in the party and, therefore, reduced his likelihood of receiving retaliation for his attempts to directly sexually coerce a female. Our data that the success rate of direct sexual coercion attempts was dependent upon presence of the mother of the aggressor support this hypothesis.

We also observed several instances of coalitionary sexual coercion (N=11) where the alpha female supported her son during his attempts to directly sexually coerce three separate females, including two parous adult females (Ana Neema and Lady), neither of whom were close associates of the alpha female (unpublished data). There are numerous studies across taxa that demonstrate females employ mechanisms (e.g., eviction and/or suppression of reproductive function, and aggression directed towards subordinates) to influence the mating success of other females as a means to increase their relative fitness contribution to the next generation (see Clutton-Brock and Huchard 2013). For this alpha female, securing mating opportunities for her son elevates her indirect fitness potential, at a low cost to her because of reduced likelihood of retaliation due to her high dominance rank and reputation for wounding targets (unpublished data). Female bonobos are known to interrupt the copulations of other females (Vervaecke and van Elsacker 2000) but this is the first evidence, to our knowledge, of female attempt to constrain female choice, through participation in direct sexual coercion that benefits her own indirect fitness.

Researchers have noted that, of the three identified forms of direct sexual coercion (forced copulations, harassment, and intimidation), forced copulations occur relatively infrequently among primates (Muller and Wrangham 2009; Paoli et al. 2009). Observations of forced copulations are rare in chimpanzees (Goodall 1986) because of the high degree of promiscuous mating where females are known to mate with all of the males during their ovulatory cycle (Stumpf and Boesch 2006; Muller et al. 2009). Given the mounting evidence that mating and reproductive skew are high in bonobos, the incentive to engage in mechanisms of direct sexual coercion as an alternate male strategy may be higher in bonobos. Several researchers, however, have reported an absence of 'coercive aggression against female in the immediate context of courtship' (Paoli et al. 2009, p. 413, citing: Wrangham 1993; Kano 1996; Parish 1994, 1996; Hohmann and Fruth 2003) and that females use sexual behavior as a form of appeasement to temper aggression from males (de Waal 1995). Paoli et al. (2009) also cite anecdotal evidence provided by Jo Thompson that describes a sequence of behaviors surrounding mating within the context of aggression that includes females exhibiting a 'grimacing expression' in the use of 'sexual activity to appease individuals' and their own observations that 'males performed strong advances toward females during periods of high excitement but they never used their physical strength to force females into sexual contact' (p. 414). These descriptions do not fit the definition of 'forced copulation,' which requires the use of physical restraint of females in the act of mating. Observations of direct sexual coercion in this study, however, were primarily in the form of harassment and intimidation (as defined above). We suggest that some observations of mating during conflict, that historically have been classified as appeasement, may be qualitatively and functionally indistinguishable from other forms of direct sexual coercion, such as harassment and intimidation.

Finally, we observed the potential induction of a stress response in female victims of sexual coercion. When targeted by males, females frequently exhibited signs of fear such as grimacing, fleeing, and defecating. We also measured urinary cortisol values across females and found that levels were significantly higher for individual female targets of direct sexual coercion on days the event took place. As discussed above, Muller and Wrangham (2009) have argued that in order for male directed aggression to qualify as sexual coercion it must impose a fitness cost to females and environmental stressors such as conflict with group members can elevate cortisol values and chronic exposure to such stress can cause a dysregulation of the circadian rhythm and a disruption of the functioning of cortisol in the body (Lupien et al. 2009; Novak et al. 2013). We found that although rates of aggression from received from males were not correlated with a disruption of circadian rhythm of cortisol values (as measured by mean AM-PM difference), female rates of direct sexual coercion received were correlated with mean AM-PM difference in cortisol values. These results suggest to us that receiving direct sexual coercion produces a greater stress response because constraint of choice has greater fitness implications than receiving non-sexually coercive aggression and is, therefore, more costly to females in terms of reproductive success.

Conclusion

In conclusion, infant handling is a distinct type of affiliative behavior that functions both as a mechanism of learning species typical maternal behaviors in young female bonobos and in a manner that may facilitate coalition formation between handlers and mothers of infants. The results presented here show that while juvenile males and females associate frequently with infants, adolescent females perform handling behaviors significantly more than do adolescent males. Furthermore, mean OT levels were correlated with handling behaviors in juvenile and adolescent females, but not in any other age-sex category. Although study design did not permit the testing of the long term consequences of associating with an infant in exchange for coalitionary support from that infant when they reach adulthood, the results presented show a positive connection between handling behaviors and coalitionary support of the handler by the mother of the infant handled. Results also showed that, during some of the study periods, handlers demonstrated a significant bias in handling related infants. Together these results on infant handling behavior in bonobos provide strong support for the ***Learning-to-Mother*** hypothesis, mixed support for the ***Alliance Formation*** and ***Kin Selection*** hypotheses, and demonstrate evidence for a mechanism that may potentially contribute to the observed lower inter-birth intervals of bonobos relative to chimpanzees.

CHAPTER V

SUMMARY REMARKS

The objective of this dissertation was to investigate previously unstudied or under-studied behavioral mechanisms that contribute to the unique social structure of bonobos. The following conclusions can be drawn from the results of the studies presented in Chapters II, III, and IV:

1. Harassment is an important part of the developmental behavioral repertoire of bonobos that functions to inform immatures about the nature of social relationships, dominance interactions, and the parameters of aggression.
2. Infant handling is a frequently occurring behavior among juvenile and adolescent bonobos that functions as a mechanism, facilitated by oxytocin, through which immature females learn maternal behaviors, group members form important alliances with powerful females, and may contribute to a reduction of the inter-birth interval in bonobos.
3. Although female bonobos exercise mate choice through proceptive sexual behaviors, male counter-strategies of sexual coercion are costly to females, function to constrain female choice, and may include support from their mothers, representing evidence of female constraint of female choice.

REFERENCES CITED

Adair Gowaty, P., Steinichen, R., & Anderson, W.W. (2002). Mutual interest between the sexes and reproductive success in *Drosophila pseudoobscura*. *Evolution*, *56*(12), 2537-2540.

Adang, O.M. (1984). Teasing in young chimpanzees. *Behaviour*, *88*(1), 98-121.

Adang, O.M. (1985). Exploratory aggression in chimpanzees. *Behaviour*, *95*(1), 138-162.

Adang, O.M. (1986). Exploring the social environment: a developmental study of teasing in chimpanzees. *Ethology*, *73*(2), 136-160.

Altmann J. 1980. *Baboon mothers and infants*. Chicago, IL: The University of Chicago Press.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266.

Altmann, J. (1990). Primate males go where the females are. Animal Behaviour, 39(1), 193-195.

Andelman, S. (1986). Ecological and social determinants of cercopithecine mating patterns. In Rubenstein, D.I., & Wrangham, R.W. (eds.), *Ecological aspects of social evolution: birds and mammals*. Princeton, NJ: Princeton University Press, 201-216.

Anderson, D.P., Nordheim, E.V., Boesch, C., & Moermond, T.C. (2002). Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In Boesch, C., Hohmann, G., & Marchant, L. (eds.), *Behavioural diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press, 90-101.

Andersson, M.B. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Anestis, S.F. (2010). Hormones and social behavior in primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(2), 66-78.

Arcadi, A.C., & Wrangham, R.W. (1999). Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates*, *40*(2), 337-351.

Badescu, I., Sicotte, P., Ting, N., & Wikberg, E.C. (2015). Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (Colobus vellerosus). *American journal of primatology*, *77*(4), 376-387.

Barrett, L., & Henzi, S.P. (2006). Monkeys, markets and minds: biological markets and primate sociality. In Kappeler, P.M., & van Schaik, C.P. (eds.), *Cooperation in primates and humans: mechanisms and evolution*. Berlin: Springer, 209-232.

Benarroch, E.E., (2013). Oxytocin and vasopressin: social neuropeptides with complex neuromodulatory functions. *Neurology*, *80*, 1521-1528.

Bercovitch, F.B. (1991). Mate selection, consortship formation, and reproductive tactics in adult female savanna baboons. *Primates*, *32*(4), 437-452.

Blersch, B.H., & Schmidt, C.R. (1992). Adoption of an additional infant by a western lowland gorilla (*Gorilla gorilla gorilla*). *Folia Primatologica*, *58*(4), 190-196.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford: Oxford University Press.

Boesch, C., Bole, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: the case of adoption. *PLoS One*, *5*(1), e8901.

Boinski, S. (1987). Mating patterns in squirrel monkeys (*Saimiri oerstedi*). *Behavioral Ecology and Sociobiology*, *21*(1), 13-21.

Boose, K.J., & White, F.J. (2012). Male bonobo (*Pan paniscus*) rank related asymmetry in mating does not support the paternity confusion hypothesis for lack of infanticide. *American Journal of Primatology*, *74*, 57-57.

Boose, K. J., & White, F.J. (2017). Harassment of adults by immatures in bonobos (*Pan paniscus*): testing the Exploratory Aggression and Rank Improvement hypotheses. *Primates*, doi: 10.1007/s10329-017-0616-9.

Boose, K.J., White, F.J., & Meinelt, A. (2013). Sex differences in tool use acquisition in bonobos (*Pan paniscus*). *American journal of primatology*, *75*(9), 917-926.

Bourke, A.F., & Franks, N.R. (1995). *Social evolution in ants*. Princeton, NJ: Princeton University Press.

Bradbury, J.W., & Vehrencamp, S.L. (1976). Social organization and foraging in emballonurid bats. *Behavioral Ecology and Sociobiology*, *1*(4), 337-381.

Bramblett, C.A. (1978). Sex differences in the acquisition of play among juvenile vervet monkeys. In Smith, E.O. (ed.), *Social play in primates*. New York, NY: Academic Press, 33-48.

Brent, L.J., Teichroeb, J.A., & Sicotte, P. 2008. Preliminary assessment of natal attraction and infant handling in wild *Colobus vellerosus*. *American Journal of Primatology*, *70*: 101-105.

Brown, J., Walker, S., & Steinman, K. (2004). *Endocrine manual for the reproductive assessment of domestic and non-domestic species*. Endocrine Research Laboratory, Department of Reproductive Sciences, Conservation and Research Center, National Zoological Park, Smithsonian Institution, Handbook, 1-93.

Buck, M.R. (1998) Female mate choice in sooty mangabeys: social constraints on mating behaviour. Ph.D. thesis, Department of Anthropology, Emory University.

Bullinger, A.F., Burkart, J.M., Melis, A.P., & Tomasello, M. (2013). Bonobos, *Pan paniscus*, chimpanzees, *Pan troglodytes*, and marmosets, *Callithrix jacchus*, prefer to feed alone. *Animal Behaviour*, *85*(1), 51-60.

Busse, C., & William, H.J. (1981). Infant carrying by male chacma baboons. *Science*, *212*(4500), 1281-1283.

Caine, N.G. & Mitchell, G.D. (1980). Species differences in the interest shown in infants by juvenile female macaques (*Macaca mulatta* and *M. radiata*). *International Journal of Primatology*, *1*, 323-332.

Caldwell, J.D., Prange, A.J., & Pedersen, C.A. (1986). Oxytocin facilitates the sexual receptivity of estrogen-treated female rats. *Neuropeptides*, *7*(2), 175-189.

Chapais B., & Gauthier C. (1993). Early agonistic experience and the onset of matrilineal rank acquisition in Japanese macaques. In Pereira, M.E., & Fairbanks, L.A., (eds.), *Juvenile primates: life history, development and behavior*. Oxford: Oxford University Press, 245-258.

Chapais, B. (1988). Rank maintenance in female Japanese macaques: experimental evidence for social dependency. *Behaviour*, *104*(1), 41-58.

Chapais, B. (1992). The role of alliances in social inheritance of rank among female primates. In Harcourt, A.H., & de Waal, F.B.M. (eds.), *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press, 29-60.

Chapman, C.A., White, F.J., & Wrangham, R.W. (1994). Party size in chimpanzees and bonobos. In Wrangham, R.W., McGrew, W.C., de Waal, F.B.M., & Heltne, P.G. (eds.), *Chimpanzee cultures*. Cambridge, MA: Harvard University Press, 41-58.

Chapman, T. (2006). Evolutionary conflicts of interest between males and females. *Current Biology*, *16*(17), R744-R754.

Charnov, E.L. (1979). Natural selection and sex change in pandalid shrimp: test of a life-history theory. *The American Naturalist*, *113*(5), 715-734.

Charnov, E.L. (1991). Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences*, *88*(4), 1134-1137.

Clarke, M.R. 1978. Social interactions of juvenile female bonnet monkeys, *Macaca radiata*. *Primates*, *19*, 517-524.

Clarke, M.R., Glander, K.E. & Zucker, E.L. 1998. Infant-nonmother interactions of free-ranging mantled howling monkeys (*Alouatta palliata*) in Costa Rica. *International Journal of Primatology*, *1*, 451-472.

Clarke, P., Pradhan, G., van Schaik, C., Muller, M.N., & Wrangham, R.W. (2009). Intersexual conflict in primates: infanticide, paternity allocation, and the role of coercion. In Muller, M.N., & Wrangham, R.W. (eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press, 42-77.

Clutton-Brock, T.H. (1989). Review lecture: mammalian mating systems. *Proceedings of the Royal Society of London B: Biological Sciences*, *236*(1285), 339-372.

Clutton-Brock, T.H., & Huchard, E. (2013). Social competition and selection in males and females. *Phil. Trans. R. Soc. B*, *368*(1631), 1-15.

Clutton-Brock, T.H., & Parker, G.A. (1995). Sexual coercion in animal societies. *Animal Behaviour*, *49*(5), 1345-1365.

Conklin-Brittain, N.L., Wrangham, R.W., & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology*, *19*(6), 971-998.

Crockford, C., Wittig, R.M., Langergraber, K., Ziegler, T.E., Zuberbühler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B*, *280*(1755), 1-8.

Cronin, K.A., De Groot, E., & Stevens, J.M. (2015). Bonobos show limited social tolerance in a group setting: a comparison with chimpanzees and a test of the Relational Model. *Folia Primatologica*, *86*(3), 164-177.

Cunningham, E.J.A., & Russell, A.F. (2000). Egg investment is influenced by male attractiveness in the mallard. *Nature*, *404*, 74-77.

Darwin, C. (1871). *Sexual selection and the descent of man*. London: John Murry.

de Waal, F.B.M. (1977). The Organization of Agonistic Relations within two Captive Groups of Java_monkeys (*Macaca fascicularis*). *Zeitschrift fur Tierpsychologie*, *44*(3), 225-282.

de Waal, F.B.M. (1986). The integration of dominance and social bonding in primates. *The Quarterly Review of Biology*, *61*(4), 459-479.

de Waal, F.B.M. (1990). Do rhesus mothers suggest friends to their offspring? *Primates 31*, 597-600.

de Waal, F.B.M. (1995). Sex as an alternative to aggression in the bonobo. In Abramson, P.R., & Pinkerton, S.D., *Sexual nature, sexual culture*. Chicago, IL: The University of Chicago Press, 37-56.

de Waal, F.B.M., & Hoekstra, J.A. (1980). Contexts and predictability of aggression in chimpanzees. *Animal Behaviour*, *28*(3), 929-937.

Dickerson, S.S., Kemeny, M.E., Aziz, N., Kim, K.H., & Fahey, J.L. (2004). Immunological effects of induced shame and guilt. *Psychosomatic Medicine*, *66*(1), 124-131.

Dolhinow, P. (1972). The north Indian langur. In Dolhinow, P. (ed.), *Primate patterns*. New York, NY: Holt, Rinehart and Winston, 181-238.

Dolhinow, P. & Murphy, G. (1982). Langur monkey (*Presbytis entellus*) development: the first 3 months of life. *Folia Primatologica*, *39*, 305-331

Douglas, P.H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., & Deschner, T. (2016). Mixed messages: wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. *BMC Evolutionary Biology*, *16*(1), 140.

Drickamer, L.C., Gowaty, P.A., & Holmes, C.M. (2000). Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Animal Behaviour*, *59*(2), 371-378.

Dugdale, H.L., Ellwood, S.A., & MacDonald, D.W. (2010). Alloparental behaviour and long-term costs of mothers tolerating other members of the group in a plurally breeding mammal. *Animal Behaviour*, *80*, 721-735

Eberle, M., & Kappeler, P.M. (2006). Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, *60*(4), 582-588.

Dunbar, R.I.M. (1982). Intraspecific variations in mating strategy. In Bateson, P.P.G., & Klopfer, P.H. *Ontogeny*. New York, NY: Springer, 385-431.

Dunbar, R.I.M. (1984). *Reproductive decisions: an economic analysis of gelada baboon reproductive strategies*. Princeton, NJ: Princeton University Press.

Dunbar, R.I.M. (2013). *Primate social systems*. New York, NY: Springer Science & Business Media.

Eberhard, W.G. (1996). *Female control: sexual selection by cryptic female choice*. Princeton, NJ: Princeton University Press.

Emery-Thompson, M. (2005). Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology*, *67*(1), 137-158.

Emlen, S.T. (1991) Evolution of cooperative breeding in birds and mammals. In Krebs, J.R., Davies, N.B. (eds.), *Behavioural ecology: an evolutionary approach*. Oxford: Blackwell, 301-337

Emlen, S.T., & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215-223.

Eriksson, J., Siedel, H., Lukas, D., Kayser, M., Erler, A., Hashimoto, C., Hohmann, G., Boesch, C., & Vigilant, L. (2006). Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus*). *Molecular Ecology*, *15*(4), 939-949.

Fairbanks, L.A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, *40*, 53-562.

Feistner, A.T.C., & Price, E.C. (1991). Food offering in New World primates: two new species added. *Folia Primatologica*, *57*, 165-168.

Feldblum, J.T., Wroblewski, E.E., Rudicell, R.S., Hahn, B.H., Paiva, T., Cetinkaya-Rundel, M., & Gilby, I.C. (2014). Sexually coercive male chimpanzees sire more offspring. *Current Biology*, *24*(23), 2855-2860.

Feldman, M., & Christiansen, F. B. (1984). Population genetic theory of the cost of inbreeding. *The American Naturalist*, *123*(5), 642-653.

Feldman, R., (2012). Oxytocin and social affiliation in humans. *Hormones and Behavior*, *61*, 380-391.

Feldman, R., Weller, A., Zagoory-Sharon, O., & Levine, A. (2007). Evidence for a neuroendocrinological foundation of human affiliation: plasma oxytocin levels across pregnancy and the postpartum period predict mother-infant bonding. *Psychological Science*, *18*(11), 965-970.

Feldman, R., Gordon, I., & Zagoory_Sharon, O. (2011). Maternal and paternal plasma, salivary, and urinary oxytocin and parent-infant synchrony: considering stress and affiliation components of human bonding. *Developmental Science*, *14*(4), 752-761

Feldman, R., Gordon, I., Schneiderman, I., Weisman, O., & Zagoory-Sharon, O. (2010). Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent-infant contact. *Psychoneuroendocrinology*, *35*(8), 1133-1141

Fernandez-Duque, E., Valeggia, C.R., & Mendoza, S.P. (2009). The biology of paternal care in human and nonhuman primates. *Annual Review of Anthropology*, *38*, 115-130.

Finkenwirth, C., Martins, E., Deschner, T., & Burkart, J.M. (2016). Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys. *Hormones and Behavior*, *80*, 10-18.

Flack, J.C., De Waal, F.B., & Waal, D. (2004). Dominance style, social power, and conflict management: a conceptual framework. In Thierry, B., Singh, M., & Kaumanns, W. (eds.) *Macaque societies: a model for the study of social organization*. Cambridge: Cambridge University Press, 157-181.

Forster, S., Cords, M. (2005). Socialization of infant blue monkeys (*Cercopithecus mitis stuhlmanni*): allomaternal interactions and sex differences. *Behaviour*, *142*, 869-896.

Francis, D.D., Champagne, F.C., & Meaney, M.J. (2000). Variations in maternal behaviour are associated with differences in oxytocin receptor levels in the rat. *Journal of Neuroendocrinology*, *12*(12), 1145-1148.

Frank, S.A. (1995). Mutual policing and repression of competition in the evolution of cooperative groups. *Nature*, *377*(6549), 520-522.

Fruteau, C., van de Waal, E., van Damme, E., & Noe, R. 2011. Infant access and handling in sooty mangabeys and vervet monkeys. *Animal Behaviour*. *81*, 153-161.

Fruth, B., Hohmann, G., & McGrew, W.C. (1999). The *Pan* species. In Dolhinow, P., & Fuentes, A. (eds.) *The non-human primates*. Mountain View, CA: Mayfield, 64-72.

Fuchs, A.R., Fuchs, F., Husslein, P., Soloff, M.S., & Fernstrom, M.J. (1982). Oxytocin receptors and human parturition: a dual role for oxytocin in the initiation of labor. *Science*, *215*(4538), 1396-1398.

Furuichi, T. (1989). Social interactions and the life history of femalePan paniscus in Wamba, Zaire. *International Journal of Primatology*, *10*(3), 173-197.

Furuichi, T. (1992). The prologed estrous of females and factors influencing mating in a wild group of bonobos (*Pan paniscus*) in Wamba, Zaire. In *Topics in Primatology Vol. 2: Behavior, Ecology, and Conservation*. Tokyo: University of Tokyo Press,179-199.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, *18*(6), 855-875.

Furuichi, T., & Hashimoto, C. (2002). Why female bonobos have a lower copulation rate during estrus than chimpanzees. In Boesch, C., Hohmann, G., & Marchant, L.F. (eds.), *Behavioural diversity in chimpanzees and bonobos*. New York, NY: Cambridge University Press, 156-167.

Furuichi, T., & Hashimoto, C. (2004). Sex differences in copulation attempts in wild bonobos at Wamba. *Primates*, *45*(1), 59-62.

Furuichi, T., Idani, G.I., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C. and Kano, T. (1998). Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, *19*(6), pp.1029-1043.

Galdikas, B.M. (1981). Orangutan reproduction in the wild. In Graham, C. E. (ed.), *Reproductive biology of the great apes: comparative and biomedical perspectives*. New York, NY: Academic Press, 281-300.

Gerloff, U., Hartung, B., Fruth, B., Hohmann, G., & Tautz, D. (1999). Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*(1424), 1189-1195.

Ginther, A.J., Snowdon, C.T. (2009). Expectant parents groom adult sons according to previous alloparenting in a biparental cooperatively breeding primate. *Animal Behaviour*, *78*, 287-297.

Gittleman, J.L. (1985). Functions of communal care in mammals. In Gireenwood, P.J., Harvey, P.H., Slutkin, M. (eds.) *Evolution*. *Essays in honour of John Maynard Smith*. Cambridge: Cambridge University Press, 187-205.

Goldizen. A. (1987). Tamarins and marmosets: communal care of offspring. In Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., & Struhsaker, T. (eds.) *Primate Societies*. Chicago, IL: University of Chicago Press, 34-43.

Goldizen, A.W., & Terborgh, J. (1989). Demography and dispersal patterns of a tamarin population: possible causes of delayed breeding. *American Naturalist*, *134*, 208-224.

Goldstone, L.G., Sommer, V., Nurmi, N., Stephens, C., & Fruth, B. (2016). Food begging and sharing in wild bonobos (*Pan paniscus*): assessing relationship quality?. *Primates*, *57*(3), 367-376.

Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Cambridge, MA: Harvard University Press.

Gordon, I., Zagoory‐Sharon, O., Schneiderman, I., Leckman, J. F., Weller, A., & Feldman, R. (2008). Oxytocin and cortisol in romantically unattached young adults: associations with bonding and psychological distress. *Psychophysiology*, *45*(3), 349-352.

Gordon, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2010a). Oxytocin and the development of parenting in humans. *Biological psychiatry*, *68*(4), 377-382.

Gordon, I., Zagoory-Sharon, O., Leckman, J.F., & Feldman, R. (2010b). Prolactin, oxytocin, and the development of paternal behavior across the first six months of fatherhood. *Hormones and Behavior*, *58*(3), 513-518

Halliday, T.R. (1983). The study of mate choice. In Bateson, P. (ed.), *Mate choice*. Cambridge: Cambridge University Press, 3-32.

Hamilton, W.D. (1964). The genetic evolution of social behavior, I, II. *Journal of Theoretical Biology*, *7*, 1- 52.

Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, *20*(5), R230-R231.

Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, *17*(7), 619-623.

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573-585.

Harlow, H.F., & Harlow, M.K. (1965). The affectional systems. In Schrier, A.M., Harlow, H.F., & Stollnitz, F. (eds.) *Behavior of nonhuman primates: modern research trends*. New York, NY: Academic Press, 287-334.

Harvey, P.H., & Clutton-Brock, T.H. (1985). Life history variation in primates. *Evolution*, *39*(3), 559-581.

Hebb, D.O., & Thompson, W.R. (1954). The social significance of animal studies. In Lindzey, G. (ed.), Handbook of social psychology, Vol. 1. Reading, MA: Addison-Wesley, 532-561.

Henzi, S.P., Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour*, *63*, 915-921.

Hinde, R.A. (1966). *Animal behavior: a synthesis of ethology and comparative psychology*. New York, NY: McGraw-Hill.

Hinde, R.A. (1976). Interactions, relationships and social structure. *Man*, *11*(1), 1-17.

Hinde, R.A. (1983). A conceptual framework. In Hinde, R.A. (ed.), *Primate social relationships*. Sunderland, MA: Sinauer Associates, 1-7.

Hine, E., Lachish, S., Higgie, M., & Blows, M.W. (2002). Positive genetic correlation between female preference and offspring fitness. *Proceedings of the Royal Society of London B: Biological Sciences*, *269*(1506), 2215-2219.

Hiraiwa, M. 1981. Maternal and alloparental care in a troop of free-ranging Japanese monkeys. *Primates*, *22*, 309-329

Hobaiter, C., Schel, A. M., Langergraber, K., & Zuberbühler, K. (2014). 'Adoption' by maternal siblings in wild chimpanzees. *PloS one*, *9*(8), e103777.

Hohmann, G., & Fruth, B. (2003a). Culture in bonobos? Between-species and within-species variation in behavior. *Current Anthropology*, *44*(4), 563-571.

Hohmann, G., & Fruth, B. (2003b). Intra-and inter-sexual aggression by bonobos in the context of mating. *Behaviour*, *140*(11), 1389-1413.

Hohmann, G., Gerloff, U., Tautz, D., & Fruth, B. (1999). Social bonds and genetic ties: kinship, association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour*, *136*(9), 1219-1235.

Holekamp, K.E., & Smale, L. (1991). Dominance acquisition during mammalian social development: the "inheritance" of maternal rank. *American Zoologist*, *31*(2), 306-317.

Hrdy, S.B. (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia primatologica*, *22*(1), 19-58.

Hrdy, S.B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In Rosenblatt, J.S., Hinde, R.A., Shaw, E., Beer, C. (eds.), *Advances in the study of behavior, vol 6*. New York, NY: Academic Press, 101-158.

Hrdy, S.B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, *1*(1), 13-40.

Hrdy, S.B. (2009). *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: The Belknap Press of Harvard University Press.

Hsu, M.J., Lin, S.I., Lin, J.F., Lin, T.J. and Agoramoorthy, G., (2015). Non-maternal infant handling in wild formosan macaques of Mount Longevity, Taiwan. *Folia Primatologica*, *86*(6), pp.491-505.

Huchard, E., Alvergne, A., Féjan, D., Knapp, L.A., Cowlishaw, G., & Raymond, M. (2010). More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons. *Behavioral Ecology and Sociobiology*, *64*(5), 769-781.

Hurlemann, R., Patin, A., Onur, O.A., Cohen, M.X., Baumgartner, T., Metzler, S., Dziobek, I., Gallinat, J., Wagner, M., Maier, W. and Kendrick, K.M., (2010). Oxytocin enhances amygdala-dependent, socially reinforced learning and emotional empathy in humans. *Journal of Neuroscience*, *30*(14), 4999-5007.

Idani, G. (1990). Relations between unit-groups of bonobos at Wamba, Zaire: Encounters and temporary fusions. *Afrian Study Monographs*, *11*, 153-186.

Idani, G. (1991). Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia primatologica*, *57*(2), 83-95.

Insel, T.R., 1992. Oxytocin - a neuropeptide for affiliation: evidence from behavioral, receptor autoradiographic, and comparative studies. *Psychoneuroendocrinology*, *17*, 3-35.

Insel, T.R., & Winslow, J.T. (1991). Central administration of oxytocin modulates the infant rats response to social isolation. *European Journal of Pharmacology*, *203*(1), 149-152

Insel, T.R., & Hulihan, T.J. (1995). A gender-specific mechanism for pair bonding: oxytocin and partner preference formation in monogamous voles. *Behavioral neuroscience*, *109*(4), 782.

Isler K, van Schaik C (2012). Allomaternal care, life history and brain size evolution in mammals. *Journal of Human Evolution*, *63*, 52-63.

Janson, C. (1985). Aggresive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, *18*(2), 125-138.

Janson, C. (1992). Evolutionary ecology of primate social structure. In Smith, E.A., & Winterhalder, B., (eds.), *Evolutionary ecology and human behavior*. New York, NY: DeGruyter, 95–130.

Jay, P.C. (1962). Aspects of maternal behavior among langurs. *Annals of the New York Academy of Sciences*, *102*(1), 468-476.

Kano, T. (1989). The sexual behavior of pygmy chimpanzees. In Heltne, G., Marquardt, L.A., *Understanding chimpanzees*. Cambridge, MA: Harvard University Press, 176–183.

Kano, T. (1992). *The last ape: pygmy chimpanzee behavior and ecology*. Stanford, CA: Stanford University Press.

Kano, T. (1996). Male rank order and copulation rate in a unit-group of bonobos at Wamba, Zaire. In McGrew, W.C., Marchant, L.F., and Nishida, T. (eds.), *Great Ape Societies*. Cambridge, MA: Cambridge University Press, 135-145.

Kappeler, P.M., & Van Schaik, C.P. (Eds.). (2004). *Sexual selection in primates: new and comparative perspectives*. Cambridge, MA: Cambridge University Press.

Kapsalis, E. (2003) Matrilineal kinship and primate behavior. In Chapais, B., & Berman, C. (eds.) *Kinship and behavior in primates*. Oxford: Oxford University Press, 153–176.

Karlamangla, A.S., Friedman, E.M., Seeman, T.E., Stawksi, R.S., & Almeida, D.M. (2013). Daytime trajectories of cortisol: demographic and socioeconomic differences—findings from the National Study of Daily Experiences. *Psychoneuroendocrinology*, *38*(11), 2585-2597.

Keddy, A.C. (1986). Female mate choice in vervet monkeys (*Cercopithecus aethiops sabaeus*). *American Journal of Primatology*, *10*(2), 125-134.

Kendrick, K.M., Keverne, E.B., & Baldwin, B.A. (1987). Intracerebroventricular oxytocin stimulates maternal behaviour in the sheep. *Neuroendocrinology*, *46*(1), 56-61

Kim, S., Fonagy, P., Koos, O., Dorsett, K., & Strathearn, L. (2014). Maternal oxytocin response predicts mother-to-infant gaze. *Brain research*, *1580*, 133-142

Kishimoto, T., Ando, J., Tatara, S., Yamada, N., Konishi, K., Kimura, N., Fukumori, A., & Tomonaga, M. (2014). Alloparenting for chimpanzee twins. *Scientific reports*, *4*, doi: 10.1038/srep06306.

Knott, C.D. (2009). Orangutans: sexual coercion without sexual violence. In Muller, M.N., & Wrangham, R.W. (eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press, 81-111.

Knott, C.D., & Kahlenberg, S.M. (2007). Orangutans in perspective: forced copulations and female mating resistance. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., & Stumpf, R.M. (eds.), *Primates in perspective*. New York, NY: Oxford University Press, 290-304.

Kohda, M. (1985). Allomothering behaviour of New and Old World monkeys. *Primates*, *26*, 28-44.

Kolm, N. (2001). Females produce larger eggs for large males in a paternal mouthbrooding fish. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1482), 2229-2234.

Kramer, K.L. (2010). Cooperative breeding and its significance to the demographic success of humans. *Annual Review of Anthropology*, *39*, 417 436.

Kuroda, S. (1979). Grouping of the pygmy chimpanzees. *Primates*, *20*(2), 161-183.

Lancaster, J.B. (1971). Play mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica*, *15*, 161-182.

Lee, P.C. (1987). Nutrition, fertility and maternal investment in primates. *Journal of Zoology London*, *213*, 409-422.

Leigh, S.R., & Blomquist, G.E. (2011). Life History In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., & Stumpf, R.M. (eds.), *Primates in perspective*. New York, NY: Oxford University Press, 418-427.

Lemasson, A., Palombit, R.A., & Jubin, R. (2008). Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. Behavioral Ecology and *Sociobiology*, *62*(6), 1027-1035.

Levine, A., Zagoory-Sharon, O., Feldman, R., & Weller, A. (2007). Oxytocin during pregnancy and early postpartum: individual patterns and maternal–fetal attachment. *Peptides*, *28*(6), 1162-1169.

Levy, F., Kendrick, K.M., Keverne, E.B., Piketty, V., & Poindron, P. (1992). Intracerebral oxytocin is important for the onset of maternal behavior in inexperienced ewes delivered under peridural anesthesia. *Behavioral neuroscience*, *106*(2), 427.

Lewis, R.J. (2002). Beyond dominance: the importance of leverage. *The Quarterly review of biology*, *77*(2), 149-164.

Lim, M.M., & Young, L.J. (2006). Neuropeptidergic regulation of affiliative behavior and social bonding in animals. *Hormones and behavior*, *50*(4), 506-517.

Lischke, A., Berger, C., Prehn, K., Heinrichs, M., Herpertz, S. C., & Domes, G. (2012). Intranasal oxytocin enhances emotion recognition from dynamic facial expressions and leaves eye-gaze unaffected. *Psychoneuroendocrinology*, *37*(4), 475-481.

Lonsdorf, E.V., Anderson, K.E., Stanton, M.A., Shender, M., Heintz, M.R., Goodall, J., & Murray, C. M. (2014). Boys will be boys: sex differences in wild infant chimpanzee social interactions. *Animal behaviour*, *88*, 79-83.

Lupien, S.J., McEwen, B. S., Gunnar, M. R., & Heim, C. (2009). Effects of stress throughout the lifespan on the brain, behaviour and cognition. *Neuroscience*, *10*(6), 434.

MacKinnon, K.C. (2011). Social beginnings: the tapestry of infant and adult interactions. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., & Stumpf, R.M. (eds.), *Primates in perspective*. New York, NY: Oxford University Press, 440-455.

Maestripieri, D. (1994). Social structure, infant handling, and mothering styles in group-living Old World monkeys. *International Journal of Primatology*, *15*(4), 531-553.

Maestripieri, D., Hoffman, C. L., Anderson, G. M., Carter, C. S., & Higley, J. D. (2009). Mother-infant interactions in free-ranging rhesus macaques: relationships between physiological and behavioral variables. *Physiology & behavior*, *96*(4), 613-619.

Malenky, R.K., & Wrangham, R.W. (1994). A quantitative comparison of terrestrial herbaceous food consumption by Pan paniscus in the Lomako Forest, Zaire, and Pan troglodytes in the Kibale Forest, Uganda. *American Journal of Primatology*, *32*(1), 1-12.

Manson, J.H. (1992). Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour*, *44*, 405-416.

Manson, J.H. (1999). Infant handling in wild *Cebus capucinus*: testing bonds between females?. *Animal Behaviour*, *57*(4), 911-921

Manson, J.H. (2003). Foreword. In Jones, C. B. *Sexual selection and reproductive competition in primates*. Norman, OK: American Society of Primatologists, xiii-xv.

Manson, J.H. (2011). Mate choice. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., & Stumpf, R.M. (eds.), *Primates in perspective*. New York, NY: Oxford University Press, 476-487.

Marson, J., Meuris, S., Cooper, R.W., & Jouannet, P. (1991). Puberty in the male chimpanzee: time-related variations in luteinizing hormone, follicle-stimulating hormone, and testosterone. *Biology of reproduction*, *44*(3), 456-460.

Marvan, R., Stevens, J.M.G., Roeder, A.D., Mazura, I., Bruford, M.W., & De Ruiter, J. R. (2006). Male dominance rank, mating and reproductive success in captive bonobos (Pan paniscus). *Folia Primatologica*, *77*(5), 364-376.

McCarthy, M.M., (1990). Oxytocin inhibits infanticide in female house mice (*Mus domesticus*). *Hormones and Behavior*, *24*, 365-375.

McCarthy, M.M., Bare, J.E., & vom Saal, F.S.V. (1986). Infanticide and parental behavior in wild female house mice: effects of ovariectomy, adrenalectomy and administration of oxytocin and prostaglandin. *Physiology and Behavior*, *36*, 17-23.

McKenna, J.J. (1979). The evolution of allomothering behaviour among colobine monkeys: function and opportunism in evolution. *American Anthropologist*, *81*, 818-840

Meaney, M.J., Lozos, E., & Stewart, J. (1990). Infant carrying by nulliparous female vervet monkeys (*Cercopitecus aethiops*). *Journal of Comparative Psychology*, *104*, 377-381.

Meyer-Lindenberg, A., Domes, G., Kirsch, P., & Heinrichs, M., (2011). Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine. *National Review of Neuroscience*, *12*(9), 524-538.

Mitani, J.C., & Watts, D. (1997). The evolution of non-maternal caretaking among anthropoid primates: do helpers help? *Behavioural Ecology and Sociobiology*, *40*, 213-220.

Muller, M.N., & Wrangham, R.W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, *55*(4), 332-340.

Muller, M.N., & Wrangham, R.W. (eds.). (2009). Sexual coercion in primates and humans. Cambridge, MA: Harvard University Press.

Muller, M.N., Thompson, M.E., Kahlenberg, S.M., & Wrangham, R.W. (2011). Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. *Behavioral Ecology and Sociobiology*, *65*(5), 921-933.

Muller, M.N., Kahlenberg, S.M., & Wrangham, R.W. (2011). Male aggression against females and sexual coercion in chimpanzees. In Muller, M.N., & Wrangham, R.W. (eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press, 184-217.

Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, *128*, 103-129.

Neff, B.D., & Pitcher, T.E. (2005). Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Molecular Ecology*, *14*(1), 19-38.

Nicolson, N. 1987. Infants, mothers, and other females. In Smuts, B., Cheney, D.L., Seyfarth, R.M, Wrangham, R.W., & Struhsaker, T.T., *Primate Societies*. Chicago, IL: University of Chicago Press, 330-342.

Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates*, *9*(3), 167-224.

Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In Hamburg, D.A., & McCown, E.R. (eds.), *The great apes*. Menlo Park, CA: Benjamin Cummings, 73-122.

Nishida, T. (1983). Alloparental behavior in wild chimpanzees of the Mahale Mountains, Tanzania. *Folia Primatologica*, *41*(1-2), 1-33.

Nishida, T. (1990). Chimpanzees of the Mahale Mountains. Tokyo: University of Tokyo Press.

Nishida, T. (2003). Harassment of mature female chimpanzees by young males in the MahaleMountains. *International Journal of Primatology*, *24*(3), 503-514.

Nishida, T., Kano, T., Goodall, J., McGrew, W.C., & Nakamura, M. (1999). Ethogram and Ethnography of Mahale Chimpanzees. *Anthropological Science*, *107*(2), 141-188.

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): implicationsfor natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*(3), 418-426.

Noe, R, & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioural Ecology and Sociobiology*, *35*, 1-11.

Noe, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology and Evolution*, *10*, 336-339.

Norris, K. (1993). Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature*, *362*(6420), 537-539.

Novak, M.A., Hamel, A.F., Kelly, B.J., Dettmer, A.M., & Meyer, J.S. (2013). Stress, the HPA axis, and nonhuman primate well-being: a review. *Applied Animal Behaviour Science*, *143*(2), 135-149.

Nunn, C.L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour*, *58*(2), 229-246.

O'Brien, T.G., & Robinson, J.G. (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour*, *119*, 30-50.

Packer, C., Lewis, S., & Pusey, A. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour*, *43*(2), 265-281.

Palthe, T.V.W., & van Hooff, J.A. (1975). A case of the adoption of an infant chimpanzee by a suckling foster chimpanzee. *Primates*, *16*(2), 231 234.

Paoli, T., Palagi, E., Tacconi, G., & Tarli, S.B. (2006). Perineal swelling, intermenstrual cycle, and female sexual behavior in bonobos (*Pan paniscus*). *American Journal of Primatology*, *68*(4), 333-347.

Paoli, T., & Palagi, E. (2008). What does agonistic dominance imply in bonobos?. In Furuichi, T. & Thompson, J. (eds.), *The Bonobos*. New York, NY: Springer Science and Business Media, 39-54.

Paoli, T. (2009). The absence of sexual coercion in bonobos. In Muller, M.N., & Wrangham, R.W. (eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press, 410-423.

Parish, A.R. (1994). Sex and food control in the “uncommon chimpanzee”: how bonobo females overcome a phylogenetic legacy of male dominance. *Ethology and Sociobiology*, *15*(3), 157-179.

Parish, A.R. (1996). Female relationships in bonobos (Pan paniscus). *Human Nature*, *7*(1), 61-96.

Parker, G.A. (1979). Sexual selection and sexual conflict. In Blum, M., & Blum, N. (eds.), *Sexual selection and reproductive competition in insects*. New York, NY: Academic Press, 123-166.

Partridge, L. (1980). Mate choice increases a component of offspring fitness in fruit flies. *Nature*, *283*(5744), 290-291.

Paul, A., & Kuester, J. (1996). Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses. *Behavioral Ecology and Sociobiology*, *39*(2), 133-145.

Paul, A. (2002). Sexual selection and mate choice. *International Journal of Primatology*, *23*(4), 877-904.

Pedersen, C.A. (1997). Oxytocin control of maternal behavior Regulation by sex steroids and offspring stimuli. *Annals of the New York Academy of Sciences*, *807*(1), 126-145.

Pedersen, C.A., & Prange, A. J. (1979). Induction of maternal behavior in virgin rats after intracerebroventricular administration of oxytocin. *Proceedings of the National Academy of Sciences*, *76*(12), 6661-6665.

Pedersen, C.A., (2013). Oxytocin regulation of maternal behavior: from rodents to humans. In: Choleris, E., Pfaff, D., & Kavaliers, M. (eds.), *Oxytocin, vasopressin and related peptides in the regulation of behavior*. Cambridge: Cambridge University Press, 148-182.

Perloe, S.I. (1992). Male mating competition, female choice and dominance in a free ranging group of Japanese macaques. *Primates*, *33*(3), 289-304.

Perry, A., Aviezer, H., Goldstein, P., Palgi, S., Klein, E., & Shamay-Tsoory, S.G. (2013). Face or body? Oxytocin improves perception of emotionsfrom facial expressions in incongruent emotional body context. *Psychoneuroendocrinology*, *38*(11), 2820-2825

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, *371*(6498), 598-599.

Poirier, F.E. (1968). The Nilgiri langur (*Presbytis johnii*) mother-infant dyad. *Primates 9*, 45-68.

Porter, L.M., & Garber, P.A. (2009). Social behavior of *callimicos*: mating strategies and infant care. In Ford, S.M., Porter, L.M., & Davis, L.C. (eds.), *The Smallest Anthropoids*. New York, NY: Springer Science and Business Media, 87-101.

Promislow, D.E., Smith, E.A., & Pearse, L. (1998). Adult fitness consequences of sexual selection in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences*, *95*(18), 10687-10692.

Pusey, A.E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour*, *28*(2), 543-552.

Pusey, A.E. (1990). Behavioural changes at adolescence in chimpanzees. *Behaviour*, *115*(3), 203-246.

Quiatt, D. (1979). Aunts and mothers: adaptive implications of allomaternal behaviour of nonhuman primates. *American Anthropologist*, *81*, 310-319.

Quinlan, R.J., & Quinlan, M.B. (2008). Human lactation, pair-bonds and alloparents: a cross-cultural analysis. *Human Nature*, *19*, 87-102.

Qvarnström, A., & Forsgren, E. (1998). Should females prefer dominant males?. *Trends in Ecology & Evolution*, *13*(12), 498-501.

Reichert, K.E., Heistermann, M., Hodges, K.J., Boesch, C., & Hohmann, G. (2002). What females tell males about their reproductive status: are morphological and behavioural cues reliable signals of ovulation in bonobos (*Pan paniscus*)?. *Ethology*, *108*(7), 583-600.

Ren, B., Li,D., Garber, P.A., & Li, M. (2012). Evidence of allomaternal nursing across one-male units in the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). *PloS one*, *7*(1), e30041.

Reynolds, J.D., & Gross, M.R. (1992). Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proceedings of the Royal Society of London B: Biological Sciences*, *250*(1327), 57-62.

Riedman, M.L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology*, *57*(4), 405-435.

Rodrigues, S.M., Saslow, L.R., Garcia, N., John, O.P., & Keltner, D. (2009). Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *Proceedings of the National Academy of Sciences*, *106*(50), 21437-21441.

Rosenbaum, S., Silk, J.B., & Stoinski, T.S. (2011). Male-immature relationships in multi_male groups of mountain gorillas (*Gorilla beringei beringei*). *American Journal of Primatology*, *73*(4), 356-365.

Rosenbaum, S., Hirwa, J.P., Silk, J.B., Vigilant, L., & Stoinski, T.S. (2015). Male rank, not paternity, predicts male-immature relationships in mountain gorillas, *Gorilla beringei beringei*. *Animal Behaviour*, *104*, 13-24.

Ross, C., & MacLarnon, A. (2000). The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. *Folia Primatologica*, *71*(1-2), 93-113.

Ross, H.E., Freeman, S.M., Spiegel, L.L., Ren, X., Terwilliger, E.F., & Young, L.J. (2009). Variation in oxytocin receptor density in the nucleus accumbens has differential effects on affiliative behaviors in monogamous and polygamous voles. *Journal of Neuroscience*, *29*(5), 1312-1318.

Rowell, T.E. (1967). A quantitative comparison of the behaviour of a wild and a caged baboon group. *Animal Behaviour*, *15*(4), 499-509.

Saito, A., & Nakamura, K. (2011). Oxytocin changes primate paternal tolerance to offspring in food transfer. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *197*(4), 329-337.

Salo, A.L., & French, J.A. (1989). Early experience, reproductive success, and development of parental behaviour in Mongolian gerbils. *Animal Behaviour*, *38*(4), 693-702.

Sapolsky, R.M., Romero, L.M., & Munck, A.U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews*, *21*(1), 55-89.

Sapolsky, R.M. (2005). The influence of social hierarchy on primate health. *Science*, *308*(5722), 648-652.

Schneiderman, I., Zagoory-Sharon, O., Leckman, J.F., & Feldman, R. (2012). Oxytocin during the initial stages of romantic attachment: relations to couples' interactive reciprocity. *Psychoneuroendocrinology*, *37*(8), 1277-1285.

Scollay, P.A., & DeBold, P. (1980). Allomothering in a captive colony of Hanuman langurs (*Presbytis entellus*). *Ethology and Sociobiology*, *1*(4), 291-299.

Scott, J.P., & Fredericson, E. (1951). The causes of fighting in mice and rats. *Physiological Zoology*, *24*(4), 273-309.

Selye, H. (1975). Stress and distress. *Comprehensive Therapy*, *1*(8), 9-13.

Silk, J.B. (1980). Kidnapping and female competition among captive bonnet macaques. *Primates*, *21*(1), 100-110.

Silk, J.B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, *57*(5), 1021-1032.

Silk, J.B., Alberts, S.C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*(5648), 1231-1234.

Silk, J.B., Rendall, D., Cheney, D.L., & Seyfarth, R.M. (2003). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology*, *109*(8), 627-644.

Small, M.F., & Rodman, P.S. (1981). Primigravidity and infant loss in bonnet macaques. *Journal of Medical Primatology*, *10*, 164-169.

Small, M.F. (1982). A comparison of mother and nonmother behaviour during the birth seasons in two species of captive macaques. *Folia Primatologica*, *38*, 99-107.

Smith, A. S., Ågmo, A., Birnie, A.K., & French, J.A. (2010). Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. *Hormones and Behavior*, *57*(2), 255-262.

Smuts, B.B., & Smuts, R.W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, *22*(22), 1-63.

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., & Wrangham, R.W. (Eds.). (2008). *Primate societies*. Chicago, IL: University of Chicago Press.

Snowdon, C.T., Pieper, B.A., Boe, C.Y., Cronin, K.A., Kurian, A.V., & Ziegler, T.E. (2010). Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. *Hormones and Behavior*, *58*(4), 614-618

Sokal, R.R., & Rohlf, F.J. (2012). *Descriptive statistics*. *Biometry, the principles and practice of statistics in biological research 4th edition*. New York, NY: Freeman and Company.

Solomon, N.G., & French, J.A. (1997). *Cooperative breeding in mammals*. Cambridge: Cambridge University Press.

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y., & Nozaki, M. (1997). Sexual selection in Japanese macaques I: female mate choice or male sexual coercion?. *Animal Behaviour*, *54*(3), 725-736.

Soltis, J. (2002). Do primate females gain nonprocreative benefits by mating with multiple males? Theoretical and empirical considerations. *Evolutionary Anthropology: Issues, News, and Reviews*, *11*(5), 187-197.

Sommer, V. (1989). Infant mistreatment in langur monkeys: sociobiology tackled from the wrong end? In Rasa, A.E., Vogel, C., & Voland, E., *The Sociobiology of Sexual and Reproductive Strategies*. London: Chapman & Hall, 110-127.

Stanford, C. (1991). The capped langur in Bangladesh: behavioural ecology and reproductive tactics. *Contributions to Primatology*, *26*, 1-181

Stanford, C. (1992). The costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behavioral Ecology and Sociobiology*, *30*, 29-34.

Stanford, C.B. (1998). The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Current Anthropology*, *39*(4), 399-420.

Stearns, S.C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.

Stevens, J.M., Vervaecke, H., De Vries, H., & van Elsacker, L. (2007). Sex differences in the steepness of dominance hierarchies in captive bonobo groups. *International Journal of Primatology*, *28*(6), 1417-1430.

Stevens, J.R. (2004). The selfish nature of generosity: harassment and food sharing in primates. *Proceedings of the Royal Society of London B: Biological Sciences*, *271*(1538), 451-456.

Strathearn, L., (2011). Maternal neglect: oxytocin, dopamine and the neurobiology of attachment. *Journal of Neu*roendocrinology, *23*, 1054-1065.

Stumpf, R.M., & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire. *Behavioral ecology and sociobiology*, *57*(5), 511-524.

Stumpf, R.M., & Boesch, C. (2006). The efficacy of female choice in chimpanzees of the Taï Forest, Côte d'Ivoire. *Behavioral Ecology and Sociobiology*, *60*(6), 749-765.

Stumpf, R.M. (2011). Chimpanzees and bonobos: inter-and intraspecies diversity. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., & Stumpf, R.M. (eds.), *Primates in perspective*. New York, NY: Oxford University Press, 340-356.

Stumpf, R.M., Martinez‑Mota, R., Milich, K.M., Righini, N., & Shattuck, M.R. (2011). Sexual conflict in primates. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(2), 62-75.

Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society of London B: Biological Sciences*, *278*(1705), 590-598.

Surbeck, M., Deschner, T., Weltring, A., & Hohmann, G. (2012). Social correlates of variation in urinary cortisol in wild male bonobos (*Pan paniscus*). *Hormones and Behavior*, *62*(1), 27-35.

Surbeck, M., & Hohmann, G. (2013). Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behavioral ecology and sociobiology*, *67*(11), 1767-1780.

Surbeck, M., Langergraber, K. E., Fruth, B., Vigilant, L., & Hohmann, G. (2017). Male reproductive skew is higher in bonobos than chimpanzees. *Current Biology*, *27*(13), R640-R641.

Takahata, Y.U., Ihobe, H.I., & Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or receptivity. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*. Cambridge, MA: Cambridge University Press, 146-155.

Tardif, S.D., Richter, C.B., Carson, R.L. (1984). Effects of sibling rearing experience on future reproductive success in two species of *Callitrichidae*. *American Journal of Primatology*, *6*, 377-380.

Tardif, S.D., Carson, R. L., & Gangaware, B. L. (1992). Infant care behavior of non‑reproductive helpers in a communal care primate, the Cotton‑top Tamarin (*Saguinus oedipus*). *Ethology*, 92(2), 155-167.

Tecot, S., & Baden, A.L. (2015). Primate allomaternal care. In Scott, R., & Kosslyn, S. *Emerging trends in the social and behavioural sciences: an interdisciplinary, searchable, and linkable resource*. Hoboken, NJ: Wiley & Sons, 1-16.

The Jane Goodall Institute. (2010). Twins! Golden & Glitter. Retrieved from: http://www.janegoodall.org/chimp-central-twins.

Thompson-Handler, N., Malenky, R.K., & Badrian, N. (1984). Sexual behavior of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur Zaire. In Susman, R.L. (ed.), *The pygmy chimpanzee: evolutionary biology and behavior*. New York, NY: Plenum, 347-366.

Thompson, M.E. (2014). Sexual conflict: nice guys finish last. *Current Biology*, *24*(23), R1125-R1127.

Thompson, M.E., & Wrangham, R.W. (2008). Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *American Journal of Physical Anthropology*, *135*(2), 171-181

Tiddi, B., Aureli, F., & Schino, G. (2010). Grooming for infant handling in tufted capuchin monkeys: a re-appraisal of the primate infant market. *Animal Behaviour*, *79*, 1115-1123.

Tokuyama, N., & Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour*, *119*, 27-35.

Trivers, R. (1972). *Parental investment and sexual selection*. Cambridge, MA: Biological Laboratories, Harvard University.

van IJzendoorn, M.H., & Bakermans-Kranenburg, M.J., (2012). A sniff of trust: meta-analysis of the effects of intranasal oxytocin administration on face recognition, trust to in-group, and trust to out-group. *Psychoneuroendocrinology*, *37*, 438-443.

van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161-311.

van Schaik, C.P., & Kappeler, P.M. (1997). Infanticide risk and the evolution of male–female association in primates. *Proceedings of the Royal Society of London B: Biological Sciences*, *264*(1388), 1687-1694.

van Schaik, C.P., Van Noordwijk, M.A., & Nunn, C.L. (1999). Sex and social evolution in primates. In Lee, P.C. (ed.), *Comparative primate socioecology*, Cambridge: Cambridge University Press, 204-231.

van Schaik, C.P., & Janson, C.H. (eds.). (2000). *Infanticide by males and its implications*. Cambridge: Cambridge University Press.

van Schaik, C.P., Pradhan, G.R., & van Noordwijk, M.A. (2004). Mating conflict in primates: infanticide, sexual harassment and female sexuality. In Kappeler, P.M., & van Schaik, C.P. (eds.), *Sexual selection in primates: new and comparative perspectives*. Cambridge: Cambridge University Press, 131-150.

Vervaecke, H., & Van Elsacker, L. (2000). Sexual competition in a group of captive bonobos (*Pan paniscus*). *Primates*, *41*(1), 109-115.

Vervafcke, H., De Vries, H., & van Elsacker, L. (2000). Function and distribution of coalitions in captive bonobos (*Pan paniscus*). *Primates*, *41*(3), 249-265.

Vogel, C. (1984). Patterns of infant transfer within two groups of common langurs (*Presbytis entellus*) near Jodphur: testing hypotheses concerning the benefits and risks. In Roonwal, M.L., Mohnot, S.M., & Rathore, N.S. (eds.), *Current Primate Research*. Jodphur: Jodphur University Press, 361-379.

Wakefield, M.L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, *85*(6), 1303-1313.

Wallen, K., & Winston, L.A. (1984). Social complexity and hormonal influences on sexual behavior in rhesus monkeys (*Macaca mulatta*). *Physiology & Behavior*, *32*(4), 629-637.

Wallis, J. (1995). Seasonal influence on reproduction in chimpanzees of Gombe National Park. *International Journal of Primatology*, *16*(3), 435-451.

Wasser, S.K. (1983). Reproductive competition and cooperation among female yellow baboons. In Wasser, S.K. (ed.), *Social behavior of female vertebrates*. New York, NY: Academic Press, 349-390.

Wasser, S.K., & Barash, D.P. (1981). The selfish 'allomother': a comment on Scollay and Debold. *Ethology and Sociobiology*, *2*, 91-93.

Watson-Capps, J.J. (2009). Evolution of sexual coercion with respect to sexual selection and sexual conflict theory. In Muller, M.N., & Wrangham, R.W. (eds.), *Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females*. Cambridge, MA: Harvard University Press, 23-41.

Watts, D.P. (1992). Social relationships of immigrant and resident female mountain gorillas. I. Male-female relationships. *American Journal of Primatology*, *28*(3), 159-181.

Watts, D.P. (2010). Dominance, power, and politics in nonhuman and human primates. In Kappeler, P.M., & Silk, J. (eds.), *Mind the gap*. Berlin, Heidelberg: Springer, 109-138.

White, F.J. (1988). Party composition and dynamics in Pan paniscus. *International Journal of Primatology*, *9*(3), 179-193.

White, F.J. (1996). Comparative socio-ecology of *Pan paniscus*. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*. Cambridge, MA: Cambridge University Press, 29-41.

White, F.J. (1998). Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality. *International Journal of Primatology*, *19*(6), 1013-1027.

White, F.J., & Lanjouw, A. (1992). Feeding competition in Lomako bonobos: variation in social cohesion. *Topics in Primatology*, *1*, 67-79.

White, F. J., & Wood, K. D. (2007). Female feeding priority in bonobos, Pan paniscus, and the question of female dominance. *American Journal of Primatology*, *69*(8), 837-850.

White, F.J., & Wrangham, R.W. (1988). Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour*, *105*(1), 148-164.

White, F.J., Waller, M.T., Cobden, A.K., & Malone, N.M. (2008). Lomako bonobo population dynamics, habitat productivity, and the question of tool use. *American Journal of Physical Anthropology*, *46*, 222.

White, F.J., Waller, M., Boose, K., Merrill, M.Y., & Wood, K.D. (2015). Function of loud calls in wild bonobos. *Journal of Anthropological Sciences*, *93*, 1-13

Wigby, S., & Chapman, T. (2004). Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution*, *58*(5), 1028-1037.

Witt, D.M., & Insel, T.R. (1991). A selective oxytocin antagonist attenuates progesterone facilitation of female sexual behavior. *Endocrinology*, *128*(6), 3269-3276.

Witt, D.M., Winslow, J.T., & Insel, T.R. (1992). Enhanced social interactions in rats following chronic, centrally infused oxytocin. *Pharmacology Biochemistry and Behavior*, *43*(3), 855-861.

Wittig, R.M., Crockford, C., Deschner, T., Langergraber, K.E., Ziegler, T.E., & Zuberbühler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proc. R. Soc. B*, *281*(1778), doi: 10.1098/rspb.2013.3096.

Woolfenden, G.E., & Fitzpatrick, J.W. (1984). *The Florida scrub jay: demography of a cooperative-breeding bird* (Vol. 20). Princeton, NJ: Princeton University Press.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75(3), 262-300.

Wrangham, R.W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature*, *4*(1), 47-79.

Wrangham, R.W., Conklin-Brittain, N.L., & Hunt, K.D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology*, *19*(6), 949-970.

Yerkes, R.M. (1925). *Almost human*. New York, NY: J. Cape.