Infant handling in bonobos (*Pan paniscus*): Exploring functional hypotheses and the relationship to oxytocin

Klaree Boose[a,*], Frances White[a], Colin Brand[a], Audra Meinelt[b], Josh Snodgrass[a]

[a] Department of Anthropology, University of Oregon, 1218 University of Oregon, Eugene, OR 97403, USA
[b] Columbus Zoo and Aquarium, Powell, OH, USA

ABSTRACT

Infant handling describes interactions between infants and non-maternal group members and is widespread across mammalian taxa. The expression of infant handling behaviors, defined as any affiliative or agonistic interaction between a group member and an infant, varies considerably among primate species. Several functional hypotheses may explain the adaptive value of infant handling including the Kin Selection hypothesis, which describes handling as a mechanism through which indirect fitness is increased and predicts a bias in handling behaviors directed toward related (genetic) infants; the Alliance Formation hypothesis, which describes handling as a social commodity and predicts females with infants will support handlers during conflict; and the Learning-to-Mother hypothesis, which describes handling as a mechanism through which handlers learn species-specific maternal behaviors and predicts that handling will occur most frequently in immature and nulliparous females. Using behavioral observation and data on urinary oxytocin, a neuropeptide hormone known to modulate maternal care and social bonds in mammals, the purpose of this study was to describe the pattern of infant handling in bonobos (*Pan paniscus*) and to explore proposed functional hypotheses. Data show that related infant-handler dyads occurred significantly more frequently than unrelated infant-handler dyads during some of the study period and that handling was positively correlated with support during conflict. Data also showed that immature and nulliparous females handled infants significantly more than other age-sex categories and exhibited higher post handling oxytocin values than other age-sex class. The trends identified in this data set provide insight into the role oxytocin may play in facilitating care-giving behaviors in young female bonobos and help to narrow the focus of future research efforts, particularly those associated with the Kin Selection, Alliance Formation, and Learning-to-Mother functional hypotheses.

1. Introduction

Group members in many species of primate exhibit a marked interest in infants, particularly newborn individuals [138,141]. This phenomenon is known as "natal attraction," and occurs when conspecifics approach, examine, touch, and smell the infants [63]. 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 [138,141]. Although care-giving is not always coupled with natal attraction, many species also exhibit allocare behaviors, where individuals other than the mother assist in the feeding, carrying, protecting, and indirect provisioning of immatures, a phenomenon that is especially prevalent in birds and mammals [30,47,125]. Several different terms have been used to describe this range of behaviors such as "allomaternal care," "allomothering," "babysitting," and "kidnapping."

While some of these terms imply specific functions and are tied to support for different hypotheses used to explain these behaviors, others are more vague and authors have most recently favored the term "infant handling" to avoid any potential confusion that may result from using terms tied to specific functional hypotheses [91,110,170]. For the purpose of this paper, infant handling refers to behaviors such as cradling, carrying, grooming (while the infant is not clinging to the mother), and aggressing the infant, etc., which are distinct from, but not mutually exclusive to, those associated with natal attraction (described above). The categorization of infant handling and natal attraction is this manner reflects the differences in fitness consequences that accompany the different categories of behaviors. Handling behaviors potentially carry both greater risk, in the form of survival of the infant and the reproductive success of the mother, and greater opportunity to learn mothering behaviors through experience and to form social bonds with the infant and/or mother. For example, handlers are

better able to aggress infants they are handling than when the infants are not clinging to their mothers, such as carrying them high into a tree and dropping them.

Infant handling occurs across a wide array of mammalian taxa [28,30,40,47,62,77,80,108,125,147] and the patterning and frequency of expression of handling behaviors varies considerably across primate species [70,157]. Many factors contribute to this variability of expression, including the type and availability of social partners, infant age [16,62,63,90,136–138] and sex [40], the dominance rank of the mother and handler [2,42,57,107,138], levels of agonism, relatedness between the handler, the infant, and the infant's mother [55,73,107,136,137], as well as the handler's age and parity ([29,103,138]; see [6] for review). Carrying, grooming, and cradling of infants by individuals other than the mother are common behaviors, whereas allonursing and adoption of infants occurs much less frequently [71,116,123]. Marmosets and tamarins perform considerable amounts of infant handling in the form of carrying, feeding, and protection [48,117,154] and Hanuman langur [62,98], capped langur [147], and squirrel monkey [181] infants spend nearly equal amounts of time with handlers 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 [27,62,98,146–148,165] whereas savanna baboon, rhesus macaque, and Japanese macaque infants spend < 5% of their time with non-mothers [103]. 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 [24,120,139,170].

Some of the variation of expression and patterning of infant handling can be attributed to the adaptive value of the behavior in relation to the type of breeding system that is characteristic of a species. As Hsu et al. [64] have noted, functional hypotheses used to explain infant handling are often divided along two theoretically different lines: (1) those where paternal care and cooperative breeding are obligate (e.g. callitrichids and pair bonded species: [38,48,121,145] and (2) those where non-maternal care is not considered essential for infant survival, such as the socially breeding species that characterize most non-human primates (see [91]). Although these differing theoretical lines are not mutually exclusive, they are often considered separately according to type of breeding system that is characteristic of a species [64].

Further teasing apart of different functional explanations is difficult for three reasons. First, the fitness benefits and/or consequences of infant handling are not always apparent and may involve all or some combination of individuals (i.e. mother, infant, and/or handler). For example, when infants are handled, mothers may obtain increased feeding time that can result in net energy gains that can improve maternal milk quality [58,62,156]. High quality milk can increase infant growth rates, allowing mothers to wean earlier and affording them increased reproductive success through better infant survival and reduced inter-birth intervals [2,3,80,81,95,156,80]. Second, producing concrete support for measures of fitness often requires specific findings available only from long-term data sets that are particularly scarce and difficult to obtain in primates. For example, young females in some species perform the majority of infant handling behaviors (e.g. colobines [6]; Chimpanzees [7]) and, while it is tempting to attribute these behaviors to a functional component related to learning species typical maternal behaviors, data on whether these females have infants that are more likely to survive than the infants of females who do not often handle infants would be needed to fully test this hypothesis. Third, the benefits of infant handling might overlap in a manner that supports several functional hypotheses. For example, kin-biased data may be the result of mutually selfish interactions among kin and can support hypotheses based on kin selection, mutualism, and reciprocal altruism [182]. In spite of these limitations, several functional hypotheses (detailed below) have been put forth in an attempt to account for the heterogeneity observed both within and between species and to explain the adaptive value of infant handling in primates (see [91] for review;

[70,101,129,145]). Although each of these functional hypotheses is categorically distinct, they generate overlapping predictions and are, therefore, not considered to be mutually exclusive.

1.1. Functional 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 [55,63]. 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 [47,62,91,139,169,170]. 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 [120,135].

Hypotheses generated from the **Biological Market** paradigm describe infant handling as a form of reciprocal altruism not dependant on relatedness [105,106], where individuals exchange handling behaviors for any social commodity, such as grooming [8,42,46,57,102,159] or potential future mating opportunities [18,65,84]. 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 [62,147]; 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 [26,91,94].

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 [32,62,79,99,125]. There is considerable support for this hypothesis in species across numerous taxa, (scrub-jays: [180]; pinnipeds: [125]; gerbils: [132]; tamarins: [155]; and vervets: [32]), where generally females demonstrate the highest rates of infant handling ([19,23,59,103,110,141,183]. **Data supporting the Learning-to-Mother hypothesis in primates is relatively scarce, however, and can be partially attributed to the methodological limitations (described above) associated with studying long-lived species.

To compensate for these limitations, researchers have begun to use novel methods to generate variables that are less temporally constraining and to help narrow the focus of future research. For example, fecal stable isotopes have been used to determine the contribution of maternal milk to infants' diets as a measurement of the effect of handling on maternal lactation effort and speed with which weaning occurs [7]. Another potential variable of value is the hormone oxytocin, a known mediator of maternal care behaviors in mammals (see [34,76,111,150]). Despite numerous studies describing the role of oxytocin in facilitating these behaviors (e.g. [34,76,111,113,150]), the relationship between oxytocin and infant handling is not known but has the potential to inform future studies designed to test functional hypotheses on the adaptive value of this complex behavior.

1.2. Oxytocin

Oxytocin, along with other neuropeptide hormones, functions as a modulator of complex social behavior and social cognition in mammals [88]. Produced by the hypothalamus and stored and secreted by the pituitary gland, oxytocin acts primarily as a neuromodulator in the brain where, once released centrally, 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. Oxytocin has

long been recognized for its functions in several aspects of reproduction including parturition, lactation, and mating [20,43,177] and has also been associated with the regulation of social behaviors (see [9,34,100] for review) such as anxiety and affiliation [68,69,178], interpersonal trust [163], recognition of emotions and empathy [66,89,114,126], pair bonding in monogamous species [67,69,130,133,143], and social bonding and food sharing in chimpanzees [25,179].

Research has also focused on the role of oxytocin as a key neuromodulator of care-giving, responsible for the facilitation and maintenance of maternal behaviors [34,76,111,113,150] and studies on animal models have significantly advanced our understanding of the neuroendocrine pathways and acute neuromodulatory effects of oxytocin on behavior. For example, injection of oxytocin stimulates the onset of species-specific maternal behaviors in rats [112]. In mice, variations in lactation-induced oxytocin levels have been found to correspond to variations in maternal behaviors [41] and administration of oxytocin has been found to suppress rates of infanticide and simultaneously increase care-giving behaviors [96,97]. In female sheep (ewes) central injection of oxytocin has been found to rapidly stimulate species typical maternal responses [75], while the administration of peridural anesthesia, which blocks the normal rise in cerebrospinal fluid (CSF) concentrations of oxytocin, was found to inhibit onset of maternal behaviors [87]. In rhesus macaques, researchers have found that variations in maternal behaviors, such as time spent grooming and nursing, are associated with variations in circulating oxytocin [92]. Oxytocin has also been implicated in the modulation of maternal behaviors in humans, particularly during pregnancy and the postpartum period. For example, peripheral oxytocin levels rise and remain high in pregnant and parturient women [35,52–54,86] relative to non-pregnant women [35,52]. Researchers have also found that oxytocin levels during pregnancy are predictive of maternal behaviors such as infant gaze, vocalizations, positive affect, and affectionate touch during the postpartum period [35] and mothers who exhibit a pattern of rising oxytocin during pregnancy and the early postpartum period self-reported stronger attachment to offspring [86]. In addition, higher oxytocin levels are associated with greater infant affect synchrony and social engagement [36,37].

Alongside the data on oxytocin's acute neuromodulatory effects, research is also being done on the organizational effects of oxytocin on the brain and its contribution to the development of species-specific behaviors salient to survival and reproductive success. Referred to as the "organizational/activation hypothesis," exposure to certain hormones during both perinatal and peripubertal development is critically important for sexual differentiation of the brain and behavior in adult individuals [115,134]. Experiments on rodents show that manipulation of oxytocin levels during early postnatal development affect pair bond formation in females, affiliative behaviors in males, sexual behavior in both males and females, and may play a role in facilitating social interactions in both males and females during peripubertal development (see [184] for summary), although researchers acknowledge that more work is needed to fully understand the organizational effects of exposure to oxytocin during development.

1.3. Objective

Although male-immature interactions have been studied in gorillas [127,128] and cases of adoption of orphans have been reported in some species of primates [10,12,60,109], relatively little is known about the social, demographic, and ecological factors that affect the expression or absence of infant handling in great apes. The most detailed studies come from chimpanzees where natal attraction and infant handling occur with varying frequency across sites (e.g. [7,63]), which may be the result of an underreporting of the behavior. Recently, however, the incorporation of molecular techniques has produced some promising insights into the adaptive value of infant handling in this long-lived species. Badescu et al. [7] have shown, through the use of fecal stable

isotope analysis and behavioral observations that in addition to nursing less often, milk contributed less to the age-specific diets of infants who were handled more frequently than infants who were handled less frequently. These results indicated that the speed with which infants were being weaned was inversely related to the amount of allocare infants received, which may influence the length of lactational amenorrhea in mothers and possibly reduce inter-birth interval times through earlier resumption of cycling.

Infant handling, to our knowledge, has not yet been studied in bonobos, a species closely related to chimpanzees. Bonobos, like chimpanzees, are a male-philopatric species that exhibit a multi-male multi-female fission-fusion community structure [5,11,72,104,171] where females generally disperse during adolescence [31,45,72,151] and reach the age of first parturition around 13–15 years [151]. Female bonobos can occupy the highest rank positions within the group [44,50,149,152] and are known to form female-female coalitions [160,174] and strong bonds with both males and females [61,173].

The purpose of this paper was to use a combination of hormonal data, behavioral observations, and known kinship and dominance hierarchy data to 1) describe the basic pattern of occurrence of infant handling in bonobos, and 2) to compare trends in the hormonal data and in the expression of infant handling behaviors to the predictions generated by the proposed functional hypotheses. We then used the trends identified to pinpoint which hypotheses are likely to yield fruitful results in areas of future research where direct measures of fitness (i.e. inter-birth intervals, number of surviving offspring, etc.) are available to more fully test these hypotheses.

1.4. Predictions

The **Kin Selection** hypothesis assumes that infant handling behaviors provide a net positive fitness benefit for mothers, infants, and/or handlers. If kin selection affects the expression of infant handling in bonobos, we expected that: 1) positive handling behaviors would occur significantly more frequently than negative behaviors; 2) individuals would handle related infants significantly more frequently than unrelated infants; and 3) although oxytocin is known to mediate kin-based care-giving behaviors between mothers and infants, we expected that oxytocin would not show a relationship to handling behaviors because handlers are, by definition, individuals other than the mother.

The **Reproductive Competition** hypothesis assumes that infant handling reduces the reproductive success of females not related to the handler by negatively impacting the survival of the infants. If handling functions as a competitive behavior among female bonobos, we expected that: 1) negative handling behaviors would occur significantly more frequently than positive behaviors; 2) individuals would direct handling behaviors toward unrelated infants significantly more frequently than related infants; 3) females would handle infants significantly more frequently than males; 4) adult females would handle significantly more frequently than adolescent or juvenile females; 5) because lower ranking individuals have less social power than higher ranking individuals, we expected that infants of lower-ranking females would be handled significantly more frequently than higher-ranking female; and 6) because oxytocin mediates the formation of social bonds through affiliative behaviors, we expected that oxytocin would show either no relationship or a negative relationship to handling behaviors among parous females.

The **By-Product** hypothesis does not ascribe any adaptive value to infant handling and assumes the behavior is a consequence of prosociality and the processes responsible for the onset of maternal behavior in females. If these processes function to prime female bonobos to be attracted to and respond to infants in a manner that simulates maternal behavior, we expected that: 1) positive handling behaviors would occur significantly more frequently than negative behaviors and 2) females would handle significantly more frequently than males. Furthermore, an alternate **By-Product** hypothesis suggests that because previous

experience and the hormones circulating during pregnancy prime maternal brains (e.g. [83]), we expected that: 3) parous females would handle more frequently than nulliparous and immature females and 4) because oxytocin mediates maternal behaviors, we expected that oxytocin levels would be positively related to handling behaviors in parous females and not in any other age-sex class.

The **Biological Market** model assumes that infant handling is a commodity that individuals perform in exchange for other social commodities, including reciprocal handling (**Reciprocity** hypothesis) and coalitionary support during conflict (**Alliance Formation** hypothesis). If infant handling is a commodity shared between female bonobos with infants, we expected that: 1) positive handling behaviors would occur significantly more frequently than negative behaviors; 2) parous females would perform handling behaviors significantly more frequently than other age-sex categories and would exchange the service of handling each other's infants; and 3) because reciprocity implies an equitable exchange and females would therefore be expected to provide similar maternal behaviors to both their own offspring as well as the offspring of reciprocity partners, we expected that oxytocin would be positively related to handling in adult females with infants, but not other age-sex classes. If infant handling is a commodity exchanged for support during conflicts in bonobos, we expected that: 1) the infants of higher-ranking females would be handled significantly more frequently than lower-ranking females; 2) handling behaviors would be positively correlated with agonistic support from mothers not related to the handler during conflicts involving the handler; and 3) although oxytocin may potentially mediate alliance formation indirectly through mechanisms of social bonding such as grooming between coalition partners, it is unlikely to mediate bonding through a third party (the infant being handled) and, therefore, we expected no relationship between oxytocin and handling behaviors.

The **Learning-to-Mother** hypothesis assumes the adaptive value of infant handling is increased survival rates of infants of females who gain knowledge of species-appropriate maternal behaviors through handling infants before their first parturition. If infant handling functions as a mechanism to provide nulliparous female bonobos the opportunity to learn species appropriate maternal behavior, then we expected that: 1) immature and nulliparous females would perform handling behaviors significantly more frequently than other age-sex categories; 2) positive handling behaviors would occur significantly more frequently than negative behaviors; and 3) in addition to facilitating maternal behaviors in parous females, if oxytocin also functions to facilitate the simulation of maternal behaviors within the context of learning species-appropriate behaviors, we expected that oxytocin would be positively related to handling behaviors in immature females and not in other age-sex categories.

2. Methods

2.1. 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) (Table 1). Daily observations usually began around 0730 h and ended between 1300 and 1700 h 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 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 × 45.7 m, 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 infants had abundant opportunity to interact with all individuals in the entire colony (see [13] for description).

Kin relationships were defined as those between related individuals and included mothers and offspring, fathers and offspring (determined by genetic testing conducted by CZA), and full and half (both paternal and maternal) siblings.

2.2. 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. [185]. For example, Thompson-Handler et al. [185] 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 to < 3 years; juvenile = 3 to < 8 years; adolescent I = 8 to < 10 years; adolescent II = 10 to < 13 years; and adult ≥13 years. These age classes vary slightly from what was reported for a wild population of bonobos (see [56,72]), where infants are sometimes categorized as individuals 0 to < 4 or < 5, and may reflect the accelerated development that can occur in captivity. Additionally, adolescents were split into two developmental categories: 1) adolescent II, where female anogenital 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 [186,151]. 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 1). 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 [72,104,171], 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 1).

2.3. Behavioral observations

Data were collected using all occurrence sampling of infant handling and agonistic events [1]. Infant handling was defined as any affiliative or agonistic interaction between a group member and an infant including cradling/holding, carrying, grooming, and aggressive behaviors such as pulling, hitting, kicking, biting, etc. 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 with infants occurring solely within the contexts of play and/or conflicts involving other group members were also excluded. For example, during conflicts

Table 1
Group composition and rank and age class assignments of the CZA bonobo colony (2011–2015).

Subject	Sex	Birth year	Rank	Age class				
				2011	2012	2013	2014	2015
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 I	*	*	*
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

* Indicates individual transferred to another zoo.
** Indicates individual not yet transferred in to CZA.

involving mothers of infants, opponents would sometimes grab and pull the infant while the infant was clinging to the mother and was not scored as infant handling.

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 min. We chose this time frame because there were often indications that the bout was not fully terminated 30–90 s after handling behaviors ceased (e.g. such as the handler following, watching, and/or attempting to retrieve the infant, and then resuming handling behaviors). We, therefore, conservatively assigned the time of 2 min in order to account for this ambiguity that frequently existed within the shorter time interval.

2.4. Urine analyses

2.4.1. 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) and were sampled randomly throughout the day. Some samples were serendipitously collected after a handling bout but not all of them (individuals were never removed from their sub-group specifically for the purpose of collecting urine). Samples were then immediately frozen and stored at −20 °C until they were packed on dry ice and shipped overnight to the Global Health Biomarker Lab at the University of Oregon in Eugene, OR where they were stored at −80 °C until time of analyses.

2.4.2. 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 [187] 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.

2.4.3. 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. [17] in the Smithsonian's Conservation and Research Center Endocrine Workbook (ppg. 21–24). 100 μl 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.) ([17], pg. 21). The displacement curve generated by these serial dilution concentrations was then compared to the standard curve by calculating the difference between the slope of the line produced by a linear regression of the serial dilution curve ($y = -0.069x + 92.58$) and the slope of the line produced by a linear regression of the standard curve ($y = -0.054x + 71.55$). No significant difference was found between the two slopes ($t = 0.0008$, df = 8, $p = .9994$), indicating that the analyte measured in bonobo urine demonstrates immunoactivity of the endogenous antigen in parallel to what was observed in the standard solution provided by the kit manufacturer.

2.4.4. 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 μl 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 μl 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 [17] 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.

2.5. Data analyses

2.5.1. Analyses of variance and frequency

All data from each year of the study period (2011–2015) were pooled unless explicitly stated otherwise. To investigate differences in types of handling behavior, we compared the total number of positive and negative handling behaviors using a one-way ANOVA in R (version 3.3.1)[122].

To test for effects of kinship on handling behaviors, we determined whether a preference for handling related infants over unrelated infants existed among handlers. The frequency of observed infant handling bouts comprised of related dyads (e.g. a juvenile handling an infant sibling) and unrelated dyads (e.g. a juvenile handling an unrelated infant) were compared to corresponding expected frequencies based on all possible related and unrelated dyads using *G* Tests of Goodness of Fit with Williams correction applied in BIOMstat (version 3.30 t). However, because proportions of related and unrelated dyads changed from year to year over the course of the study, as some infants changed age-classes and became juveniles and new infants were born into the study group (see Table 1), these data were not pooled and frequency analyses were conducted for each study year to account for the existing differences in availability of related infants across handlers during the entire study period.

We conducted a two-way ANOVA to investigate the effects of age and sex on handling rate. To account for changes in group composition over the course of the study (e.g. three adolescent females transferred to new zoos and a new adolescent female from another zoo was brought into the group, see Table 1) as well as differences in number of hours of observation, handling data for each individual for each year were first calculated as rates using the following equation:

$$\frac{\text{handling bouts/number of available infants}}{\text{hours of observation}} = \text{handling rate }(r)$$

This rate was then used as the unit of analysis. A Shapiro-Wilk normality test revealed the handling rate data were non-normally distributed and were therefore ln-transformed. We tested for the fixed effects of age and sex, as well as an interaction between age and sex, using R (version 3.3.1, 2015). Post-hoc planned comparisons were used to investigate significant differences in handling rates across age classes within sex using the R package 'lsmeans' [85]. These data were visualized using the package 'ggpubr' [74].

To determine if individuals were preferentially handling the infants of high or low ranking mothers, we compared frequency rates of handling across all infants using *G* Tests of Goodness of Fit with Williams correction applied in BIOMstat (version 3.30t). Because number of hours of observation differed between study years, the total amount each infant was handled was divided by the number of observation hours for each infant to obtain a rate of handling for each infant. Assuming an equal likelihood of being handled, expected frequency ratios were then entered as 1:1:1:1 [144].

2.5.2. 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, 2015).

Linearity in the dominance rank of adults was found to be complete and significant (Landau's *h* = 0.476, *p* < .01) and adults were ordered into a linear dominance hierarchy and assigned a unique rank number where 1 represents the highest-ranking individual (Table 1). 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 [188,152,160] only counts of coalitionary support that were performed by females (with infants) unrelated to the handler were included in the analyses.

2.5.3. Oxytocin

In order to identify a potential relationship between oxytocin and infant handling, baseline oxytocin values were established first for each individual and then compared to mean oxytocin values from samples collected after infant handling bouts. Although the exact temporal connection between central oxytocin, where neuromodulation occurs, and peripheral oxytocin, measured as urinary levels, remains somewhat unclear [22], experimental studies have demonstrated that the clearance rate for oxytocin is between 30 and 60 min [4] and that neuropeptide hormones can pool in urine within an hour [124]. We therefore averaged the oxytocin values from samples that were collected within one hour of no occurrences of grooming, sexual, or handling behaviors observed in the target individual to establish baseline values. We then averaged the oxytocin values from samples that were collected within one hour of at least one infant handling bout and no occurrences of additional grooming or sexual behavior in the target individual and compared these values to the corresponding baseline values in each target individual using descriptive statistics.

3. Results

3.1. 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 predicted that positive handling behaviors would occur significantly more frequently than negative handling behaviors, while the **Reproductive Competition** hypothesis predicted that negative handling behaviors would 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 (F = 8.71, df = 1, *p* < .05).
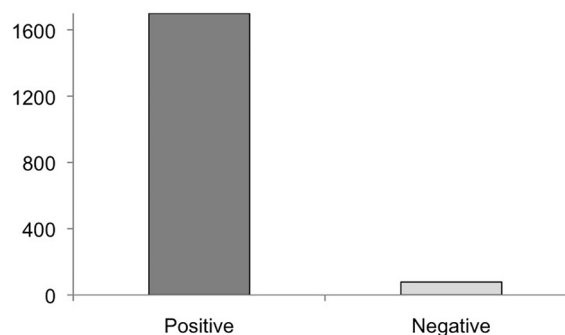

Fig. 1. Frequency distribution of type of infant handling behavior.

3.2. Kin bias

The **Kin Selection** and **Reproductive Competition** hypotheses generated contrasting predictions regarding kin bias in handling frequency. The **Kin Selection** hypothesis predicted that infant handling dyads between related individuals would occur significantly more frequently than between unrelated individuals and the **Reproduction Competition** hypothesis predicted that infant handling dyads between unrelated individuals would occur more frequently than between related individuals. As stated above, because proportions of related and unrelated dyads changed from year to year over the course of the study (see Table 1), these data were not pooled and frequency analyses were conducted for each study year to account for the existing differences in availability of related infants across handlers during the entire study period. We found that for three of the study years infant handling dyads between related individuals occurred significantly more frequently than expected and less frequently than expected between unrelated individuals (2011: G = 19.72, df = 1, $p < .01$; 2012: G = 222.54, df = 1, $p < .01$; 2014: G = 31.86, df = 1, $p < .01$). Infant handling dyads between unrelated individuals occurred significantly more frequently than expected and less frequently than expected between related individuals for the 2013 study period (G = 15.38, df = 1, $p < .01$). There was no significant difference in expected frequencies of related and unrelated dyads for the 2015 study period (G = 0.234, df = 1, $p = .314$).

3.3. Age-sex class distribution among handlers

All non-infant individuals were observed handling infants over the course of the entire study period. The **Reproductive Competition** and **By-Product** hypotheses predicted that females would handle significantly more frequently than would males and, alternatively, that parous females would handle infants significantly more frequently than would immature and/or nulliparous females. The results of the two-way ANOVA testing the effects of age and sex on handling showed that while there was no significant difference in handling between males and females (F = 0.443, df = 1, $p = .509$), there was a significant difference in handling across age categories (F = 41.465, df = 2, $p < .001$) and a significant interaction between age and sex categories (F = 38.835, df = 2, $p < .001$). Post-hoc planned comparisons showed that adult females handled significantly less frequently than both juvenile (df = 54, $p < .001$) and adolescent (df = 54, $p < .001$) females (Fig. 2).

The **Reciprocity** hypothesis predicted that parous females would handle infants significantly more frequently than other age-sex categories of handlers. There were no observations of reciprocal infant handling among adult females and, as stated above, adult females did
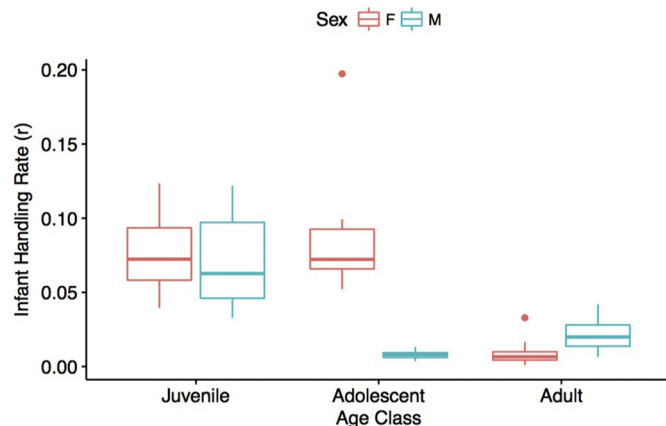
not handle infants significantly more frequently than any other age class (Fig. 2). The **Learning-to-Mother** hypothesis predicted that immature and nulliparous females would handle significantly more frequently than other age-sex categories of handlers and, as stated above, we found that juvenile and adolescent females handled infants significantly more frequently than adult females and more frequently than adult males (Fig. 2). We also found that, although mean adolescent female handling rate ($r = 0.0928$) was much higher than the mean adolescent male handling rate ($N = 2$, $r = 0.0080$), mean handling rates were similar for juvenile females ($N = 3$, $r = 0.0770$) and juvenile males ($N = 2$, $r = 0.0714$) (Fig. 2).

3.4. Rank effects and coalitionary support

All infants in this study were observed being handled and no significant difference in handling frequency was found among the infants (G = 0.12, df = 3, $p = .500$), indicating that neither the infants of high-ranking females nor the infants of low-ranking females were preferentially handled. 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 predicted that infants of lower ranking females would be handled significantly more frequently than the infants of higher ranking females and the **Alliance Formation** hypothesis predicted the opposite, where infants of higher ranking females would 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 ($p = .0824$, df = 2, $R^2 = 0.696$; Fig. 3).

The **Alliance Formation** hypothesis also predicted that individuals would 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 ($p < .05$, df = 26, $R^2 = 0.128$; Fig. 4).

3.5. Oxytocin

401 urine samples were collected from 18 individuals (mean number of samples per individual = 22.27; range = 13–40) during each year in the study period with the exception of 2011. Of the 401 urine samples assayed for oxytocin, 161 were collected from targets within one hour of no observations of grooming, sexual, or handling behavior and 79 samples were collected from targets within one hour of handling without observation of grooming or sexual behavior. The **Reproductive Competition** hypothesis predicted that oxytocin values measured after handling would not differ from baseline levels or would be lower than baseline levels and the **Kin Selection** and **Alliance**
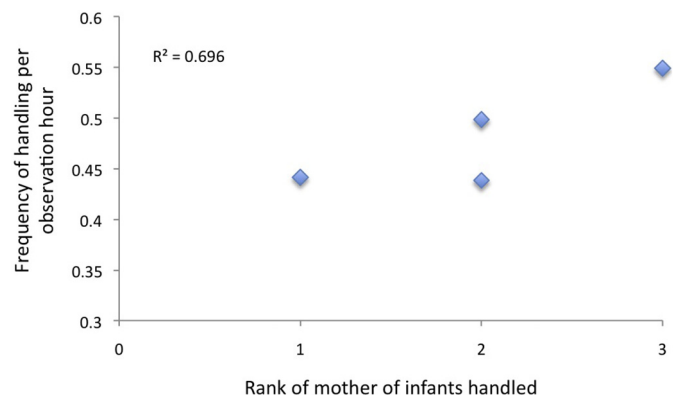

Fig. 2. Frequency distribution of handling behaviors across age-sex classes.

Fig. 3. Frequency distribution of handling behaviors received for each infant by rank of mother.
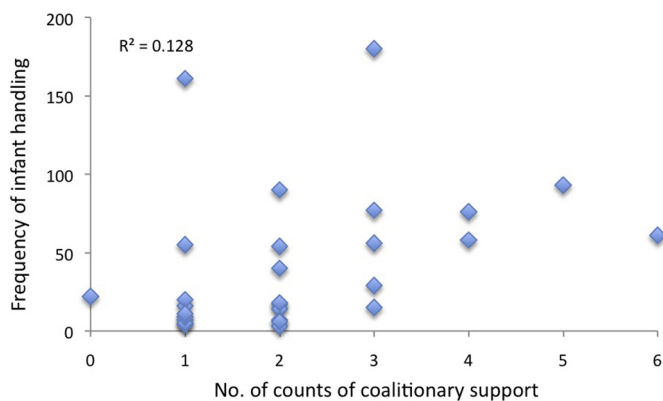
Fig. 4. Frequency distribution of handling behaviors performed by amount of coalitionary support received from unrelated mothers of infants.

Formation hypotheses also predicted that oxytocin values measured after handling would not differ from baseline levels. We found that mean post-handling oxytocin levels were slightly higher than mean oxytocin baseline levels across all handlers ($N = 18$, post handling mean = 1319.95 pg mg^{-1} creatinine, SD = 195.21 pg mg^{-1} creatinine; baseline mean = 1177.93 pg mg^{-1} creatinine, SD = 389.98 pg mg^{-1} creatinine). The *By-Product* hypothesis predicted that oxytocin values measured after handling would be higher than baseline levels in parous females and would not differ from baseline levels in any other age-sex class; the *Reciprocity* hypothesis predicted that post handling oxytocin values would be higher than baseline values in adult females with infants; and the *Learning-to-Mother* hypothesis predicted that post handling oxytocin values would be higher than baseline values in immature females but would not differ from baseline levels in other age-sex classes. We found that mean post-handling oxytocin levels were higher than mean oxytocin baseline levels in both adolescent and juvenile females, and were lower than baseline levels in all other age-sex categories with the greatest degree of negative change in adult females (Fig. 5).

4. Discussion

The purpose of this paper was to describe the basic pattern of occurrence of infant handling in bonobos and to compare trends in the hormonal data and in the expression of these behaviors to predictions generated by the proposed functional hypotheses. It is important to note that the variables used in this study were primarily descriptive in

nature and that the results presented here should be considered exploratory. Despite the limitations associated with these descriptive measures (discussed above), our data were useful in pinpointing the functional hypotheses that should be further investigated using direct measures of fitness such as inter-birth intervals and differential survival rates in infants.

Although reports of infant handling in wild bonobos are scarce [72,101], the handling of infants was a common phenomenon in this captive group. Over the course of five study years (2011–2015) we observed 1778 handling bouts between infants and group members other than the mother, occurring at a rate of about two every three hours. Our finding that infant handling may occur frequently in some populations and not in others is somewhat similar to the reported variation of infant handling in wild chimpanzees. While rare in some populations (e.g. Gombe: [51,162]), infant handling occurs more often in others (e.g. Mahale: [104]; and Ngogo: [7]). At Ngogo, some infants may be handled frequently enough to reduce lactational effort in mothers, allowing them to accelerate the weaning process for their offspring [7]. The unusual demographic features of the Ngogo community, namely that females do not always transfer out of their natal group [166,167], and the relatively high abundance of food and relatively low seasonal variance in food availability [118,119] result in lower feeding competition and higher presence of maternal kin. Badescu et al. [7] hypothesize that these ecological and demographic features facilitate infant handling behaviors through lowered female reproductive competition and reduced likelihood of aggression directed at infants. Relaxed feeding competition and increased presence of maternal kin are also features characteristic of our study population and may help explain the high frequency of occurrence of infant handling in the CZA bonobos.

At Mahale, mothers preferentially select kin over non-kin to handle their infants and the adaptive value of infant handling may be tied, at least partially, to mechanisms of kin selection whereby handlers increase their indirect fitness by handling related infants [104]. As discussed in the introduction, mechanisms of kin selection to explain the adaptive value of infant handling have primarily been invoked in species that practice cooperative or communal breeding [15,30], but there are examples of kin bias in other primate species (e.g. cercopithecines [110]). The *Kin Selection* hypothesis [55,63] suggests that handling provides direct and/or indirect fitness gains to the mother and/or handler. Mothers benefit from increased feeding time and net energy gains, which in turn improve maternal milk quality, increasing infant growth rates and shortening weaning times, which may decrease inter-birth intervals, improving reproductive success. Handlers benefit their
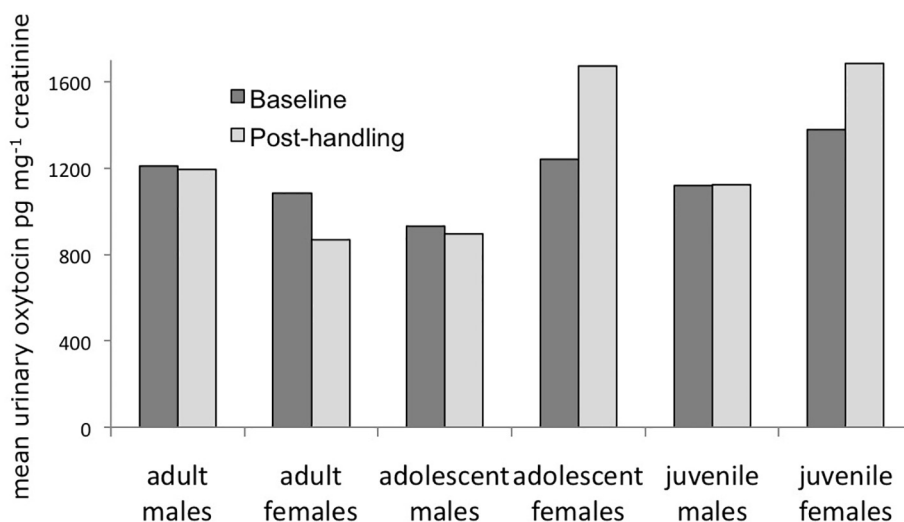

Fig. 5. Baseline and post-handling urinary oxytocin levels across age-sex classes.

own indirect fitness through improved reproductive success of related mothers and/or infants. There is considerable evidence that humans practice extensive allocare among kin (see [78]) but direct measures of the degree to which infant handling may provide fitness gains in other great ape species is largely unknown. In this study population, all group members interacted regularly with all of the infants but handlers exhibited a significant bias toward related infants during some of the study periods. Post-handling oxytocin values were not expected to differ from baseline levels and while our data showed that post-handling levels were slightly higher than baseline levels, this trend is most likely being driven by high post-handling levels in nulliparous and immature females, who frequently handled related infants. These data suggest that mechanisms of kin selection may be at work in bonobos and future studies on the adaptive value of infant handling should focus on the relationship between handling, weaning time, inter-birth intervals, and the differential survival rates of infants who are handled by kin and those handled by non-kin.

The **Reproductive Competition** hypothesis [47,62,91,139,169,170] 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. Our data showed 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 although post-handling oxytocin levels were slightly lower than baseline levels in parous females, which support the **Reproductive Competition** hypothesis, aggressive behaviors directed toward infants in the context of handling were infrequent and usually mild (i.e. pulling on the infant). Silk [138] 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 [14] 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 [138] 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. Furthermore, while the trends in our results can not directly reject the **Reproductive Competition** hypothesis, the relatively high abundance and low seasonal variation in food availability characteristic of bonobo habitats [21,172,173,175] also suggest that feeding competition may not be a strong selective force influencing the frequency of negative handling behaviors and future studies that investigate alternate functional hypotheses may yield more fruitful results.

The **Reciprocity** hypothesis [62,147] 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 or that post-handling oxytocin levels would be higher than baseline levels in these females. These results are interesting given the strong natal attraction and frequency of handling among the immature female bonobos in our study group but should be interpreted with care due to our small sample size. Future studies on a larger population with multiple parous females with and without infants and measurements of differential survival rates and weaning times of infants and frequency of reciprocal handling would more adequately address this question. 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 [91]. 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 [21,93,172,173,175,176]. Although bonobos, including those in this study population, form linear dominance hierarchies ([149]; this population: [14]), females exhibit intrasexual social tolerance within the context of feeding [188]. Future studies should address whether measures of social tolerance (i.e. proximity during feeding) and relaxed feeding competition (i.e. food abundance and seasonal availability) are related to frequency of infant handling in bonobos and whether they influence any differential expression of handling frequency in parous females and other age-sex categories.

The **Alliance Formation** hypothesis also describes infant handling as a social commodity, namely a service that can be exchanged for coalitionary support during conflicts. The trends in our data offer mixed support for this hypothesis. 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 [164] and in wild populations, female coalitions also function to maintain dominance over males [160,174]. 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 [160]. While the results presented in this paper may provide potential insight into these observations, further studies are needed to tease apart the contribution of other measures of affiliation (i.e. grooming and sociosexual behavior) between handlers and mothers to isolate the connection between infant handling and the observed patterning of coalitionary support.

The **By-Product** hypothesis posits that infant handling has no inherent adaptive value but is instead the result of selection for infant responsiveness because females who respond promptly and frequently to infant signals should make good mothers [120,135]. The predictions generated from this hypothesis overlap with predictions generated from the other hypotheses explored in this paper where our results supported the prediction that positive handling behaviors should occur more frequently than negative handling behaviors but did not support the prediction that females should handle infants more frequently than males. Furthermore, the alternate **By-Product** hypothesis predicted that

parous females would be more attracted to and motivated to handle infants than immature and nulliparous females as a result of the priming effect of hormones on maternal brains (e.g. [83]). Post-handling oxytocin levels were expected to be higher than baseline levels in parous females and our data did not show this trend. Although our data did not support either prediction, it would be interesting to explore the connection between parity, measures of infant responsiveness, and infant survival, as well as the relationship between parity and proclivity to handle the infants of other females to establish the adaptive value of responsiveness to infants in bonobos and whether infant handling may be a by-product of this reproductive consequence. In addition, while experimental studies delineating the neuromodulaory effects of oxytocin on maternal behaviors may be prohibitively difficult and ethically questionable, more studies using non-invasive techniques are needed to differentiate the types of behaviors (i.e. maternal, sexual, affiliative, etc.) connected to the endogenous oxytocin system.

The trends in our data also provided some 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. Primate infants, particularly among the great ape species, take a long time to develop and reach maturity (see [82,151]). 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 [161]. In spite of the observation of widespread natal attraction across primate species, as well as the apparent adaptive value that infant handling can afford to nulliparous females, there is relatively little actual support for the **Learning-to-Mother** hypothesis in the form of direct measures of fitness variables such as inter-birth intervals and infant survival rates. For example, through the use of longitudinal data on a captive group of vervet monkeys, [32] was able to demonstrate a connection between allocare and reduced inter-birth intervals in the mothers and increased survival in first live-born among handlers providing allocare. What many studies have been able to show, however, are that mechanisms of **Learning-to-Mother** may be at play through descriptive accounts of the expression of handling behaviors and the patterning of handling behavior across age-sex classes. For example, at Mahale, nulliparous adolescent females are the most frequent handlers, although adult males also show interest in handling infants, albeit to a lesser degree [104]. 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 as immature males were also frequently observed handling infants (Fig. 2). Our data support the prediction that post-handing oxytocin levels should be higher than baseline levels in nulliparous and immature females and not in other age-sex categories. While this result highlights an intriguing area of potential research, more studies differentiating between types of behaviors and their relationship to oxytocin are needed in bonobos. For example, oxytocin is thought to facilitate the formation of social bonds among non-kin in chimpanzees [25] and it is possible that infant handling, particularly among non-kin individuals, represents a type of social bonding behavior. Our result showing that post-handling levels are only elevated in nulliparous and immature females, however, suggested to us that infant handling alone may not be functioning as mechanism of social bonding in bonobos. It is interesting, however, to consider the role interactions with infants may play in influencing social relationships in bonobo society. Females often occupy powerful positions in the group hierarchy and the infants of high-ranking females in particular may represent a type of social passport that provides less socially well-connected or peripheral group members the opportunity to form social bonds and coalitionary alliances with these females.

In conclusion, the trends in our data showed that infant handling is a frequently expressed behavior performed mostly by nulliparous and immature females in this study population. The exploratory data

presented here offer support for some of the predictions outlined in the introduction, namely those generated by the **Kin Selection**, **Alliance Formation**, and **Learning-to-Mother** hypotheses and provide direction for future studies. While long-term studies incorporating direct measures of fitness are necessary to confirm the assumptions of most of the functional hypotheses, molecular techniques such as the fecal stable isotope data from field studies at Ngogo [7] as well as the incorporation of hormonal measures such as the oxytocin data presented in this study can help refine our understanding of the physiological and behavioral pathways through which the adaptive value of infant handling is expressed. The data presented here also offer further insight into the complex social dynamics of bonobos and can inform our understanding of the behavioral repertoire that may have been present in the last common ancestor. Relative to the other extant great ape species, modern humans exhibit markedly increased levels of allocare behaviors that are part of a suite of adaptations that reduce the energetic demands of care-giving and contribute to our relatively low inter-birth intervals. While the adaptive value of infant handling in non-human primates is continuing to be investigated through the testing of functional hypotheses, data demonstrating the capacity for these behaviors are an important tool for understanding the evolution of mechanisms that contribute to reproductive success in humans and our hominid ancestors.

Ethical note

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study protocol was approved by the University of Oregon Institutional Animal Care and Use Committee (IACUC). All data were collected using observations of spontaneous behavior at the Columbus Zoo and Aquarium (CZA), an Association of Zoos and Aquariums (AZA) accredited and United States Department of Agriculture (USDA) regulated institution in Columbus, Ohio, USA. CZA adheres to the welfare and husbandry standards outlined by the AZA and USDA.

References

[1] J. Altmann, Observational study of behavior: sampling methods, Behaviour 49 (3) (1974) 227–266.
[2] J. Altmann, Baboon Mothers and Infants, The University of Chicago Press, Chicago, 1980.
[3] J. Altman, S.C. Alberts, Growth rates in a wild primate population: ecological influences and maternal effects, Behav. Ecol. Sociobiol. 57 (2005) 490–501.
[4] J.A. Amico, J.S. Ulbrecht, A.G. Robinson, Clearance studies of oxytocin in humans using radioimmunoassay measurements of the hormone in plasma and urine, J. Clin. Endocrinol. Metab. 64 (1987) 340–345.
[5] D.P. Anderson, E.V. Nordheim, C. Boesch, T.C. Moermond, Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire, in: C. Boesch, G. Hohmann, L. Marchant (Eds.), Behavioural Diversity in Chimpanzees and Bonobos, Cambridge University Press, Cambridge, 2002, pp. 90–101.
[6] I. Bădescu, P. Sicotte, N. Ting, E.C. Wikberg, Female parity, maternal kinship,

infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*), Am. J. Primatol. 77 (4) (2015) 376–387.

[7] I. Bădescu, D.P. Watts, M.A. Katzenberg, D.W. Sellen, Alloparenting is associated with reduced maternal lactation effort and faster weaning in wild chimpanzees, R. Soc. Open Sci. 3 (11) (2016) 160577.

[8] L. Barrett, S.P. Henzi, Monkeys, markets and minds: biological markets and primate sociality, in: P.M. Kappeler, C.P. van Schaik (Eds.), Cooperation in Primates and Humans: Mechanisms and Evolution, Springer, Berlin, 2006, pp. 209–232.

[9] E.E. Benarroch, Oxytocin and vasopressin: social neuropeptides with complex neuromodulatory functions, Neurology 80 (2013) 1521–1528.

[10] B.H. Blersch, C.R. Schmidt, Adoption of an additional infant by a western lowland gorilla (*Gorilla gorilla gorilla*), Folia Primatol. 58 (4) (1992) 190–196.

[11] C. Boesch, H. Boesch-Achermann, The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution, Oxford University Press, USA, 2000.

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

[13] K.J. Boose, F.J. White, A. Meinelt, Sex differences in tool use acquisition in bonobos (*Pan paniscus*), Am. J. Primatol. 75 (9) (2013) 917–926.

[14] K.J. Boose, F.J. White, Harassment of adults by immatures in bonobos (*Pan paniscus*): testing the exploratory aggression and rank improvement hypotheses, Primates 58 (4) (2017) 493–504.

[15] A.F. Bourke, N.R. Franks, Social Evolution in Ants, Princeton University Press, 1995.

[16] L.J. Brent, J.A. Teichroeb, P. Sicotte, Preliminary assessment of natal attraction and infant handling in wild *Colobus vellerosus*, Am. J. Primatol. 70 (1) (2008) 101–105.

[17] J. Brown, S. Walker, K. Steinman, 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, 2004, pp. 1–93.

[18] C. Busse, W.J. Hamilton, Infant carrying by male chacma baboons, Science 212 (4500) (1981) 1281–1283.

[19] N.G. Caine, G.D. Mitchell, Species differences in the interest shown in infants by juvenile female macaques (*Macaca mulatta* and *Macaca radiata*), Int. J. Primatol. 1 (1980) 323–332.

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

[21] C.A. Chapman, F.J. White, R.W. Wrangham, Party size in chimpanzees and bonobos, in: R.W. Wrangham, W.C. McGrew, F.B.M. de Waal, P.G. Heltne (Eds.), Chimpanzee Cultures, Harvard University Press, Cambridge, MA, 1994, pp. 41–58.

[22] P.S. Churchland, P. Winkielman, Modulating social behavior with oxytocin: how does it work? What does it mean? Horm. Behav. 61 (3) (2012) 392–399.

[23] M.R. Clarke, Social interactions of juvenile female bonnet monkeys, *Macaca radiata*, Primates 19 (3) (1978) 517–524.

[24] M.R. Clarke, K.E. Glander, E.L. Zucker, Infant–nonmother interactions of free-ranging mantled howling monkeys (*Alouatta palliata*) in Costa Rica, Int. J. Primatol. 19 (3) (1998) 451–472.

[25] C. Crockford, R.M. Wittig, K. Langergraber, T.E. Ziegler, K. Zuberbühler, T. Deschner, Urinary oxytocin and social bonding in related and unrelated wild chimpanzees, Proc. R. Soc. B 280 (1755) (2013) 20122765.

[26] F.B.M. de Waal, Do rhesus mothers suggest friends to their offspring? Primates 31 (4) (1990) 597–600.

[27] P. Dolhinow, G. Murphy, Langur monkey (*Presbytis entellus*) development: the first 3 months of life, Folia Primatol. 39 (3–4) (1982) 305–331.

[28] H.L. Dugdale, S.A. Ellwood, D.W. MacDonald, Alloparental behaviour and long-term costs of mothers tolerating other members of the group in a plurally breeding mammal, Anim. Behav. 80 (4) (2010) 721–735.

[29] M. Eberle, P.M. Kappeler, Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*), Behav. Ecol. Sociobiol. 60 (4) (2006) 582–588.

[30] S.T. Emlen, Evolution of Cooperative Breeding in Birds and Mammals, in: J.R. Krebs, N.B. Davies (Eds.), Behavioural Ecology: An Evolutionary Approach, 3rd edition, Blackwell, Oxford, 1991, pp. 301–337.

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

[32] L.A. Fairbanks, Reciprocal benefits of allomothering for female vervet monkeys, Anim. Behav. 40 (3) (1990) 553–562.

[34] R. Feldman, Oxytocin and social affiliation in humans, Horm. Behav. 61 (3) (2012) 380–391.

[35] R. Feldman, A. Wller, O. Zagoory-Sharon, A. Levine, Evidence for a neuroendocrinological foundation of human affiliation: plasma oxytocin levels across pregnancy and the postpartum period predict mother–infant bonding, Psychol. Sci. 18 (11) (2007) 965–970.

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

[37] R. Feldman, I. Gordon, O. Zagoory-Sharon, Maternal and paternal plasma, salivary, and urinary oxytocin and parent–infant synchrony: considering stress and affiliation components of human bonding, Dev. Sci. 14 (4) (2011) 752–761.

[38] E. Fernandez-Duque, C.R. Valeggia, S.P. Mendoza, The biology of paternal care in human and non-human primates, Annu. Rev. Anthropol. 38 (2009) 115–130.

[40] S. Förster, M. Cords, Socialization of infant blue monkeys (*Cercopithecus mitis*

stuhlmanni): allomaternal interactions and sex differences, Behaviour 142 (7) (2005) 869–896.

[41] D.D. Francis, F.C. Champagne, M.J. Meaney, Variations in maternal behaviour are associated with differences in oxytocin receptor levels in the rat, J. Neuroendocrinol. 12 (12) (2000) 1145–1148.

[42] C. Fruteau, E. van de Waal, E. van Damme, R. Noë, Infant access and handling in sooty mangabeys and vervet monkeys, Anim. Behav. 81 (1) (2011) 153–161.

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

[44] T. Furuichi, Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba, Int. J. Primatol. 18 (6) (1997) 855–875.

[45] U. Gerloff, B. Hartung, B. Fruth, G. Hohmann, D. Tautz, Intracommunity relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples, Proc. R. Soc. Lond. B Biol. Sci. 266 (1424) (1999) 1189–1195.

[46] A.J. Ginther, C.T. Snowdon, Expectant parents groom adult sons according to previous alloparenting in a biparental cooperatively breeding primate, Anim. Behav. 78 (2) (2009) 287–297.

[47] J.L. Gittleman, Functions of communal care in mammals, in: P.J. Gireenwood, P.H. Harvey, M. Slutkin (Eds.), Evolution: Essays in Honour of John Maynard Smith, Cambridge University Press, Cambridge, 1985, pp. 187–205.

[48] A. Goldizen, Tamarins and marmosets: communal care of offspring, in: B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, T. Struhsaker (Eds.), Primate Societies, University of Chicago Press, Chicago, 1987, pp. 34–43.

[50] L.G. Goldstone, V. Sommer, N. Nurmi, C. Stephens, B. Fruth, Food begging and sharing in wild bonobos (*Pan paniscus*): assessing relationship quality? Primates 57 (3) (2016) 1–10.

[51] J. Goodall, Through a Window: My Thirty Years with the Chimpanzees of Gombe, Houghton Mifflin Company, Boston, MA, 1990.

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

[53] I. Gordon, O. Zagoory-Sharon, J.F. Leckman, R. Feldman, Oxytocin and the development of parenting in humans, Biol. Psychiatry 68 (4) (2010) 377–382.

[54] I. Gordon, O. Zagoory-Sharon, J.F. Leckman, R. Feldman, Prolactin, oxytocin, and the development of paternal behavior across the first six months of fatherhood, Horm. Behav. 58 (3) (2010) 513–518.

[55] W.D. Hamilton, The genetic evolution of social behavior II, J. Theor. Biol. 7 (1) (1964) 1–52.

[56] C. Hashimoto, Context development of sexual behavior of wild bonobos (*Pan paniscus*) at Wamba, Zire, Int. J. Primatol. 18 (1) (1997) 1–21.

[57] S.P. Henzi, L. Barrett, Infants as a commodity in a baboon market, Anim. Behav. 63 (5) (2002) 915–921.

[58] K. Hinde, L.A. Milligan, Primate milk: proximate mechanisms and ultimate perspectives, Evol. Anthropol. 20 (1) (2011) 9–23.

[59] M. Hiraiwa, Maternal and alloparental care in a troop of free-ranging Japanese monkeys, Primates 22 (3) (1981) 309–329.

[60] C. Hobaiter, A.M. Schel, K. Langergraber, K. Zuberbühler, Adoption'by maternal siblings in wild chimpanzees, PLoS One 9 (8) (2014) e103777.

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

[62] S.B. Hrdy, Care and exploitation of nonhuman primate infants by conspecifics other than the mother, in: J.S. Rosenblatt, R.A. Hinde, E. Shaw, C. Beer (Eds.), Advances in the Study of Behavior, vol. 6, Academic Press, New York, 1976, pp. 101–158.

[63] S.B. Hrdy, Mothers and Others: The Evolutionary Origins of Mutual Understanding, The Belknap Press of Harvard University Press, Cambridge, MA, 2009.

[64] M.J. Hsu, K.I. Lin, J.F. Lin, T.J. Lin, G. Agoramoorthy, Non-maternal infant handling in wild formosan macaques of Mount Longevity, Taiwan, Folia Primatol. 86 (6) (2015) 491–505.

[65] E. Huchard, A. Alvergne, D. Fejan, L.A. Knapp, G. Cowlishaw, M. Raymond, More than friends? Behavioural and genetic aspects of heterosexual associations in wild chacma baboons, Behav. Ecol. Sociobiol. 64 (5) (2010) 769–781.

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

[67] T.R. Insel, T.J. Hulihan, A gender-specific mechanism for pair bonding: oxytocin and partner preference formation in monogamous voles, Behav. Neurosci. 109 (4) (1995) 782.

[68] T.R. Insel, J.T. Winslow, Central administration of oxytocin modulates the infant rats response to social isolation, Eur. J. Pharmacol. 203 (1) (1991) 149–152.

[69] T.R. Insel, Oxytocin – a neuropeptide for affiliation: evidence from behavioral, receptor autoradiographic, and comparative studies, Psychoneuroendocrinology 17 (1) (1992) 3–35.

[70] K. Isler, C. van Schaik, Allomaternal care, life history and brain size evolution in mammals, J. Hum. Evol. 63 (1) (2012) 52–63.

[71] P.C. Jay, Aspects of maternal behavior among langurs, Ann. N. Y. Acad. Sci. 102 (1) (1962) 468–476.

[72] T. Kano, The Last Ape: Pygmy Chimpanzee Behavior and Ecology, Stanford University Press, Stanford, 1992.

[73] E. Kapsalis, Matrilineal kinship and primate behavior, in: B. Chapais, C.M. Berman

(Eds.), Kinship and Behavior in Primates, Oxford University Press, New York, 2004, pp. 153–176.

[74] A. Kassambara, ggpubr: 'ggplo2' Based Publication Ready Plots. R package version 0.1.6, https://CRAN.R-project.org/package=ggpubr, (2017).

[75] K.M. Kendrick, E.B. Keverne, B.A. Baldwin, Intracerebroventricular oxytocin stimulates maternal behaviour in the sheep, Neuroendocrinology 46 (1) (1987) 56–61.

[76] S. Kim, P. Fonagy, O. Koos, K. Dorsett, L. Strathearn, Maternal oxytocin response predicts mother-to-infant gaze, Brain Res. 1580 (2014) 133–142.

[77] M. Kohda, Allomothering behaviour of new and old world monkeys, Primates 26 (1) (1985) 28–44.

[78] K.L. Kramer, Cooperative breeding and its significance to the demographic success of humans, Annu. Rev. Anthropol. 39 (417) (2010) 436.

[79] J.B. Lancaster, Play mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*), Folia Primatol. 15 (3–4) (1971) 161–182.

[80] P.C. Lee, Nutrition, fertility and maternal investment in primates, J. Zool. 213 (3) (1987) 409–422.

[81] P.C. Lee, The meaning of weaning: growth, lactation, and life history, Evol. Anthropol. 5 (3) (1996) 87–96.

[82] S.R. Leigh, G.E. Blomquist, Life history, in: C.J. Cambell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, R.M. Stumpf (Eds.), Primates in Perspective, 2nd edition, Oxford University Press, Oxford, 2011, pp. 418–428.

[83] G. Leng, S.L. Meddle, A.J. Douglas, Oxytocin and the maternal brain. Curr. Opin. Pharmacol, 8 (6) (2008) 731–734.

[84] A. Lemasson, R.A. Palombit, R. Jubin, Friendships between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments, Behav. Ecol. Sociobiol. 62 (6) (2008) 1027–1035.

[85] R.V. Lenth, Least-square means: the R package lsmeans, J. Stat. Softw. 69 (1) (2016) 1–33.

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

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

[88] M.M. Lim, L.J. Young, Neuropeptidergic regulation of affiliative behavior and social bonding in animals, Horm. Behav. 50 (4) (2006) 506–517.

[89] A. Lischke, C. Berger, K. Prehn, M. Heinrichs, S.C. Herpertz, G. Domes, Intranasal oxytocin enhances emotion recognition from dynamic facial expressions and leaves eye- gaze unaffected, Psychoneuroendocrinology 37 (4) (2012) 475–548.

[90] K.C. MacKinnon, Social beginnings: the tapestry of infant and adult interactions, in: C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder, R.M. Stumpf (Eds.), Primates in Perspective, Oxford University Press, New York, 2011, pp. 440–455.

[91] D. Maestripieri, Social structure, infant handling, and mothering styles in group-living Old World monkeys, Int. J. Primatol. 15 (4) (1994) 531–553.

[92] D. Maestripieri, C.L. Hoffman, G.M. Anderson, C.S. Carter, J.D. Higley, Mother–infant interactions in free-ranging rhesus macaques: relationships between physiological and behavioral variables, Physiol. Behav. 96 (4) (2009) 613–619.

[93] R.K. Malenky, R.W. Wrangham, A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda, Am. J. Primatol. 32 (1) (1994) 1–12.

[94] J.H. Manson, Infant handling in wild *Cebus capucinus*: testing bonds between females? Anim. Behav. 57 (4) (1997) 911–921.

[95] G.M. McCabe, L.M. Fedigan, Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica, Int. J. Primatol. 28 (4) (2007) 837–851.

[96] M.M. McCarthy, Oxytocin inhibits infanticide in female house mice (*Mus domesticus*), Horm. Behav. 24 (3) (1990) 365–375.

[97] M.M. McCarthy, J.E. Bare, F.S.V. vom Saal, Infanticide and parental behavior in wild female house mice: effects of ovariectomy, adrenalectomy and administration of oxytocin and prostaglandin F2α, Physiol. Behav. 36 (1) (1986) 17–23.

[98] J.J. McKenna, The evolution of allomothering behaviour among colobine monkeys: function and opportunism in evolution, Am. Anthropol. 81 (4) (1979) 818–840.

[99] M.J. Meaney, E. Lozos, J. Stewart, Infant carrying by nulliparous female vervet monkeys (*Cercopithecus aethiops*), J. Comp. Psychol. 104 (4) (1990) 377–381.

[100] A. Meyer-Lindenberg, G. Domes, P. Kirsch, M. Heinrichs, Oxytocin and vasopressin in the human brain: social neuropeptides for translational medicine, Nat. Rev. Neurosci. 12 (9) (2011) 524–538.

[101] J.C. Mitani, D. Watts, The evolution of non-maternal caretaking among anthropoid primates: do helpers help? Behav. Ecol. Sociobiol. 40 (4) (1997) 213–220.

[102] Y. Muroyama, Exchange of grooming for allomothering in female patas monkeys, Behaviour 128 (1) (1994) 103–129.

[103] N. Nicolson, Infants, mothers, and other females, in: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, W. Wrangham, T.T. Struhsaker (Eds.), Primate Societies, University of Chicago Press, Chicago, 1987, pp. 330–342.

[104] T. Nishida, The social group of wild chimpanzees in the Mahale Mountains, Primates 9 (3) (1968) 167–224.

[105] R. Noë, P. Hammerstein, Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating, Behav. Ecol. Sociobiol. 35 (1) (1994) 1–11.

[106] R. Noë, P. Hammerstein, Biological markets, Trends Ecol. Evol. 10 (1995) 336–339.

[107] T.G. O'Brien, J.G. Robinson, Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness, Behaviour 119 (1) (1991) 30–50.

[108] C. Packer, S. Lewis, A. Pusey, A comparative analysis of non-offspring nursing, Anim. Behav. 43 (2) (1992) 265–281.

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

[110] A. Paul, J. Kuester, Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses, Behav. Ecol. Sociobiol. 39 (2) (1996) 133–145.

[111] C.A. Pedersen, Oxytocin control of maternal behavior regulation by sex steroids and offspring stimuli, Ann. N. Y. Acad. Sci. 807 (1) (1997) 126–145.

[112] C.A. Pedersen, A.J. Prange, Induction of maternal behavior in virgin rats after intracerebroventricular administration of oxytocin, Proc. Natl. Acad. Sci. 76 (12) (1979) 6661–6665.

[113] C.A. Pedersen, Oxytocin regulation of maternal behavior: from rodents to humans, in: E. Choleris, D. Pfaff, M. Kavaliers (Eds.), Oxytocin, Vasopressin and Related Peptides in the Regulation of Behavior, Cambridge University Press, Cambridge, 2013, pp. 148–182.

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

[115] C.H. Phoenix, R.W. Goy, A.A. Gerall, W.C. Young, Organizing action of prenatally administered testosterone propionate on the tissues mediating mating behavior in the female Guinea pig, Endocrinology 65 (3) (1959) 369–382.

[116] F.E. Poirier, The Nilgiri langur (*Presbytis johnii*) mother-infant dyad, Primates 9 (1–2) (1968) 45–68.

[117] L.M. Porter, P.A. Garber, Social behavior of callimicos: mating strategies and infant care, in: S.M. Ford, L.M. Porter, L.C. Davis (Eds.), The Smallest Anthropoids, Springer, Boston, 2009, pp. 87–101.

[118] K.B. Potts, Nutritional ecology and reproductive output in female chimpanzees (*Pan troglodytes*): variation among and within populations, in: Clancy KBH, K. Hinde, J.N. Rutherford (Eds.), Building Babies: Primate Development in Proximate and Ultimate Perspective, Springer Science + Business Media, New York, 2013, pp. 83–100.

[119] K.B. Potts, E. Baken, S. Ortmann, D.P. Watts, R.W. Wrangham, Variability in population density is paralleled by large differences in foraging efficiency in chimpanzees (*Pan troglodytes*), Int. J. Primatol. 36 (6) (2015) 1101–1119.

[120] D. Quiatt, Aunts and mothers: adaptive implications of allomaternal behaviour of nonhuman primates, Am. Anthropol. 81 (2) (1979) 310–319.

[121] R.J. Quinlan, M.B. Quinlan, Human lactation, pair-bonds and alloparents: a cross-cultural analysis, Hum. Nat. 19 (1) (2008) 87–102.

[122] R Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, 2015.

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

[124] T.L. Reyes, A.M. Galinsky, J.N. Hoffmann, H.M. You, T.E. Ziegler, M.K. McClintock, Social peptides: measuring urinary oxytocin and vasopressin in a study of older adults at risk for dehydration, J. Gerontol. B Psychol. Sci. Soc. Sci. 69 (8) (2014) S229–S237.

[125] M.L. Riedman, The evolution of alloparental care and adoption in mammals and birds, Q. Rev. Biol. 57 (4) (1982) 405–435.

[126] S.M. Rodrigues, L.R. Saslow, N. Garcia, O.P. John, D. Keltner, Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans, Proc. Natl. Acad. Sci. 106 (50) (2009) 21437–21441.

[127] S. Rosenbaum, J.P. Hirwa, J.B. Silk, L. Vigilant, T.S. Stoinski, Male rank, not paternity, predicts male–immature relationships in mountain gorillas, *Gorilla beringei beringei*, Anim. Behav. 104 (2015) 13–24.

[128] S. Rosenbaum, J.B. Silk, T.S. Stoinski, Male–immature relationships in multi-male groups of mountain gorillas (*Gorilla beringei beringei*), Am. J. Primatol. 73 (4) (2011) 356–365.

[129] C. Ross, A. MacLarnon, The evolution of non-maternal care in anthropoid primates, a test of the hypotheses, Folia Primatol. 71 (1–2) (2000) 93–113.

[130] H.E. Ross, S.M. Freeman, L.L. Spiegel, X. Ren, E.F. Terwilliger, L.J. Young, Variation in oxytocin receptor density in the nucleus accumbens has differential effects on affiliative behaviors in monogamous and polygamous voles, J. Neurosci. 29 (5) (2009) 1312–1318.

[132] A.A. Salo, J.A. French, Early experience, reproductive success, and development of parental behavior in Mongolian gerbils, Anim. Behav. 38 (1989) 693–702.

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

[134] K.M. Schulz, H.A. Molenda-Figueira, C.L. Sisk, Back to the future: the organizational-activational hypothesis adapted to puberty and adolescence, Horm. Behav. 55 (5) (2009) 597–604.

[135] P.A. Scollay, P. DeBold, Allomothering in a captive colony of Hanuman langurs (*Presbytis entellus*), Ethol. Sociobiol. 1 (4) (1980) 291–299.

[136] J.B. Silk, S.C. Alberts, J. Altmann, Social bonds of female baboons enhance infant survival, Science 302 (5648) (2003) 1231–1234.

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

[138] J.B. Silk, Why are infants so attractive to others? The form and function of infant handling in bonnet macaques, Anim. Behav. 57 (1999) 1021–1032.

[139] J.B. Silk, Kidnapping and female competition in captive bonnet macaques,

Primates 21 (1) (1980) 100–110.

[141] M.F. Small, A comparison of mother and nonmother behaviour during the birth seasons in two species of captive macaques, Folia Primatol. 38 (1–2) (1982) 99–107.

[143] C.T. Snowdon, B.A. Pieper, C.Y. Boe, K.A. Cronin, A.V. Kurian, T.E. Ziegler, Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins, Horm. Behav. 58 (4) (2010) 614–618.

[144] R.R. Sokal, F.J. Rohlf, Descriptive Statistics. Biometry, the Principles and Practice of Statistics in Biological Research, 4th edition, Freeman and Co., New York, 2012.

[145] N.G. Solomon, J.A. French, Cooperative Breeding in Mammals, Cambridge University Press, Cambridge, 1997.

[146] V. Sommer, Infant mistreatment in langur monkeys: socio-biology tackled from the wrong end? in: A.E. Rasa, C. Vogel, E. Voland (Eds.), The Sociobiology of Sexual and Reproductive Strategies, Chapman & Hall, London, 1989, pp. 110–127.

[147] C.B. Stanford, Costs and benefits of allomothering in wild capped langurs (*Preshytis pileatta*), Behav. Ecol. Sociobiol. 30 (1) (1992) 29–34.

[148] C.B. Stanford, The capped langur in Bangladesh: behavioural ecology and re-productive tactics, Contributions to Primatology, Vol. 26 Karger Medical and Scientific Publishers, 1991.

[149] J.M. Stevens, H. Vervaecke, H. De Vries, L. van Elsacker, Sex differences in the steepness of dominance hierarchies in captive bonobo groups, Int. J. Primatol. 28 (6) (2007) 1417–1430.

[150] L. Strathearn, Maternal neglect: oxytocin, dopamine and the neurobiology of at-tachment, J. Neuroendocrinol. 23 (11) (2011) 1054–1065.

[151] R.M. Stumpf, Chimpanzees and Bonobos: inter- and intraspecies diversity, in: C.J. Campbell, A. Fuentes, K.C. MacKinnon, R.M. Stumpf, S.K. Bearder (Eds.), Primates in Perspective, 2nd edition, Oxford University Press, New York, 2011, pp. 340–356.

[152] M. Surbeck, G. Hohmann, Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*), Behav. Ecol. Sociobiol. 67 (11) (2013) 1767–1780.

[154] S.D. Tardif, R.L. Carson, B.L. Gangaware, Infant-care behavior of non-reproductive helpers in a communal-care primate, the cottontop tamarin (*Saguinus oedipus*), Ethology 92 (2) (1992) 155–167.

[155] S.D. Tardif, C.B. Richter, R.L. Carson, Effects of sibling rearing experience on fu-ture reproductive success in two species of Callitrichidae, Am. J. Primatol. 6 (4) (1984) 377–380.

[156] S.D. Tardiff, The bioenergetics of parental behavior and the evolution of allopar-ental care in marmosets and tamarins, in: N.G. Solomon, J.A. French (Eds.), Cooperative Breeding in Mammals, Cambridge University Press, Cambridge, UK, 1996, pp. 11–33.

[157] S. Tecot, A.L. Baden, Primate allomaternal care, in: R. Scott, S. Kosslyn (Eds.), Emerging Trends in the Social and Behavioural Sciences: An Interdisciplinary, Searchable, and Linkable Resource, Wiley & Sons, Hoboken, 2015, pp. 1–16.

[159] B. Tiddi, F. Aureli, G. Schino, Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market, Anim. Behav. 79 (5) (2010) 1115–1123.

[160] N. Tokuyama, T. Furuichi, Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba, Anim. Behav. 119 (2016) 27–35.

[161] R. Trivers, Parental Investment and Sexual Selection, Vol. 136 Biological Laboratories, Harvard University, Cambridge, MA, 1972.

[162] J. van Lawick-Goodall, My Friends the Wild Chimpanzees, National Geographic Society, Washington, DC, 1967.

[163] M.H. Van IJzendoorn, M.J. Bakermans-Kranenburg, 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 (3) (2012) 438–443.

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

[165] C. Vogel, Patterns of infant transfer within two groups of common langurs (*Presbytis entellus*) near Jodphur: testing hypotheses concerning the benefits and risks, in: M.L. Roonwal, S.M. Mohnot, N.S. Rathore (Eds.), Current Primate Researches. Jodphur, Jodphur University Press, 1984, pp. 361–379.

[166] M.L. Wakefield, Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda, Int. J. Primatol. 29 (4) (2008) 907–929.

[167] M.L. Wakefield, Social dynamics among females and their influence on social structure in an East African chimpanzee community, Anim. Behav. 85 (6) (2013) 1303–1313.

[169] S.K. Wasser, Reproductive competition and cooperation among female yellow baboons, in: S.K. Wasser (Ed.), Social Behavior of Female Vertebrates, Academic Press, New York, 1983, pp. 349–390.

[170] S.K. Wasser, D.P. Barash, The selfish 'allomother': a comment on Scollay and Debold, Ethol. Sociobiol. 2 (2) (1981) 91–93.

[171] F.J. White, Party composition and dynamics in *Pan paniscus*, Int. J. Primatol. 9 (3) (1988) 179–193.

[172] F.J. White, Comparative socio-ecology of *Pan paniscus*, in: W.C. McGrew, L.F. Marchant, T. Nishida (Eds.), Great Ape Societies, Cambridge University Press, Cambridge, 1996, pp. 29–41.

[173] F.J. White, Seasonality and socioecology: the importance of variation in fruit abundance to bonobo sociality, Int. J. Primatol. 19 (6) (1998) 1013–1027.

[174] F.J. White, K.D. Wood, Female feeding priority in bonobos, *Pan paniscus*, and the question of female dominance, Am. J. Primatol. 69 (8) (2007) 837–850.

[175] F.J. White, R.W. Wrangham, Feeding competition and patch size in the chim-panzee species *Pan paniscus* and *Pan troglodytes*, Behaviour 105 (1) (1988) 148–164.

[176] F.J. White, M. Waller, K.J. Boose, M.Y. Merrill, K.D. Wood, Function of loud calls in wild bonobos, J. Anthropol. Sci. 93 (2015) 1–13.

[177] D.M. Witt, T.R. Insel, A selective oxytocin antagonist attenuates progesterone fa-cilitation of female sexual behavior, Endocrinology 128 (6) (1991) 3269–3276.

[178] D.M. Witt, J.T. Winslow, T.R. Insel, Enhanced social interactions in rats following chronic, centrally infused oxytocin, Pharmacol. Biochem. Behav. 43 (3) (1992) 855–861.

[179] R.M. Wittig, C. Crockford, T. Deschner, K.E. Langergraber, T.E. Ziegler, K. Zuberbühler, Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees, Proc. R. Soc. B 281 (1778) (2014) 20133096.

[180] G.E. Woolfenden, J.W. Fitzpatrick, The Florida Scrub Jay: Demography of a Cooperative Breeding Bird, Princeton University Press, Princeton, 1984.

[181] J.D. Baldwin, The ontogeny of social behaviour of squirrel monkeys (Saimiri sciureus) in a seminatural environment, Folia Primatologica 11 (1-2) (1969) 35–79.

[182] Bernard Chapais, Primate nepotism: what is the explanatory value of kin selec-tion? Int. J. Primatol. 22 (2) (2001) 203–229.

[183] N. Nicolson, Weaning and the development of independence in olive baboons, Ph.D. thesis Harvard University, Cambridge, Massachusetts, 1982.

[184] Travis V. Miller, Heather K. Caldwell, Oxytocin during development: possible organizational effects on behavior, Front. Endocrinol. 6 (2015) 76.

[185] Nancy Thompson-Handler, Richard K. Malenky, Noel Badrian, Sexual behavior of Pan paniscus under natural conditions in the Lomako Forest, Equateur, Zaire, MA, The pygmy chimpanzee. Springer, Boston (1984) 347–368.

[186] Jocelyne Marson, et al., Puberty in the male chimpanzee: progressive maturation of semen characteristics, Biology of reproduction 44 (3) (1991) 448–455.

[187] Leslie J. Seltzer, Toni E. Ziegler, Non-invasive measurement of small peptides in the common marmoset (Callithrix jacchus): a radiolabeled clearance study and endogenous excretion under varying social conditions, Horm. Behav. 51 (3) (2007) 436–442.

[188] Hilde Vervaecke, Han de Vries, Linda van Elsacker, Function and distribution of coalitions in captive bonobos (Pan paniscus), Primates 41 (3) (2000) 249–265.