HHS Public Access

Author manuscript

Horm Behav. Author manuscript; available in PMC 2019 February 12.

Published in final edited form as:

Horm Behav. 2017 May ; 91: 107–121. doi:10.1016/j.yhbeh.2017.03.004.

Neuroendocrine Control in Social Relationships in Non-Human Primates: Field Based Evidence

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Abstract

Primates maintain a variety of social relationships and these can have fitness consequences. Research has established that different types of social relationships are unpinned by different or interacting hormonal systems, for example, the neuropeptide oxytocin influences social bonding, the steroid hormone testosterone influences dominance relationships, and paternal care is characterized by high oxytocin and low testosterone. Although the oxytocinergic system influences social bonding, it can support different types of social bonds in different species, whether pair bonds, parent-offspring bonds or friendships. It seems that selection processes shape social and mating systems and their interactions with neuroendocrine pathways. Within species, there are individual differences in the development of the neuroendocrine system: the social environment individuals are exposed to during ontogeny alters their neuroendocrine and socio-cognitive development, and later, their social interactions as adults. Within individuals, neuroendocrine systems can also have short-term effects, impacting on social interactions, such as those during hunting, intergroup encounters or food sharing, or the likelihood of cooperating, winning or losing. To understand these highly dynamic processes, extending research beyond animals in laboratory settings to wild animals living within their natural social and ecological setting may bring insights that are otherwise unreachable. Field endocrinology with neuropeptides is still emerging. We review the current status of this research, informed by laboratory studies, and identify questions particularly suited to future field studies. We focus on primate social relationships, specifically social bonds (mother-offspring, father-offspring, cooperative breeders, pair bonds and adult platonic friendships), dominance, cooperation and in-group / out-group relationships, and examine evidence with respect to the ‘tend and defend’ hypothesis.

Keywords

oxytocin; prolactin; tend-and-defend; social bonds; in-group / out-group; cooperation

Introduction

Social relationships are formed through repeated social interactions between the same individuals (Hinde, 1983, Cheney and Seyfarth, 1986). In mammals, social relationships are

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underpinned by a number of neuroendocrinological systems (Broad et al., 2006; Maestripieri, 2010; van Anders et al., 2011; Goodson, 2013; Chang et al., 2013; Brent et al., 2014; Rilling and Young, 2014; Crespi, 2015; Numan and Young 2016). Over the last couple of decades, laboratory research has led to increased understanding of the functions, effects, and interactions of different hormones in the body and brain, and their impact on emotions, social cognition, behavior and social interactions. How this complex interplay of hormones, brain activity and behavior contributes to the formation and maintenance of different types of social relationships is beginning to be understood (Broad et al., 2006; Maestripieri, 2010; van Anders et al., 2011; Goodson, 2013; Chang et al., 2013; Brent et al., 2014; Rilling and Young, 2014; Crespi, 2015; Numan and Young, 2016).

One prevalent type of social relationship is the social bond, in which an animal shows a preference or selectivity to affiliate with a particular individual. Social bonds can occur between kin: mothers or fathers and their offspring, family groups, or within cooperative breeding groups (Silk, 2009; Cheney and Seyfarth, 2008; Snowdon, 2015), between breeding pairs, and in platonic friendships between unrelated adults (Snowdon, 2015; Langergraber et al., 2007, 2009; Schulke et al., 2010). Another prevalent type of social relationship is based on shows of dominance and subordination resulting in dominance relationships (Bergman et al., 2003; Cheney and Seyfarth, 2008). Relationships between social groups also exist, and are defined by hostility in the case of territorial species, or neutral or affiliative interactions in less territorial species (Wrangham, 1980; Herbinger et al., 2001).

Broadly speaking, clarity is emerging in terms of which endocrine systems are principally involved in which types of relationships. Social bonds are influenced by neuropeptides, such as oxytocin, vasopressin and prolactin (Rilling and Young, 2014; Storey and Ziegler, 2016). Oxytocin, for example, fosters partner-specific preferences for affiliation, and is key in facilitating mother-offspring bonds (Rilling and Young, 2014). Testosterone mediates dominance relationships (Muller, 2017, this issue). However, less is known about how hormones interact, such as between oxytocin and testosterone, or each of these hormones with the HPA axis (van Anders et al., 2011; Carter, 2014; Crespi et al., 2015; Trumble et al., 2015).

Not only social relationships but also certain contexts or behaviors can trigger the release of hormones, precipitating positive or negative feedback loops or cascade reactions that can down or up regulate other hormones. For example, in some contexts, oxytocin release may be subject to a positive feedback mechanism whereby oxytocin may promote affiliative behavior, which may in turn promote further oxytocin release. Oxytocin simultaneously down-regulates HPA axis activity (Bethlehem et al., 2014; Sanchez et al., 2015), such as occurs during social buffering. Here, during exposure to a stressor, affiliation or support from a bond partner that triggers oxytocin release, may result in reduced cortisol release (Heinrichs et al., 2003; Sanchez et al., 2015 Cavanaugh et al. 2016; Wittig et al., 2016). However, hormonal interactions are not yet fully understood. In some contexts, hormones seem to oppose each other, such as the low testosterone and high oxytocin levels observed during early fatherhood. In other contexts, the same hormones seem to facilitate each other (Trumble et al. 2015). Sexual activity, hunting and in-group / out-group contexts, for

example, involve simultaneously high oxytocin, testosterone and glucocorticoid concentrations (Sobolewski et al., 2012a,b; Trumble et al., 2015; Wittig et al., 2016; Samuni et al., 2017).The resulting social behavior from hormonal interactions priming or suppressing activation in specific brain areas (Donaldson and Young, 2008; Rilling and Young, 2014; Bosch et al., 2016), can facilitate or impede cooperation (Soares et al., 2010; Trumble et al., 2015), contest (Beehner et al., 2006), or responses to stressors (Hennessey et al., 2009; Young et al., 2014; Wittig et al., 2016), which likely facilitate or impede relationships such as social bonds (Cacioppo et al., 2015).

While the processes between neuroendocrine systems and behavior are highly conserved across mammals, from rodents to humans, functional shifts are apparent between species (Goodson, 2013). For example, in two closely related rodent species, prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*), maternal care of offspring is facilitated by oxytocin circuitry. However, only prairie voles form pair bonds, and only in this species, does oxytocin circuitry facilitate partner-specific preferences in adult male-female interactions (Numan and Young, 2016). Thus, an animal's mating and social system has a considerable impact on the influence and functionality of neuropeptides, which in turn influence brain activity and behavior. Natural selection likely drives the dramatic shifts in the differing propensity to form and maintain certain relationships observed between species.

Within the primate order, the diversity of social and mating systems results in a broad array of social relationships, between and within species (Cheney and Seyfarth, 2008). Chacma baboons, for example, have enduring mother-daughter bonds, dominance relationships, short-term sexual consortships and male-female 'friendships' to protect offspring from potential infanticide. Playback studies have shown that these relationships are not only evident to humans but are also highly salient to the baboons, such that baboons monitor each of these relationships in other baboons (Bergman et al., 2003; Crockford et al., 2007; Cheney and Seyfarth, 2008). Strikingly, one individual can be party to all of these relationships simultaneously, and actively engage in each type of relationship within minutes of each other. An adult female can be simultaneously a mother, a daughter, hold a position within the dominance hierarchy and be on a sexual consortship. We will examine what is known about how hormones interact to facilitate or impede different social relationships and social interactions.

A key theory for explaining oxytocin involvement in different affiliative relationships is that neuroendocrine circuitry which facilitates the formation of mother-offspring bonds has been co-opted to support other relationships, such as pair bonds, adult platonic friendships and in-group / out-group relationships (Broad et al., 2006; Crespi, 2015). Throughout this review, we examine the extent to which maternal behavior to 'tend and defend' is observed in other social relationships, social interactions and contexts and is supported by similar neuroendocrinological mechanisms.

Taken together, a highly malleable and complex picture of primate life emerges, where social context and social relationships are in constant flux and juxtaposition, played out within particular mating and social systems. Many shifts between social context and

relationship types involve neuroendocrine and hormonal interplay, that in and of itself is malleable and multifaceted. Hence, primates offer an excellent model system to examine the interchange and nuance between social life and supporting endocrine systems.

Here, we review the hormonal mechanisms mediating social relationships in wild and free-ranging nonhuman primates. Understanding of neuroendocrine involvement in social events has predominantly come from laboratory studies on animals (Hennessy et al., 2009; Carter 2014; Rilling and Young, 2014), including human and nonhuman primates (Chang et al., 2013; Hostinar et al., 2014; Trumble et al., 2015). By extending research to primates in their natural habitats, where a natural range of mating, social dynamics, and social contexts are possible, we are likely to acquire a more complete understanding of how hormonal systems support and influence sociality between individuals and across species, and hence how hormonal systems may impact on selection and adaptation of primate sociality and social relationships.

The use of field endocrinology to study social relationships has been of interest to primatologists for many years. An expanding array of noninvasive methods now makes it possible to measure changes in neuropeptide and steroid hormone levels, without disrupting social behavior (Crockford et al., 2013; Wittig et al., 2014, 2015, 2016; Samuni et al., 2017). Furthermore, methods are not limited to correlational studies, where averaged hormone concentrations are correlated with rates of behavior across time (Engh et al., 2006; Crockford et al., 2008; Wittig et al., 2008; Young et al., 2014). Event-sampling is also possible, where single naturally-occurring social interactions can be targeted, enabling within-subject test-control type study designs in wild animals (Crockford et al., 2013; Wittig et al., 2014, 2015, 2016; Samuni et al., 2017). Sampling naturally-occurring social interactions avoids potential contextual confounds introduced by laboratory settings (Brown et al., 2016), and enables sampling of contexts difficult to replicate in captivity, such as intergroup encounters or hunting (Sobolewski et al., 2012a,b; Wittig et al., 2016; Samuni et al., 2017).

Hence, the focus of this review is to revisit current knowledge of neuropeptides and their influence on social relationships, and how this knowledge can inform future field studies. Within primates, we will provide evidence from wild and free-ranging apes, Old World and New World monkeys, and prosimians, showing endocrine involvement, in particular, during social interactions and relationships. Specifically, we will examine studies where oxytocin, opiates, prolactin, glucocorticoids and androgen levels were measured to determine their role in social relationships. Finally, we suggest questions that are ready to be answered in wild-living primates.

Social bonds

Mother-offspring bonds—A primate infant enters the world helpless and in need of forming a strong attachment to its mother to survive. In mammals, the mother-infant bond is a special form of attachment where an infant's welfare depends upon maternal care throughout the period of lactation and in some species, beyond lactation (Bowlby, 1969; Ainsworth, 1982). Primates have highly dependent offspring that are slow to mature and require a heavy investment. Therefore, most primate births are single offspring with a long

adolescent period and a high cost of infant fatality (Hrdy, 2009). Hormonal and neurohormonal mechanisms have ensured that mothers are well primed to form strong social bonds with their infants, and therefore, increase their offsprings' likelihood to survive (Rilling and Young, 2016). Likewise, infants are primed with attachment-seeking behavior, which facilitates the success of mothers' nurturing behavior (Bowlby, 1969; Broad et al., 2006).

The interplay between hormonal and sensory input between mother and infant is conserved across mammals. Attachment results from hormonal priming of the mother via pregnancy hormones, the interaction of the embryonic trophoblast cells of the placenta (where production of several hormones regulate maternal physiology, metabolism and behavior), and sensory input derived from the infant stimulus (Heap, 1994). Centrally released oxytocin coordinates the onset of maternal nurturing behavior at parturition in many rodents (Ross and Young, 2009; Numan and Young, 2016). Both an oxytocin antagonist, or oxytocin antiserum, infused into the brain block the onset of maternal behavior in rats after they have given birth (van Leengoed et al., 1987). In addition, oxytocin facilitates the formation of selective mother–infant bonds in other mammals such as sheep and probably most primates (Ross and Young, 2009; Numan and Young, 2016). Oxytocin activates the reward system in response to infant stimuli to regulate maternal appetitive behaviors (Atzil et al., 2017). Human maternal bonding has been associated with striatal dopamine function in the recruitment of the cortico-striatal-amygdala brain network supporting affiliation. Synchronous maternal behavior (where the mother responds to the infant stimuli) is associated with increased dopamine responses (Feldman, 2017). Thus, the integration of oxytocin and dopamine from striatal tissue supports the formation of maternal – infant bonds (Numan and Young, 2016).

Oxytocin, and the associated nanopeptide, arginine-vasopressin, have a number of neuromodulatory effects, which have been encoded into the genomes of animal species separated by 600 million years of evolution from invertebrates to mammals (Garrison et al., 2012; Donaldson and Young, 2008). Behavioral effects of oxytocin evolved along with reproduction-relevant morphological traits (Lockard, et al., 2016). Behaviors related to reproduction, including mate selection (Insel et al., 1998), copulation (Garrison et al., 2012) and provisioning (Marlin et al., 2015), are implicated as being facilitated by oxytocin, through stimulation of central brain areas that regulate associated behavior. In invertebrates, Lockard et al. (2016) examined oxytocin's role in reproductive behavior across a variety of species with diverse reproductive strategies to reveal how the system has been remodeled by relatively small genetic changes. This illustrates how slowly evolving genes can generate rapidly evolving behaviors. It is thus likely that in mammals, as sociality evolved from primarily a mother-infant bond to other types of social bonds (e.g. Numan and Yong 2016), such as pair bonds and platonic adult bonds, so has oxytocin likely influenced both physiology and behavior, differentially facilitating different social bonds.

Mother-offspring relationships and cognition—The evolution of motherhood and maternal care of offspring is associated with cognition that likely aids the rearing and survival of offspring (Albin-Brooks et al., 2017). A fundamental component of any social relationship is social recognition, such that two individuals can recognize each other and

engage in repeated patterns of behavior, whether in dominance or bonded relationships (Gabor et al., 2012). The neuroendocrine control of social recognition involves oxytocin, vasopressin and their interaction with gonadal hormones, estrogen and testosterone. Oxytocin exerts stimulation of the medial amygdala that in both sexes is essential for social recognition. By regulating oxytocin production in the hypothalamus and its receptors in the medial amygdala, estrogens facilitate social recognition. Testosterone also influences social recognition in males of some species, primarily through the vasopressin V1a receptor. Therefore, there are sex differences in the neuroendocrine control of social cognition (Gabor et al., 2012).

Maternal responsiveness and parenting quality also require social and spatial memory, as well as flexibility in attention (Albin-Brroks et al., 2017). Hippocampal-dependent tasks assessing spatial learning and memory indicate that cognitive benefits occur in new mothers where spatial memory increases and is a long-term change (Lambert et al., 2005; Hoekzema et al., 2016). Oxytocin mediates the motherhood-induced enhancement in spatial memory (Tomizawa et al., 2003), affect learning and memory (Gur et al., 2014). Social recognition memory is mediated by the olfactory systems in rodents. Sensory neurons via the olfactory epithelium and vomeronasal organ project to the medial amygdala where information is transferred to the hippocampus via the lateral septum (Bielsky and Young, 2004). Primates likely use other sensory signals as well as olfactory for social recognition, such as sight and vocal sounds, and all of these stimuli are involved in social memory (Proverbio, 2017). In humans, oxytocin has been shown to facilitate memory for faces but may cause impairment of learning and memory outside of the social domain (Boccia et al., 2007; Guastella et al., 2008).

In general, research suggests that similar sub-cortical brain areas to those used in mother-offspring and pair-bond interactions in rodents, are also used in humans in mother-offspring relationships (Broad et al., 2006; Numan and Young, 2016). Importantly, humans additionally seem to have more generalized use of oxytocin neurocircuitry, expressing nurturing, empathetic or cooperative behavior outside of the mother-offspring relationship, in other affilative social relationships or social contexts (Rilling and Young 2014; Numan and Young, 2016). Greater cortical involvement in social cognition processes may explain why humans show some emancipation from neurohormonal control in terms of social interactions and relationships (Broad et al., 2006; Numan and Young, 2016). A fascinating question is the degree to which non-human primates might also show cortical involvement, and whether this varies across primates.

Hormonal mediation of individual differences in mothering styles—A nurturing mothering style seems essential for the development of a secure attachment from the infant to the mother (Rilling and Young, 2014). The attachment can impact on the infants' neuroendocrine processes, which in turn alters neural development, and then impacts on stress regulation, emotional, cognitive and social engagement well into adulthood (Sanchez et al., 2015; Hammock, 2015; Gunnar and Hostinar, 2015). This can lead to changes in the offspring's own mothering style when becoming a mother, and to their social skills in general (Rilling and Young, 2014). The mothering style, whether nurturing or neglecting, can also influence stress regulation as well as emotions and social behavior (Gunnar and

Hostinar, 2015). An early adverse relationship between the mother and infant can cause severe developmental psychopathology (Heim et al., 2000; Sanchez et al., 2005). In free-ranging rhesus macaques, *Macaca mulatta,* mother-reared individuals had higher oxytocin levels in cerebrospinal fluid (CSF) than nursery-reared individuals. Those with lower levels of oxytocin expressed maladaptive social and self-regulatory behaviors (Winslow et al., 2003). Oxytocin also promotes reward behavior, having a direct effect on dopamine release and is a component of the establishment and maintenance of social bonds (Shahrokh et al., 2010) such that parturition and suckling provide a positive effect or reward to the mother (Franceschini et al., 1989). Given the implications of these findings for human relationships, this is an area of great interest where field data on mother – offspring behavior, accompanying changes in hormone levels, and offspring development, could provide important comparative data. Long-term field projects also have the opportunity to examine how mothering styles influence offspring's behavior over time and even across generations, in animals living under natural environmental conditions.

Maternal behavior is also facilitated by estrogen (Fahrbach et al., 1985; McCarthy, 1994). Oxytocin's influence on maternal behavior is regulated by the expression of the estradiol receptor alpha (ERα) in the medial preoptic area (MPOA) of the hypothalamus (Fahrbach et al., 1985; Numan and Sheehan, 1997). In rats, the expression ERα in the MPOA appears to precipitate individual differences in maternal behavior for mother-infant interactions as well as generational effects so that when female offspring become mothers, their own maternal style is similar to their mothers' (Champagne et al., 2006). While MPOA involvement has been found in rats, it is not known it if is analogous in primates (Rilling & Young 2014).

As with oxytocin, prolactin is involved in both lactation and in maternal care (Freeman et al., 2000; Bridges et al., 1990). It facilitates maternal responsiveness to pups in rats (Bridges and Ronsheim, 1990). Prolactin elevation during gestation coincides with rising estrogen and declining progesterone and the onset of maternal behavior (Carter, 1998). Estradiol is involved in the expression of both oxytocin and prolactin receptors in the vertebrate brain (Champagne et al., 2001). Oxytocin has receptors on the prolactin lactotrophs located in the anterior pituitary and oxytocin stimulates prolactin secretion (Kennett and McKee, 2012). Oxytocin and prolactin are both involved in maternal care, and work in concert in their roles in lactation and maternal care. Prolactin is a pleiotropic hormone with the widest range of physiological actions of any molecule in the body (Gratten, 2015), such as in reproductive, metabolic, osmoregulatory and immunoregulatory systems (Ben-Jonathan et al., 2006). Prolactin has not yet been examined in free-ranging primates in mother-infant contexts.

Neurotransmitters, such as opioids, oxytocin and the monoamines, have also been linked to variation in mothering styles (Maestripieri, 2010). At a neural level, the endogenous opioid peptides form a common substrate for different types of social attachment in primates (Schino and Troisi, 1992). Inhibiting opioid release with naloxone, increases social interactions among juvenile rhesus monkeys, and juveniles maintain higher proximity to their mothers. Juveniles increase their demand for social comfort from their mothers and other group companions (Schino and Troisi, 1992).

Oxytocin acts through binding to the oxytocin receptor, a G protein-coupled receptor encoded by a single gene in mammals (Gimpl and Fahrenholz, 2001). Studies on the free-ranging rhesus monkeys at Cayo Santiago, Puerto Rico, have shown that the mu-opioid receptor gene with the G allele variant correlated with prevalence of a cautious mothering style, where mothers restrain infants limiting their exploration and mother-infant separation (Higham et al., 2011; Mandalaywala et al., 2014). Thus, for both macaque infants and their mothers, behaviors associated with separation appear to be influenced by opioid gene variation. Additionally, nursing mothers with higher rather than lower oxytocin levels are also more likely to have the G allele. Even so, at least some of the variation in mothering style was found to be inheritable in the rhesus macaque (Maestripieri, 2003).

HPA axis activity in mothers also impacts on mothering styles. Some studies showed that higher levels of cortisol or glucocorticoids have negative impacts on maternal care. For example, in wild Assamese macaques, *Macaca assemensis*, prenatal fecal glucocorticoid levels were correlated with higher rejection rates of mothers towards offspring (Berghänel et al., 2016). Similarly, in baboons (*Papio hamadryas* sp.) in free-ranging corrals, mothers with higher postpartum fecal glucocorticoid levels displayed more stress-related behaviors and maintained less contact with their infants (Bardi et al., 2004). High circulating cortisol levels appear to enhance arousal and responsiveness to infant stimuli in young, relatively inexperienced female primates, but interfere with the expression of maternal behavior in older and more experienced mothers (Saltzman and Maestripieri, 2011). Of note, prolactin levels following birth are important for maternal motivation and depressed prolactin levels occur when glucocorticoids are high (Carini and Nephew, 2013). The regulation of hormones and hormonal systems requires a delicate balance, which can be altered by many environmental factors.

The impact of early adversity on offspring—Early adversity can impact on later social skills and mothering style. A possible precipitating factor is that adversity also acts as a profound stressor, which can result in dysregulation of the stress response through the hypothalamic-pituitary-adrenal axis (HPA). A detailed description of HPA axis functioning can be found in Sanchez et al., (2015). In brief, stressor-specific pathways activate the hypothalamic paraventricular nucleus (PVN) to secrete corticotropin-releasing hormone (CRH). CRH stimulates the release of adrenocorticotropic hormone (ACTH) from the anterior pituitary into the circulation. ACTH stimulates the synthesis and release of the glucocorticoids, mainly cortisol in primates, from the adrenal gland, which produces a catabolic effect (metabolic breakdown of larger molecules to smaller ones, releasing energy). The limbic regions of the brain, amygdala and hippocampus, and the ventromedial prefrontal cortex (vmPFC) regulate the negative feedback system to down regulate HPA activity (Sanchez et al., 2015).

Early adversity can leave individuals particularly vulnerable to HPA axis dysregulation, which can have knock-on effects on immune-response systems and gene expression, resulting in long-term deleterious health effects (Slavich and Cole, 2013). Infant rhesus monkeys that rate high on early life adversity have been found to have a dysregulation of the stress response as juveniles (Petrullo et al., 2016). The dysregulation was exhibited by attenuated cortisol reactivity along with an elevated salivary alpha amylase response as

opposed to juveniles with lower ratings of early adversity showed the symmetry of the stress biomarkers. Thus, in primates, well-regulated glucocorticoid release, particularly during brain development, facilitates usual maturation of the brain and appropriate feedback within the HPA axis. Normal development of these systems is in part dependent upon the quality of parental care. For example, rhesus macaque mothers function as an external regulator of infant HPA axis activity by preventing stress-induced activation from potential threats (Levine et al., 1985; Sanchez et al., 2015; Gunnar and Hostinar, 2015). In the squirrel monkey, infants display adverse vocal and behavioral anxiety, when separated from a mother's care, but are buffered from separation anxiety by the group if the infant remains with them (Coe et al., 1978). Thus, the psychosocial development of a primate infant is dependent upon the nurturing care not only of mothers, but also of other caregivers. These examples indicate that there are two potential mechanisms here: one is that mothers can reduce their offspring's exposure to stressors, and two, that mothers may reduce the perceived threat of the stressor.

Other studies show potential long-term effects of mothers' HPA axis activity, both before and after birth, on offspring's HPA axis activity, years later across mammals (Love et al., 2005). In primates, investigations in wild living Amboseli baboons (*Papio cynocephalus*) revealed that the dominance rank mothers had at the son's conception differentially influenced fecal glucocorticoid levels of pubescent sons. Sons of lower-ranked mothers had higher fecal glucocorticoid levels than those of higher-ranked mothers (Onyango et al., 2008). Studies of wild chimpanzees (*Pan troglodytes)* at Gombe, showed that mothers' prenatal dominance rank and fecal glucocorticoid levels impacted especially on sons' fecal glucocorticoid levels in the first decade of development (pre-pubescent). Those with low-ranking, rather than high-ranking, mothers showed greater fecal glucocorticoid decreases with age (Murray et al., 2016). Persistence of maternal influences derived from the perinatal period may signal organizational effects of mothers on their son's HPA axis. Persistent, long-term elevations of glucocorticoid levels could lead offspring to have adverse effects on their lifetime fitness (Slavich and Cole, 2013). Continued investigation of primates living under natural ecological and social conditions, will provide insights into the physiological mechanisms influencing social relationships and their impact on life-history variability in natural primate populations.

Paternal care and allo-parenting—The mother-infant bond remains important in biparental and cooperative breeding monkeys, but with others to care for the infant, the bond may be strongest with the individual that provides the most care. In the bi-parental species of primates, such as in the titi monkey (*Callicebus moloch*) (Mason and Mendoza, 1998) and in the common marmoset (*Callithrix Jacchus*) (Ziegler and Sosa, 2016), paternal care may also influence infant survival. Extensive research in captivity has shown that a paternal-infant bond in common marmosets exists and the father's involvement plays an important part in the health and well-being of his offspring (Ziegler and Sosa, 2016). Titi monkey males are the primary carrier of infants, with the exception that the mother primarily cares for them during lactation (Mason 1966; Mendoza and Mason 1986b). Interestingly, while titi monkey fathers care for infants, studies have shown they lack a selective bond towards their offspring (Hoffman et al. 1995; Mendoza and Mason 1986). Titi fathers show no behavioral or

physiological separation distress in response to separation from their infants. In contrast, the infant shows increased vocalizations and plasma cortisol levels. This effect is seen even when the mother is present (Hoffman et al. 1995; Mendoza and Mason 1986). As with the titi monkey, father owl monkeys (*Aotus azarai*) contribute extensively to infant care and by the second week postpartum the infant is almost exclusively transported by the male. Males also play with the infant and encourage weaning by food sharing (Huck et al., 2014). It is possible that the father-infant bond is stronger than the mother-infant bond in certain species.

During marmoset parenting and with other allocaregivers, prolactin is elevated during physical contact with infants (Dixson, 1982; Mota et al., 2000). In hypothalamic explants, experienced fathers' oxytocin and prolactin levels are significantly higher than levels found in non-fathers (Woller et al., 2012). Oxytocin stimulates the release of prolactin in the pituitary during reproductive events and there are oxytocin receptors on the lactotrophes that produce prolactin (Grattan, 2015). Increases in prolactin and oxytocin may promote parenting behavior by interacting with reward centers, and also other social interactions outside of parenting appear to be promoted through similar processes (Snowdon and Ziegler, 2015). In males, prolactin has important interactions with both estradiol and testosterone, particularly in the contexts of reproductive functioning and parental behavior (Ziegler et al., 2009; van Anders et al, 2012). Prolactin and testosterone levels have a negative correlation in many animals, including birds, such that prolactin levels decrease and testosterone levels rise during the breeding season, and the reverse occurs during the birthing season (Logan and Wingfield 1995; Gubernick and Nelson, 1989). Prolactin's inverse relationship with testosterone levels during parenting has been demonstrated in captive marmosets and humans (Ziegler et al., 2009; van Anders et al, 2012). When bi-parental males show maternal-like behaviors to their offspring, this coincides with decreased testosterone levels, such as in common marmosets, cotton-top tamarins *Saguinus oedipus,* and humans (Saltzman & Ziegler, 2014). It is suggested that changes in testosterone levels regulate the secretion of prolactin through a feedback mechanism that is conserved from rats to humans (Gill-Sharma, 2009). Estradiol enhances prolactin release from the pituitary and increased prolactin lowers testosterone. Dopamine is the main inhibitor of prolactin and is produced in the arcuate nucleus of the hypothalamus (Freeman et al., 2000). Estradiol has a direct effect on decreasing hypothalamic dopamine and thereby stimulates the release of prolactin, as was demonstrated in a study of marmoset hypothalamic explants from experienced fathers (Woller et al., 2012).

Since prolactin is involved in the regulation of weight in bi-parental male marmosets and tamarins, this hormone could be the link between affiliation and improved metabolism. Elevated prolactin postpartum, when males are actively caring for infants, may work to prevent excessive weight loss in males during their added energetic demands (Ziegler et al., 2009). Metabolic regulation tissue such as the liver, pancreas, adipose tissue and brain all contain prolactin receptors and are regulated by prolactin (Luque et al., 2016). In pregnant females and during lactation, prolactin promotes fat deposition or mobilization to ensure optimal nutrition for the offspring (Grattan, 2015). Father marmosets have increased prolactin during body contact with their offspring. This may promote improved regulation of metabolic function during the energetically demanding period of carrying large and heavy

infants. Further data is needed on prolactin's role in contact affiliation under different social conditions and between species that express different social patterns and relationships. Prolactin levels may be difficult to monitor under field conditions and acute changes are unlikely to be detectable using collection methods available in the wild. However, changes in fecal testosterone levels may reflect behavioral changes in fathers, such as the amount of time spent with their offspring (van Anders et al, 2012).

Cooperative breeders, such as the common marmoset, show group care-taking behaviors towards infants and increased levels of urinary oxytocin during the early postpartum period when all group members are carrying infants (Finkenwirth et al., 2016). Additionally, infant licking and proactive food sharing are positively linked to increased urinary oxytocin levels across group members (Finkenwirth et al., 2016). Administration of oxytocin within the brain facilitates paternal food sharing in marmosets (Saito and Kakamura, 2011). Also, when the group shares infant caretaking, urinary oxytocin levels are elevated in all group members (Finkenwirth et al., 2016). Thus, diverse patterns of paternal care are apparent across species, with variation in relative parental effort between mother and father, and in cooperative breeders, between other group members.

To our knowledge, no study on father's hormones and paternal behaviors for any bi-parental species in the wild has been published to date. Much of this is due to the difficulty in collecting hormone samples from wild living bi-parental species, most of which are small New World monkeys that are mainly arboreal and can be obscured by brush and branches. However, fecal collection is feasible in some monkeys, such as the common marmoset where pregnancy and social influences on fertility have been documented (Albuquerque et al., 2001). Therefore, studies examining glucocorticoid and testosterone excretion during reproductive events are likely feasible in callitrichid mothers, fathers and offspring with noninvasive sample collection.

Though less well defined and examined, males living in multi-male multi-female social systems sometimes exhibit certain aspects of parental care. In chacma baboons (*Papio ursinus*), for example, where infanticide occurs at high rates following alpha male takeovers, potential fathers take on a protective role for infants. Although they rarely engage in infant carrying or grooming, ex-alpha males spend more time in close proximity to infants than other males and risk incurring costs whilst defending infants under attack from dominant males (Palombit et al., 1997). Additionally, adult male chimpanzees who do not usually engage in paternal care, are known to adopt orphans, including daily carrying, grooming, food sharing and nest sharing (Boesch et al., 2008). Monitoring the extent of androgen level decline and potential increases in oxytocin levels with infant births and infant care in males across species could identify endocrinological mechanisms that support shifting strategies from competition for dominance to infant care and protection (Storey and Ziegler, 2016; Trumble et al., 2015).

Pair bonds

New World Monkeys—A pair bond is defined as a specific, mutual and enduring preference between an adult male and a female, potentially leading to reproduction. The pair bond ensures males continue to remain during the female's pregnancy and participate in

parental care of the offspring (Mason and Mendoza, 1998). Most of what we know of pair bonding in nonhuman primates is the result of neuroendocrine and genetic work in captive New World monkey species, specifically titi monkeys, cotton-top tamarins and two species of marmosets, the common marmoset and the Wied's black tufted-eared marmoset, *Callithrix kuhlii*.

Testing the strength of the pair bond by measuring changes in circulating cortisol levels, locomotion and movement as a response to separation anxiety has illustrated the strong bond between titi monkey mates (Mason and Mendoza, 1998). When paired titi monkeys are separated, both the male and the female respond with increased circulating cortisol concentrations. However, titi monkey parents do not show a similar heightened cortisol response to separation from their offspring (Mason and Mendoza, 1998).

Oxytocin can influence social behavior within a pair bond. Male marmosets (*Callithrix penicillata)* initiated huddling with their pair bond partner more after treatment with intranasal oxytocin, and they reduced proximity and huddling from their pair bond partner after treatment with an oxytocin receptor antagonist (Smith et al., 2010). Intranasal oxytocin also increased the amount of grooming females received from their long-term mates, indicating a neuromodulatory role of central oxytocin activity on social behavior (Smith et al., 2010). When measuring endogenous urinary oxytocin in cotton-top tamarin pairs, mates showed similar levels to each other, and variation in oxytocin levels positively correlated with rates of affiliative and sexual behavior between the pairs (Snowdon et al., 2010). Similar results were found for the common marmoset, where strongly bonded marmoset pairs within a family (primarily the breeding male and female) showed synchronized longitudinal fluctuations of urinary oxytocin levels (Finkenwirth et al., 2015). Pair bonds maintain stability within the group, with the mated pair establishing a bond that lasts through pregnancy and rearing of offspring. These studies suggest that oxytocin levels can serve as an addition to behavioral observation in the assessment of pair bond strength between two individuals.

Oxytocin and prolactin both appear to be involved in the bonding process between mates. Prolactin and oxytocin are both involved in contact affiliation and pair bonding in the cotton-top tamarin (Snowdon et al., 2010; Snowdon and Ziegler, 2015). While studies of pair bonding in mammals have focused mainly on oxytocin's role, both oxytocin and prolactin trigger release of the other in reproductive functions. Prolactin exhibits a sustained surge with copulation and orgasm in males and females and is likely associated with social reward, which facilitates the bonding process (Gratten et al., 2015; Egli et al., 2010). Thus, oxytocin and prolactin may both be important in pair bonding.

Social buffering—Pair-bonded species have been key in assessing neuroendocrine involvement in social buffering, whereby social support from bond partners can downregulate HPA axis activity during exposure to a stressor (Heinrichs et a., 2004; Tops et al., 2007; Hennessey et al., 2009; Seltzer et al., 2010; Gunnar and Hostinar, 2015; Wittig et al., 2016). When experiencing a stressor with rather than without a pair-bond partner, voles showed oxytocin released in the brain is concurrent with a reduction in corticosterone and anxiety-related behaviors (Smith and Wang, 2014; Burkett et al., 2016). In marmoset pairs,

an oxytocin antagonist resulted in higher urinary cortisol levels during the stressor, suggesting that the oxytocin system may inhibit the stress-induced rise in cortisol levels. Under certain social contexts, oxytocin operates in the hypothalamus by inhibiting CRH and hence down regulation of HPA axis activity (Bosch et al., 2016). Corticotrophin releasing factor receptors (CRFR2) are located on oxytocinergic neurons and axon terminals regulating the release of oxytocin, with a potential feedback loop between the hypothalamic oxytocin system and the forebrain CRF system, impacting affective and social behaviors in times of stress (Dabrowska et al., 2011).

Non-invasive studies in human and non-human primates concur that when social support is available from a bond partner after experiencing a stressor, oxytocin levels increase and cortisol levels decrease more quickly than in control conditions with no bond partner present following a stressor (Tops et al., 2007; Seltzer et al., 2010; Wittig et al., 2016). For species where urine collection is difficult, glucocorticoids could potentially act as an indicator of social buffering effects. .

Old World monkeys—Unlike New World monkeys, few Old World monkeys and apes are considered to be pair-bonded or cooperative breeders. However, there are several gibbon species that are socially monogamous and exhibit pair-bonds (Reichard, 1995). Several lemur species show bi-parental care, and even cooperative breeding. For example, the red-bellied lemur (*Eulemur rubriventer*) exhibits pair living within stable family groups (Tecot et al., 2015). This species might be especially interesting, as females often give birth to twins, and older offspring participate in infant care (Tecot et al., 2015). Further studies on bi-parental gibbon and lemur species should provide important evolutionary data about how pair bonding and mating systems are associated.

Although many primate species do not have enduring pair bond relationships, other types of male-female reproductive relationships exist, such as harems or multi-male multi-female groups, where males sometimes engage females in either short term sexual consortships as a mate-guarding strategy, or in longer-term relationships where bonds extend outside of the mating period (Palombit et al., 1997). There has been limited examination of the hormonal involvement of these relationships. Moscovice and Ziegler (2012), however, measured urinary oxytocin levels in cycling female chacma baboons (*Papio ursinus*) including during consortships, possibly conducting the first non-invasive study of oxytocin in wild primates. They found that estrous females, especially those in consortship with a male, had significantly higher urinary oxytocin levels than pre- or post-estrous females. Also there was a positive correlation between females' urinary oxytocin levels and greater proximity maintained by consortship pairs (Moscovice and Ziegler, 2012). They concluded that behavioral and physiological changes associated with the maintenance of short-term inter-sexual relationships corresponded with changes in peripheral urinary oxytocin levels in this baboon (Moscovice and Ziegler, 2012).

Only one field study to date has examined prolactin in relation to different social styles of male behavior towards females (Phillips-Conroy et al., 2013). This study examined three species of wild baboons, hamadryas (*Papio hamadryas*), anubis and kinda (*Papio kindae*), throughout development. Prolactin was measured from blood, which was collected from the

baboons during anesthesia in the field. Prolactin levels reflected the different social styles of the baboon species: young hamadryas baboon males showed prolactin elevations coinciding with their abduction of young females. These males showed extensive grooming and even carrying of their young females, and females sometimes then remained as part of the male's harem until after sexual maturity. In a baboon species comparison, the kinda baboons had elevated prolactin levels compared with hamadryas baboons, presumably related to their uniquely high levels of grooming behavior towards females and immature baboons. In contrast, the anubis baboon males showed consistently lower levels of prolactin throughout development. These results indicate a broader role played by prolactin in sociality in that prolactin may facilitate social contact or the formation of affiliative relationships, as is the case in mother – infant bonds.

Social bonds in adult platonic relationships

A highly significant finding in ethology in the last 20 years is that maintaining adult social bonds increases reproductive success and longevity in primates (House et al., 1988; Silk et al., 2003; Silk et al., 2010; Schülke et al., 2010; Archie et al., 2014). Most studies have focused on kin relationships, such as mother-daughter and sister relationship in matrilineal Old World primates, such as baboons (Silk et al., 2003, 2009, 2010). Patrilineal species such as muriquis (*Brachyteles hypoxanthus arachnoides*) (Strier, 2011) and chimpanzees (Langergraber et al., 2007) show similar patterns. There is some evidence that enduring non-kin, socially bonded, platonic, relationships, or 'friendships' (Seyfarth and Cheney, 2012) also accrue reproductive benefits. For example, Schulke et al. (2010) found that maternally unrelated adult Assamese macaque males, which maintain close social bonds with other males, father more offspring in the following mating season. Assamese macaque males with close social bonds are also more likely to form coalitions against competitor males and rise in dominance rank, resulting in increased paternity success. Male chimpanzees that share close social bonds with non-kin males, and form coalitions against dominant males, also gain higher rates of copulations with potentially fertile females (Duffy et al., 2007). Thus, close social bonds may form, even with non-kin, when the result is a predictable cooperation partner with whom cooperating increases an individuals' reproductive success.

Sociality may have evolved as an environmental coping strategy. Affiliative and aggressive tendencies in rhesus macaques have been found to have genetic variation in the serotonin loci involved in serotonergic signaling (Brent et al., 2013). Therefore, temperaments would have a genetic basis in nonhuman primates as they do in humans. There is an adaptive significance to having genetic variations of the serotonin transporter linked polymorphic region. Low-expressing alleles are linked to hypervigilant tendencies that could be adaptive during periods of elevated competition while high-expressing alleles are linked with calmer temperaments and benefit from normal levels of competition (Dobson and Brent, 2013). Both types of temperaments would be adaptive under different social conditions and therefore these variants could be conserved. How friendships are formed and maintained between adults, however, remains unclear and will be addressed below.

Adult social bonds are likely co-opted from mother-offspring bonds—Hormonal mechanisms are likely to have been co-opted from mother-infant bonding into more flexible

bond structures, like pair bonds, adult platonic bonds and even in-group support in the face out-group threat (e. g., Broad et al., 2006; Rilling and Young, 2014; Crespi, 2015; Numan and Young, 2016). One way to further examine this hypothesis is to determine if the hormonal responses involved in social interactions between mothers and offspring are also involved in other close social relationships. Bonded individuals show a common set of behaviors, broadly grouped as tending to the bond partner through grooming or food sharing, and coming to their defense when under threat by offering agonistic support. De Dreu et al. (2012) used the term 'tend-and-defend' for behavior elicited during laboratory-induced in-group / out-group contexts. We suggest this term is equally intrinsic to maternal nurturing behavior. Maternal tend-and-defend behaviors are supported by the oxytocin system (Rilling and Young, 2014). We examine whether tend-and-defend behaviors occurring in other close social relationships are supported by the oxytocin system. We also examine whether engaging in the same behaviors outside of close social relationships involves the oxytocin system, such as when grooming, food sharing, pup-guarding, consolation contexts, or during in-group / out-group contexts. We also discuss whether co-opting of neuroendocrine circuitry that supports tend-and-defend behaviors is also likely to facilitate cooperative exchanges in general, when there are benefits to be gained from cooperation.

In some primate species, particularly some apes (Langergraber et al., 2007; Surbeck et al., 2011), maternal nurturing endures years after lactation ends and likely increases offspring survival. In chimpanzees, for example, lactation ends at 4–5 years of age, but offspring orphaned aged between 1–5 years typically do not survive (Goodall, 1986; Boesch et al., 2010; Thompson et al., 2012). Indeed reliance on mothers continues for several years beyond lactation and those orphaned in the first years after weaning can show considerable retardation in physical development (Goodall, 1986), a phenomenon less likely to occur, if orphans are adopted by other adults (Boesch et al., 2010).

In some primate species, offspring of the non-dispersing sex, which remain and reproduce in their natal group, continue to share mother-offspring bonds throughout life, such as mother-daughter relationships in chacma baboons (Silk, 2009), and mother-son relationships in bonobos (Surbeck et al., 2011) and chimpanzees (Goodall, 1986). To ensure on-going nurturing, bonded relationships between offspring of both sexes and their mothers (Curley & Keverne, 2005), mechanisms for oxytocin release have likely evolved beyond current known triggers of oxytocin release, such as parturition and suckling. Offspring may co-opt into their platonic adult relationships, the requisite hormonal and socio-cognitive systems, which supported their bonding behavior to their mothers when they were young (Rilling and Young, 2014; Burkett et al., 2016). This may explain why not only adult females, with neuroendocrine systems adapted for infant care, but also adult males are able to maintain stable, platonic social bonds. Male chimpanzees (Langergraber et al., 2007) and Assamese macaques (Schulke et al., 2010; Kalbitz et al., 2015) both form and maintain close social bonds with non-kin over years. Chimpanzee females also maintain same sex non-kin platonic bonds over years (Langergraber et al., 2007; Langergraber et al., 2009, Crockford et al., 2013, Wittig et al., 2014).

In wild chimpanzees, grooming between adult kin and non-kin bond partners, but not between non-bond partners has been shown to be associated with higher urinary oxytocin levels than resting controls, suggesting that the grooming *per se* is not associated with elevated oxytocin levels, but that the bond itself is influential (Crockford et al., 2013). This result corresponds with recent human studies showing that affiliative touch alone was not sufficient for stimulating oxytocin release (Uvnas-Moberg et al., 1993; Seltzer et al., 2010; 2012). The results support the hypothesis that adult platonic social bonds in primates, whether between kin or non-kin, are associated with, and may be mediated by oxytocin. The next crucial step would be to repeat this result in other species.

Food sharing has been shown to be associated with significantly higher oxytocin levels than grooming with friends in wild chimpanzees (Wittig et al., 2014). However, unlike grooming, oxytocin levels were not significantly different depending on the friendship status of the sharing partners, although the sample size of non-friends was small. For both, grooming and food sharing, giving or receiving the service did not impact significantly on urinary oxytocin levels. Since oxytocin release is critical for bond formation in rodents (Insel et al., 1995), one possible explanation for these results is that while moderate release of oxytocin can maintain existing bonds, large releases of oxytocin may be necessary for establishing new bonds (Wittig et al., 2014). This hypothesis, however, remains to be tested.

Another social behavior that seems integrally linked with both oxytocin levels and underlying social bonds, is consolation – or affilation, offered to one experiencing a stressor such as a conflict. Bystanders are more likely to offer consolation when it is their close bond partner is experiencing a stressor rather than another individual (Clay et al. 2013). Pair-bonded prairie voles, whose partner had received a stressor during separation, were more likely to have increased plasma corticosterone levels and to groom partners when they returned, than those who had been separated without receiving a stressor (Burkett et al., 2016). Consolation behavior and raised corticosterone levels were not observed in a non-pair bonded vole species, the meadow vole (Burkett et al., 2016) under the same conditions. In the pair-bonded voles, exposure to a stressed cage mate was associated with activity in the anterior cingulate cortex. An oxytocin receptor antagonist infused in this brain area abolished the partner-directed response. Furthermore, immunocytochemistry and use of an oxytocin agonist showed the consolation display was oxytocin-mediated, principally activating brain receptors in the anterior cingulate cortex, the part of the brain where human emotional empathy is also active (Dvash & Shamay-Tsoory, 2014). The role and function of consoling, and the defining of consoling on a behavioral level, are relatively controversial, particularly in primate studies in the context of post-conflict management (Wittig and Boesch, 2010; de Waal and van Roosmalen, 1979; Schino, 2004). Non-invasive simultaneous assessment of cortisol and oxytocin concentrations is likely to provide insight into the underlying mechanisms of consolation and other post-conflict affiliative behavior as well as how these behaviors function within relationships. It seems likely that consolation also constitutes a ‘tend-and defend’ nurturing behavior co-opted from mother-offspring neuroendocrine circuitry.

In-group / out-group effects—In-group / out-group effects are ubiquitous in humans and are described as affiliation and trust being increased in the in-group and distrust and

aggression being simultaneously increased towards the out-group (Choi and Bowles, 2007; De Dreu, 2012). In-group / out-group effects can also be construed as being co-opted from mother-infant mechanisms, as while mothers must be nurturing to offspring they must simultaneously defend offspring against outside threats (Hahn-Holbrook et al., 2011; Crespi 2015). Humans are apparently prone to behaving with more affiliation, generosity and trust towards in-group than out-group members, whether they are of the same nationality, tribe, school or sport team (De Dreu, 2012). The strong human tendency to form an in-group / out-group dichotomy, even from young ages (Buttelmann et al., 2013; Engelmann et al., 2013, Over, 2016), can rapidly and dramatically impact on our behavior. This is the case whether the dichotomy is real, such as the devastating and rapid turning of one people against another in the Rwandan genocide, or is experimentally fabricated (Zimbardo, 1973; Buttelmann et al., 2013; Engelmann et al., 2013; Over, 2016).

Administered oxytocin has been shown to be a powerful mediator of the in-group / out-group response (De Dreu, 2012; Stallen et al., 2012). However, few if any, human studies have measured naturally released oxytocin in in-group / out-group contexts. Although evolutionary causes have been speculated about (De Dreu, 2012), little empirical data on either administered or naturally released oxytocin in in-group / out-group contexts exists outside of humans (Trumble et al., 2015; Samuni et al., 2017).

One type of behavior associated with group defense is territorial behavior. Primate species show varying degrees of territorial behavior. Even closely related species, like within *Pan,* can show considerable variation in tolerance towards out-groups, ranging from invariably hostile in chimpanzees (Mitani et al., 2010) to considerable tolerance in bonobos (Itani, 1990; Surbeck et al. 2017). The variation in this behavior likely depends on socio-ecological factors such as the availability of food or sexual partners and the extent of competition that there is over these key resources (Wrangham, 1980). This variation makes nonhuman primates a good model for examining the evolutionary pressures, constraints and mechanisms of in-group / out-group effects.

In terms of mechanisms, a recent study in wild chimpanzees showed that immediately before and during intergroup conflict, both males and females had significantly higher urinary oxytocin levels compared to controls. Also, elevated hormone levels were positively correlated with greater cohesion during intergroup conflicts, and not with the level of potential threat posed by rival groups, nor with intragroup affiliative social interactions (polyadic grooming). Coordinated (hunting) behavior also showed raised urinary oxytocin levels compared to polyadic grooming, but intergroup conflict contexts were significantly higher than hunting contexts. Thus, oxytocinergic system involvement when experiencing out-group threat is not uniquely human and potentially engenders cohesion and cooperation (Samuni et al., 2017). Studies during intergroup encounters on other primate species are likely to be highly informative in determining whether oxytocin-mediated in-group / out-group effects occur in other territorial species.

In sum, nurturing tend-and-defend behaviors observed in social bond relationships outside of the mother-offspring bond involve oxytocin activity. This includes grooming between bond partners, cooperative behavior such as food sharing and pup-guarding, as well as in in-

group / out-group contexts. These findings support the theory that tend-and-defend behaviors outside of maternal care are underpinned by similar neuroendocrinologocal circuitry, likely co-opted from that already in place to facilitate maternal care and mother-offspring bonds.

Cooperation and tolerance—Another framework in which neurohormones have been frequently discussed is within the remit of cooperation (Soares et al., 2010). For example, oxytocin levels have been shown to enhance trust and generosity in humans (Kosfeld, 2005; Declerk, 2010; MacDonald and MacDonald, 2010; De Dreu, 2012; Arueti et al; 2013; Rilling and Young, 2014; Crespi, 2015; Feng et al., 2015a & b; but see also Christensen et al., 2014 where trust did not relate to oxytocin levels). Furthermore, cooperation is an inherent part of mother-offspring interactions, starting with the primary form of food sharing, lactation, and other maternal nurturing, protective and supportive behaviors, such as grooming, consoling and offspring defense. Studies on cooperation in kin and pair bonds indicate oxytocin involvement. In free-ranging, cooperative breeding meerkats, administering oxytocin increased the rate of a broad range of cooperative offspring care behaviors (such as pup-feeding and pup-guarding), even in non-parents (Madden et al., 2010). Also, the cooperatively breeding common marmoset had high urinary oxytocin levels during cooperative behaviors towards infants including food sharing and infant licking (Finkenwirth et al., 2016). Few studies, however, have examined oxytocin in contexts of cooperation between non-kin, platonic contexts outside of humans (Soares et al., 2010). Recently, Samuni et al. (2017) showed high levels of urinary oxytocin during hunting and territorial patrolling, two contexts in which chimpanzees seem to share a common goal and coordinate their behavior at a group level, irrespective of kinship.

The building blocks of cooperation have been suggested as tolerance towards conspecifics, social recognition, assessment of the social environment, social memory and learning, temporal discounting, partner choice and social bonding (Soares et al., 2010). It is uncontroversial that primate social life routinely utilizes a similar skill set, even outside of mother-offspring or pair-bonded relationships. Most of these features are underpinned by oxytocin. Thus, oxytocin system is arguably a key facilitator of cooperation. In species in which the oxytocin system can be flexibly co-opted to support adult platonic close social relationships, as demonstrated in chimpanzees and humans, it is conceivable that cooperation is facilitated, even in the absence of a social bond. Such a mechanism may explain the emergence of group-level cooperation in chimpanzees, and more extensively in humans, although this idea requires further testing.

Tolerance, cooperation and the emergence of social bonds show considerable variation across primate species, such as in terms of when and with whom social bonds are likely to form (pair bonds, paternal bonds, friendships and so on). Humans alone express considerable within-species variance in tolerance and cooperation (Henrich, 2004; Henrich et al., 2004). Tolerance, for example, across relationships or across societies ranges from open and inclusive to highly exclusive and hostile. Cooperation levels can be context specific, individual or societal, ranging from highly cooperative to highly obstructive. This indicates that while neuroendocrinological systems are conserved, the social contexts which stimulate these systems seem relatively plastic across species, and also between individuals

within a species (Goodson, 2013). Primates living in their natural social and ecological environment provide a model in which cross-species comparisons of behavioral and hormonal interactions could reveal important insights into evolutionary pressures and constraints into cooperation, as well as the underlying neuroendocrine processes that facilitate cooperation.

Putting neuroendocrinological findings into a socio-ecological context—Social experience can alter brains, in part through hormonal activation patterns influencing receptor distributions and changing the size of different cortical and subcortical brain areas (Sallet et al., 2011; Rilling and Young, 2014). These changes in the brain seem related to changes in social behavior, resulting in individuals who are more or less nurturing (Rilling and Young, 2014), more or less social or dominant (Sallet et al., 2011), and potentially also more or less aggressive or cooperative (Soares et al., 2010; De Dreu, 2012; Kalcher-Sommersguter et al., 2015). Thus, to fully understand the extent that social experience can alter the brain and neuroendocrinological processes, comparing animals that have had exposure to limited social experience to those with extensive social experience seems of paramount importance. To consider an extreme example, take a rhesus macaque or chimpanzee who from birth has lived in isolation or in paired housing with one other individual. How would its brain look compared with the brain of a wild-living conspecific, nurtured and supported by its mother in the first years of life and living within the milieu of complex social relationships that constitute daily life for group-living primates?

Group-living requires that primates like macaques and chimpanzees learn who is likely to be affiliative and who aggressive to them, their place in the dominance hierarchy and how to rise in dominance rank. Individuals need to navigate social competition at food to ensure access to food, how to gain access to the best sexual partners, to avoid predators, to maintain close social bonds to aid own reproductive success and survival, and to nurture offspring so that they survive (Cheney and Seyfarth, 2008). The ecological environment most likely influences the social environment (Wrangham, 1980; Sterck et al., 1997). Food and mate competition experienced in wild groups may be crucial for providing the context for cooperative relationships to emerge. If food and mate competition are altered or removed in captivity, through food provisioning, contraception or small group sizes, cooperative relationships and social bonds may not occur as frequently or intensely (Kalcher-Sommersguter et al., 2015). For example, for multi-male multi-female species living in one-male groups in captivity, there is not the possibility to experience male-male competition, nor to form cooperative relationships with other males to over-power dominate individuals. To experience the full range of possible ecological challenges and resulting social relationships, both positive and negative, requires studying wild animals that live in their natural social and ecological environment.

Practical considerations for non-invasive field endocrinology—Non-invasive methods of sample collection enable the measurement of the endogenous production of some hormones. Glucocorticoids, androgens, estrogens and more recently, oxytocin and prolactin, can be measured from urine, and steroids can also be measured in feces, hair and saliva (Behringer and Deschner, 2017; Koran et al., 2002; Kapoor et al. 2014; see Horvat-

Gordon (2005) for potential issues with salivary oxytocin). Behringer and Deschner (2017), this issue, provide an excellent review of appropriate sampling protocols for different hormones and substrates. Some substrates are easier to access in certain species than others, for example, most pair-bonded primates are small and arboreal, living in high canopies. Here, urine will be problematic, given the limited visibility at canopy level, and the small volume of urine. Also, the clearance time window from secretion of the hormone to excretion into the substrate in question must be taken into account when determining which substrate is most appropriate for a particular research question or feasible within the constraints of the species and their environment.

Some questions require examining broad correlations of hormone levels over extended periods, such as breeding periods, or social upheaval versus stability. Here, researchers might measure hormones in substrates that incorporate hormone concentrations over longer time periods, such as steroids in feces in Old World primates with an excretion window of upwards of 24 hours (Bahr et al., 2000; Engh et al.; 2006; Crockford et al., 2008; Wittig et al., 2008; Young et al., 2014; Behringer and Deschner, 2017). Questions that require single event sampling to capture the impact of a single social interaction, require substrates with a short excretion window, over minutes or hours, such as in saliva or urine (Amico et al., 1987; Sobolewski et al., 2012a,b; Crockford et al., 2013; Wittig et al., 2014; Wittig et al., 2016), or feces in some new world primates, where gut passage time can be up to 7 hours (Wheeler et al., 2013).

The nature of the hormone and of hormone release must also be considered, particularly in studies on wild populations where immediate storage may not be possible. Oxytocin, for example, is a nine amino acid peptide, which is secreted in pulses and has a short half-life in blood due to the enzymatic activity (Leng and Sabatier, 2016). Thus, a substrate with too short an excretion window may create problems in terms of capturing the pulsed secretion (Leng and Sabatier, 2016; Behringer and Deschner, 2016). Urine, however, accumulates hormone concentrations between urinations, due to clearance of oxytocin from the blood by the kidneys and little enzymatic breakdown once in the urine (Leng and Sabatier, 2016). Thus, using repeated sampling of urine may provide a relatively robust medium for capturing within-individual changes in hormonal activity across different social contexts. Oxytocin is stable at pH of 5 (Reyes et al., 2014). The pH of urine varies across and within species. In western chimpanzees, for example, 37% of urine samples are pH < 7 (pH of 5 or 6). Urine acidity can change with diet such that after meat eating, 60% of chimpanzee urine samples were acidic (Leendertz et al., 2010). Oxytocin can be stabilized in urine by either freezing samples directly after collection or adding acid to the urine.

The central versus peripheral oxytocin debate—The uses of peripheral measurements of oxytocin have been critically discussed (Leng and Sabatier, 2016). It is central oxytocin released in the brain that promotes behavioral change. However, central oxytocin can only be measured invasively. Peripheral oxytocin concentrations are expected to reflect central oxytocin concentrations when secreted simultaneously. However, when coordinated release occurs is not yet clear. Neuroanatomy supports the possibility of coordinated release. Oxytocin is synthesized in the paraventricular nucleus and supraoptic nucleus within the hypothalamus. Both oxytocin and vasopressin are stored in the neural

lobe of the pituitary for peripheral release into the blood. Additionally, oxytocin is also released via axons into various parts of the brain (Donaldson and Young, 2008; Knobloch et al., 2012). Of the few studies conducted, some show simultaneous release of central and peripheral oxytocin and others do not (MacDonald & Feifel 2013; Crockford et al., 2014). Torner et al. (2017) have shown that during exposure to a stressor, oxytocin is released both centrally and peripherally but via different pathways. Although more studies are required, discrepancies across studies may indicate that different release patterns are dependent on social context.

Furthermore, a number of studies have demonstrated predicted behavioral responses associated with elevated levels of peripheral oxytocin (reviewed in Crockford et al. 2014), and more recently, central release of oxytocin has been reflected in both plasma and urine (Francis et al., 2016). However, studies linking endogenous peripheral oxytocin to certain social behaviors or contexts have also produced conflicting results. It is likely that a substantial proportion of this confusion is due to poor or missing hormone extraction and validation procedures, crucial steps to ensuring reliable measurements of peripheral oxytocin (Leng and Sabatier, 2016). The accumulated evidence suggests that urinary oxytocin measures, that have been subjected to extraction and validation procedures, do reflect central oxytocin release, providing a noninvasive method to examine neuroendocrine underpinnings of social relationships in free ranging nonhuman primates. However, further studies examining coordinated release are required.

Future questions and directions

Environmental influences impact endocrine and neural systems and their development even before birth. These environmental events can also influence development and adult sociality, affecting fitness, health, reproduction and longevity. Environmental influences, such as mothering style or trauma may change an individuals' disposition to be more or less social, more or less nurturing, or more or less cooperative (Rilling and Young, 2014). While the hardware – the neuroendocrine systems and neural pathways – seems relatively conserved across animals, the software – the emergent social behavior and relationships – seems relatively malleable, flexibly adjusting to the social environment to which an animal is exposed during its lifetime. The particular types of social relationships which neuroendocrine systems support also seem flexibly altered by natural and sexual selection processes, as evidenced by the social and mating system changes in closely related species that are supported by these conserved neuroendocrine systems.

Laboratory studies have been crucial, and will remain crucial, for understanding these processes. However, given the extensive environmental influences on social development, to fully understand how neuroendocrine systems operate on neural and physical development and thus impact on social behavior, examining these systems in wild animals living in their natural social and ecological environment is also of paramount importance. This is especially likely to be the case for species that live in large social groups, where captive housing can extensively alter their social group structure, as well as food and mate competition dynamics. Below, we pose several questions suitable for addressing in wild primate settings.

1. What causes social bonding neuroendocrinological circuitry to support different types of social relationship in different species?—Laboratory and wild studies suggest that irrespective of the bond type the underlying neuroendocrinological circuitry involved is similar. Probably the most consistent and conserved across mammals is the mother-offspring bond, where marked preferences for own mothers and own offspring are apparent in many mammal species (e. g., Rilling and Young, 2014; Fleming et al., 1999). However, this is not the case in rodents (Numan and Young, 2016). While oxytocin facilitates maternal care in rodents as in other mammals, rodents rarely show a preference for their own offspring compared to another's offspring (see house mice: Weidt et al., 2008; rats: Numan and Young, 2016). Thus, while rodent mothers show nurturing behavior, they do not form selective bonds with their offspring. It is possible that selective mother-offspring bonds for animals that produce offspring in nests or burrows, like many rodents, or in kin groups, like cooperative breeders, bring fewer benefits, compared to animals that produce offspring in large social groups with low relatedness, like sheep and Old World primates. While at least parts of the neuroendocrine system are conserved across mammals, primates seem to have greater higher order processing in cortical regions of the brain, like areas involved in the perception of the social bond. . Mirror neurons are one likely component of the higher order processing and it is hypothesized they are involved in the transmission of attachment (Botbol, 2010).

Whether a specific type of social bond emerges in a given species seems highly dependent on the social system and is likely contingent on whether benefits accrue from selective bond maintenance. Social bonds between adults likely arise when benefits are gained from sustained, predictable cooperation, such as when bi-parental care increases offspring survival, or when predictable rather than opportunistic coalition formation increases reproductive success. It seems likely that neuroendocrinological circuitry can be flexibly co-opted to support social bonds where they provide fitness benefits through cooperation. How this emerges requires investigation. Further studies are called for to determine if social bonded relationships across species, especially among adults, are always underpinned by the oxytocinergic system.

2. Do hormonal systems influencing pair bonds differ from those influencing other types of male and female sexual relationships, such as in one-male units?—The hormonal systems influencing pair bonds have been extensively examined, but little is known about endocrinological involvement in male and female relationships within other mating systems. What happens for example in one-male units, or in promiscuous mating systems? Examining the neuroendocrinological involvement in these systems in different primate species could inform us about the variability seen in human mating patterns.

3. How fast and flexible is the synchrony between neuroendocrine systems, social relationships and ever-changing social contexts?—Neuroendocrine systems moderate long-term mating strategies that may operate over months or years, such as pair bonds or dominance-driven promiscuous mating systems. Male reproductive success in pair-bonded species is likely, in part, to depend on the synchrony and cooperation

expressed within the pair bond and in paternal care, supported by high prolactin and oxytocin and low testosterone levels (Storey and Ziegler, 2016; Trumble et al., 2015). In contrast, male reproductive success in dominance-driven promiscuous mating systems is likely dependent on testosterone-supported fighting prowess (Muller, 2017, this issue). A shift in mating strategy, or in associated social relationships, may precipitate hormonal shifts. In wild chacma baboons, for example, males rising in dominance rank maintained higher fecal testosterone levels than males falling in rank, but only during periods when dominance ranks were being contested (Beehner et al., 2006). When an alpha male falls in rank, his behavior can shift dramatically, showing a drop in aggression rates and a rise in proximity to offspring likely to be their own. In new fatherhood, testosterone concentrations drop, and oxytocin and prolactin levels increase, corresponding to a shift from dominance displays to infant nurturing behavior (van Anders, 2011; Crespi, 2015; Trumble et al., 2015). Thus, do reproduction strategies and maintenance of associated social relationships, which can persist over months or years, require relatively stable hormone profiles over time or only during periods of change?

While mating strategies and social relationships are ongoing, neuroendocrine systems simultaneously moderate short-term social contexts and social interactions that can be ever-changing throughout the day. In hunting and intergroup contest, urinary testosterone, cortisol and oxytocin concentrations are simultaneously high, in both humans and chimpanzees (Sobolewski et al., 2012a,b; Trumble et al., 2015, Wittig et al., 2016; Samuni et al., 2017). Within party aggression increases urinary glucocorticoid levels (Wittig et al., 2015), and grooming with bond partners in chimpanzees co-occurs with high urinary oxytocin and low urinary glucocorticoid concentrations (Crockford et al., 2013; Wittig et al., 2016). Thus, studies have started to show highly dynamic and intricately coordinated interplay between neuroendocrine systems and behavior, which can simultaneously support long-term reproduction strategies and social relationships, *and* ever-changing social contexts and social interactions. How does this flexible synchrony take place, with hormones simultaneously supporting long-term mating strategies and social relationships as well as short-term social interactions?

4. What causes individual variation in how hormonal and neurohormonal systems interact with emotions, social cognition and social behavior?—Genes, maternal environment, and the wider environment, during development have all been demonstrated to impact on hormonal systems, and on subsequent neurocognitive development, as well as on gene expression (Slavich and Cole, 2013). The subsequent impact on adult social behavior is a current key topic in human health research, likely requiring intense inter-disciplinary research to unravel. How much can genetics account for variation across individuals? How different can mothering styles be and how profound are the effects on offspring? Is variation more or less extreme in humans than non-human mammals? If genes, the mothers' prenatal environment, and mothering style, all impact on offspring's sociality, how much can later social and environmental experience compensate? In parallel with laboratory studies, examining these patterns in animals that live in the social and ecological environment in which they have evolved and are adapted to live in, enabling animals to grow up in and experience a society that encompasses a full range of social

relationships, with all their complexity, will be critical for reaching a full understanding of this complex picture.

Conclusions

In summary, the use of non-invasive hormone sampling during the daily life of wild animals can determine neuroendocrine influence on social behavior, and the influence of social behavior on neuroendocrine systems. This expanding approach promises to provide further information on hormonal mechanisms that support different social strategies used by primates living in different social systems, the resulting social relationships that they form and maintain, as well as on the ever-changing social interactions in which they engage. Examining context-specific effects of neuropeptides and other interacting hormones across different primate social systems will likely give insights into selection pressures on variation in social bonds, including mothering-styles and attachment, cooperation and in-group/out-group effects. Studies to date suggest that 'tend-and-defend' behavior supported by the oxytocin system in mammalian mothers, is also supported by the oxytocin system in other close social bond relationships, as well as during cooperative and territorial behavior outside of close social relationships. Whether flexibility in the oxytocin system has facilitated the evolution of group-level collective action, as seen in chimpanzees in hunting and territorial contexts, and in humans in these and many additional contexts, remains to be determined.

We have discussed a number of important research questions that could be addressed in a variety of primate species. With currently available methods and the continued development of new methods to measure hormones and neurochemicals non-invasively, we hope that many of these questions will be explored in a multitude of primate species in the future, and thereby provide a rich resource for understanding the processes impacting the evolution of sociality and variability in social relationships.

Acknowledgements

The authors would like to thank Verena Behringer, two anonymous reviewers and Special Issue editor, James Higham for helpful comments on the manuscript. Funding was provided by an European Union Research Council starting grant No. 679787, and the Max Plank Institute of Evolutionary Anthropology, Leipzig, Germany for Catherine Crockford, and the Wisconsin National Primate Research Center, University of Wisconsin for Toni E. Ziegler grant NIH P51OD011106.

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Table 1.

Future questions suitable for within and between species comparisons in wild primate settings.

	Future Questions and Directions
1	***What causes social bonding neuroendocrinological circuitry to support different types of social relationship in different species?***
2	***Do hormonal systems supporting pair bonds differ from those influencing other male and female sexual relationships, such as in one-male units?***
3	***How fast and flexible is the synchrony between neuroendocrine systems, social relationships and ever-changing social contexts?***
4	***What causes individual variation in how hormonal and neurohormonal systems interact with emotions, social cognition and social behavior?***