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Social Monogamy in Nonhuman Primates: Phylogeny, Phenotype, and Physiology

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Monogamy as a social system has been both a scientific puzzle and a sociocultural issue for decades. In this review, we examine social monogamy from a comparative perspective with a focus on primates, our closest genetic relatives. We break down monogamy into component elements, including pair-bonding and partner preference, mate guarding or jealousy, social attachment, and biparental care. Our survey of primates shows that not all features are present in species classified as socially monogamous, in the same way that human monogamous relationships may not include all elements—a perspective we refer to as "monogamy à la carte." Our review includes a survey of the neurobiological correlates of social monogamy in primates, exploring unique or common pathways for the elemental components of monogamy. This compilation reveals that the components of monogamy are modulated by a suite of androgenic steroids, glucocorticoid hormones, the nonapeptide hormones oxytocin and vasopressin, and other neurotransmitter systems (e.g., dopamine and opioids). We propose that efforts to understand the biological underpinnings of complex human and animal sociosexual relationships will be well served by exploring individual phenotypic traits, as opposed to pursuing these questions with the assumption that monogamy is a unitary trait or a species-specific characteristic.

Monogamy in humans has fascinated and puzzled both social and natural scientists for decades. Research has focused on the evolutionary pressures that may have selected for monogamous traits, the potential adaptive functions of monogamy, and determinants of monogamy at all levels of analysis from cells to cultures. Among nonscientists, monogamy has been an important topic of discussion from a host of diverse perspectives for centuries, including moral, ethical, religious, political, and cultural perspectives. Many long-standing and current debates among U.S. politicians in what has been referred to as the "culture war" focus on the role of monogamy within the context of religion, marriage, and family life (Brandon, 2013). Monogamy clearly represents an important scholarly topic in the biological and social sciences and continues to be a flash point for the general public.

The interest in monogamy as a social and mating system in humans is somewhat surprising, given the relatively low prevalence of this trait across the globe. Estimates based on ethnographic analyses (Dow & Eff, 2013; Marlowe, 2000) have suggested that the incidence of monogamy as a defined cultural standard is relatively rare. According to these analyses, 82% of cultures permit men to marry multiple women, 1% permit the converse (i.e., women are permitted to marry multiple men), and 17% of socioethnic groups have monogamous marriage as a cultural norm. The actual incidence of monogamy as a relationship system, as a proportion of the population, among humans is probably higher than 17%, given that while single male:multiple female marriages or relationships are permitted in cultures classified as polygynous, most men do not have sufficient resources to support more than one wife or partner, or not all males choose to have multiple female marriages.

The present review explored the neurobiological mechanisms underlying the traits associated with monogamy as a social system from a comparative perspective, focusing on our closest genetic relatives, the nonhuman primates (NHPs). Considerable knowledge regarding the evolution, ecology, and neurobiology of monogamy has emerged from laboratory studies of prairie voles (*Microtus ochrogaster*; Carter, Devries, & Getz, 1995; Freeman & Young, 2013; Johnson & Young, 2015). While informative

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on a number of levels, the vole model has notable limitations regarding our appreciation of the evolution and ecology of monogamy and its underlying neurobiology. In primates, including humans, social complexity is thought to play a large role in the elaboration of the primate brain, especially aspects of the "social brain" (Dunbar & Shultz, 2007; Platt, Seyfarth, & Cheney, 2016; Seyfarth & Cheney, 2002). As a consequence, the processing of social information, the capacity and duration of social memory, and the potential for social flexibility and conditional social responses are particularly sophisticated in nonhuman primates, and are thus more likely to reflect similar processes in humans. As a consequence, if we are interested in searching for the "fingerprints" of natural selection on the social brain, and in scrutinizing those aspects of the social brain that predispose some species or individuals to engage in monogamous versus nonmonogamous relationships, then the study of our closest genetic relative may be the best heuristic for understanding human monogamy.

Our goal in this review was to explore the neurobiological substrates of monogamous social relationships in primates. While we recognize that decisions about engaging in monogamous versus nonmonogamous sociosexual relationships in humans are not limited to heterosexual partners (Dunbar & Shultz, 2007; Macedo, 2015; Whitton, Weitbrecht, & Kuryluk, 2015), the NHP literature focuses primarily on male–female relationships, and our discussion is thus limited to this context. We begin by exploring some definitional issues in the study of monogamy and why this topic has been somewhat intractable to study from a scientific perspective. We follow these definitional issues with a discussion on the diversity of mating systems, their evolutionary and phylogenetic origins of monogamy in nonhuman primates, and the specific behavioral traits that comprise monogamous relationships in NHPs. The review includes a detailed analysis of the neural and endocrine substrates that underlie the social traits that lead to, or are a consequence of, monogamous relationships in NHPs. We provide a roadmap for exploring the neurobiology of the social brain in humans, with the goal of identifying features of the primate social brain that are relevant to individual social decisions about investment in, and fidelity to, a partner in a relationship.

Definitional Issues in the Study of Monogamy

The first definitional issue in the study of monogamy involves identifying the biological level being addressed (Gowaty, 1996). At its most fundamental definition, monogamy can be defined at the level of genes: *genetic monogamy*. According to this definition, monogamy is present when the genes contained in gametes from one individual combine only with the genes contained in gametes from a second individual. This fundamental definition has little to do with either the common notion of monogamy or the use of the term in natural and social sciences. Further, it can also lead to some interesting conundrums. For instance, consider an invertebrate species with external fertilization in which males and females are completely solitary, never engage in a single social interaction, and distribute sperm and egg into the environment. If gametes from one individual only combine with gametes of one other individual, this species *would* qualify as monogamous. Alternatively, an otherwise loving and committed human couple who conceive via in vitro fertilization from an unrelated sperm or egg donor *would not* qualify as genetically monogamous. While popular culture suggests that extrapair (i.e., nonmonogamous) paternity is frequent, recent analyses have suggested that these rates are low both historically and in contemporary times, at least in Western cultures (Larmuseau, Matthijs, & Wenseleers, 2016). Nonetheless, departures from genetic monogamy do occur in human populations.

A second level of monogamy can be defined as *sexual monogamy*: partners engage in exclusive sexual interactions with each other. Sexual monogamy is viewed as the cultural norm in most Western societies, despite the relatively high prevalence of polygamy across human societies. Monogamy and nonmonogamy are often viewed as two sides of the same coin, yet a growing number of people (4% to 5% of Americans; Conley, Moors, Matsick, & Ziegler, 2013; Conley, Ziegler, Moors, Matsick, & Valentine, 2013) are adopting another approach, called consensual nonmonogamy (i.e., an agreement between two partners that one or both of them will have other sociosexual relationships). Among human couples that would categorize themselves as monogamous, the incidence of sexual relationships outside an established couple indicates that sexual infidelity occurs annually among 2% to 4% of couples (Fincham & May, 2017). From the perspective of animal research, the classification of species as sexually monogamous versus nonmonogamous is limited by the observational acuity and persistence of the observer, and there are many examples of cryptic mating outside monogamous relationships (Arnqvist & Kirkpatrick, 2005; Digby, 1999; Griffith, Owens, & Thuman, 2002).

The most common level of analysis for monogamy excludes the strict criteria of genetic and sexual monogamy: *social monogamy*. We explore the details of social monogamy in detail in this review, but, briefly, it is characterized by a number of important features, including spatial and temporal proximity of a single male–female pair, exclusion of unfamiliar adult individuals from the home range, corearing of offspring, and the existence of a strong social attachment (pair bond) between the adult male and female. This multivariate definition of monogamy poses its own issues with regard to measurement and classification of species and/or individuals as socially monogamous, in the following sense: Biologists and psychologists that study unidimensional and univariate traits have a relatively simple task in terms of definition and measurement of the trait of interest. A biologist interested in measuring canine tooth length in a carnivore, body mass in a rodent, or the color and intensity

of redness in the sex-skin swelling of a female baboon simply needs a caliper, a balance, or a spectrometer. A psychologist studying emotional intelligence, reaction time, or brain activity requires an emotional intelligence scale, a stopwatch, or functional magnetic resonance imaging (fMRI). As we will see in this review, monogamy is anything but a simple unitary trait. Biologists or sociologists studying social monogamy in nonhuman animals or humans have a much more difficult task. Social monogamy can involve numerous elemental components, including partner preference, sexual jealousy, cohabitation, coordinated activity, social support, distress upon separation, partner fidelity, and a host of other social profiles. The following question is therefore critical: Does a species (or individual) need to express all elements, some elements, or only one element to be classified as socially monogamous? We make clear in our discussion that just as there are both species and individual differences in unitary traits (canine length or reaction time), there can be important differences within and among species in the way that the component elements of social monogamy are expressed. This notion is not new (e.g., Díaz-Muñoz & Bales, 2016; Mendoza, Reeder, & Mason, 2002) but provides an important conceptual tool to understand the neurobiological substrates of these traits associated with these social relationships.

In our review, we refer to this approach as *monogamy à la carte*. The concept derives from two strategies of preparing and ordering meals at a restaurant: ordering a full meal with appetizers, main meal, and dessert that are set and invariable (*prix fixe*) and ordering individual items one by one from the menu (*à la carte*). By way of analogy, there is a revolution in the discussion of the diagnosis of mental disorders, moving away from the *Diagnostic and Statistical Manual of Mental Disorders*, Fifth Edition (*DSM*-5), which has broad definitions of mental disorders that are treated as unitary phenomena (e.g., autism, schizophrenia) toward what is referred to as research domain criteria (RDoC; Insel, 2014; Insel et al., 2010). This latter approach identifies and dissects individual components or phenotypes of a mental disorder (e.g., are affective/emotional systems or language function altered in a person?). For example, it is more likely for basic and clinical scientists to gain insights into the neurobiological basis of emotional dysregulation as a phenotype than to discover meaningful biological correlates of the broad clinical diagnosis of "depression." In the same way, therefore, students of social monogamy are more likely to find neurobiological substrates of individual components of social monogamy (e.g., mate guarding, male responsiveness to infants, social preference for a partner) than they would in an unfruitful search for the neural substrates of "social monogamy."

This review first documents the distribution of social monogamy among NHPs, and summarizes current, but certainly still controversial, hypotheses regarding the evolutionary selective pressures that may have led to one or more of the cluster of traits associated with social monogamy. The bulk of our discussion focuses on what is known about the underlying neurobiology of these traits individually. The main section of the review explores the knowledge base regarding pair-bonding, mate guarding, social attachment, and biparental care. From the mechanistic side, we review the available data for five major endocrine, neuroendocrine, and neurotransmitter systems: sex-steroid hormones, glucocorticoids, the hypothalamic neuropeptides oxytocin and vasopressin, dopamine, and opioid-like neurotransmitters. A brief summary of these five neurobiological measures can be found in Table 1 for readers who are interested in refreshing their memories. This presentation makes it immediately apparent to even the casual reader that there are many gaps in our knowledge of primate social neurobiology, and many cases in which mechanisms associated with social monogamy have been assessed in only one or a few socially monogamous species.

Phylogenetic Distribution of Social Monogamy

In Western societies, individuals are accustomed to identifying their romantic relationships as monogamous; this view is often regarded as a hallmark trait of human romantic relationships. Yet both within and across human societies, the presence and rigidity of monogamy is anything but universal, and more broadly, the presence of monogamy is a relatively rare mating system found across all mammals (Kleiman, 1977). While approximately 90% of bird species are classified as monogamous (Cockburn, 1998), less than 10% of mammalian species are classified as monogamous (Kleiman, 1977; Lukas & Clutton-Brock, 2013). The distribution of social monogamy across mammalian clades is also widely variable. For instance, nearly one-third of primate species are recognized as monogamous, while ungulates, including giraffes, pigs, hippos, deer, cattle, and whales, have very few species characterized as monogamous (Lukas & Clutton-Brock, 2013). This variation in mammalian monogamy raises an important question concerning which evolutionary and social pressures select for, or favor, monogamy. Living in social groups may be a requisite for social monogamy, but, importantly, social living itself does not explain the presence or likelihood of monogamy. Nearly one-quarter of nonmonogamous mammalian species live in social groups and possess sophisticated social relationships (Lukas & Clutton-Brock, 2013). Notwithstanding this rich social complexity found among primates, the ecological, social, and neurobiological components that constitute monogamy remain a stimulating and puzzling evolutionary question for biologists, psychologists, and sociologists alike.

The evolutionary history of mating systems in NHPs shows that both monogamy and polygamy have emerged independently across many separate primate families. Of the two primary mating strategies, polygamy emerged first. Computational models suggest that harem polygyny was among the first of these strategies to have evolved in the

Table 1. *Neurobiology Primer*

System	Properties
1. Sex steroids	The primary regulatory sex steroids involved in social behavior are (1) androgens (testosterone and its precursors; e.g., androstenedione, DHEA), (2) estrogens (primarily estradiol, but also upstream and downstream steroids estrone and estriol), and (3) progestogens (progesterone). These compounds are synthesized primarily in the testes, ovaries, and corpora lutea, respectively, although some synthesis can occur either peripherally in the adrenal cortex or centrally in the brain. In the brain, steroid hormones bind with intracellular receptors, and these complexes subsequently act in the nucleus as a factor to alter DNA transcription and ultimately neuronal function.
2. Glucocorticoids	In all primates, the most common glucocorticoid (GC) hormone is cortisol. Cortisol is synthesized in the adrenal gland and released into circulation, controlled by a regulatory system that involves hippocampal control of hypothalamic releasing hormone (CRH) and pituitary trophic hormones (ACTH). Like sex steroids, GCs affect cell function via intracellular GC receptors and regulate a host of organismal end points, including metabolism, immunology, cardiovascular function, and cognitive and behavioral responses. Glucocorticoids thus regulate peripheral metabolic responses to stressors and mediate important elements of mood, emotion, sensory processes, and cognition in the brain.
3. Oxytocin and vasopressin	These closely related nine-amino acid neuropeptides are synthesized in the supraoptic and paraventricular nuclei of the hypothalamus. The genes regulating the synthesis of oxytocin (OT) and arginine vasopressin (AVP) are located in close proximity on the same chromosome, and the neuropeptides differ by only two amino acids. Classic peripheral actions of these neuropeptides —smooth muscle contractions in the uterus and mammary gland (OT) and conservation of water and vasoconstriction (AVP)—are mediated by release from the posterior pituitary into the general circulation. Hypothalamic neurons synthesizing OT and AVP also project widely to important regions in the "social brain," including the amygdala, nucleus accumbens, bed nucleus of the stria terminalis, and the anterior cingulate cortex. The neuropeptides are classic neuromodulatory agents, altering the likelihood of neural activity (either enhancing or inhibiting) in the regions in the brain where they are released.
4. Dopamine	The catecholamine neurotransmitter dopamine (DA) is synthesized primarily in two major regions of the midbrain: the substantia nigra and the ventral tegmental area. The former is involved in motor regulation, while the latter regulates primary reward mechanisms (although there is growing evidence of overlap in substantia nigra and ventral tegmental area projections). Like the neuropeptides, DA is a modulatory neurotransmitter, altering the probability of action potentials in regions involved in reward processes, associative learning, and cognitive function through mesolimbic and mesocortical projections.
5. Opioids	Neurons throughout the brain synthesize endogenous opioid-like neuropeptides in three families: endorphins, enkephalins, and dynorphins; likewise, receptor targets for these peptides are distributed throughout the brainstem, cerebellum, midbrain, and forebrain. Many of these peptide-receptor connections are implicated in pain perception, but the distribution of neurons and receptors in regions relevant for the social brain (e.g., nucleus accumbens, limbic system, and multiple lobes of the cerebral cortex) implicates opioids in social processes, especially social reward.

Note. Several neuroendocrine and neurotransmitter systems are implicated in regulating some of the important features of social phenotypes, including those associated with pair-living, socially monogamous primates. In the social brain, these systems interact in complex ways to produce social behavior and ultimately contribute to the formation and preservation of social relationships. Here we provide the fundamental properties of each system.

strepsirrhines, (prosimian primates including lemurs, lorisoids) originally in loris around 42 million years ago (mya) and later again in lepilemurs about 36 mya. Monogamy later emerged in lemur families around 28 mya, followed by New World monkeys (NWMs) around 26 mya, and finally among the gibbons around 19 mya (Opie, Atkinson, & Shultz, 2012; Figure 1). Given the phylogenetic distance and broad ecological differences among primates, it is likely that monogamy emerged in response to multiple ecological and life-history conditions. Therefore, it should not be surprising if the social phenotype of monogamy varies considerably across primate species as well.

How Might Evolution "Select" for Social Monogamy and Its Associated Traits?

The evolutionary causes and consequences of social monogamy in primates require that monogamous traits confer greater reproductive and social advantages than would otherwise result from simply maximizing the number of mating opportunities. Social monogamy is inherently complex and multifaceted; there is no master key and lock answer to explain all forms of monogamy. However, the diversity of social living in NHPs offers exciting opportunities to explore some of the social and biological nuances that facilitate strong social bonds and monogamous relationships. NHPs live in a variety of social environments ranging from solitary nocturnal living to living in large social groups with hundreds of individuals. Thus, given that monogamy is an amalgamation of many social phenotypes, there are many perspectives through which one can view monogamy.

The emergence of monogamy, especially in primates, has been viewed through several theoretical lenses, including female sociospatial dispersion (monogamy is common in cases where females are intolerant of other females and are distributed spatially so that males are unable to secure access to multiple females; Lukas & Clutton-Brock, 2013); and predation and male infanticide (monogamy is associated with high risk of infanticide; Opie, Atkinson, Dunbar, & Shultz, 2013a; Shultz, Opie, & Atkinson, 2011). Each of these perspectives has engendered robust debate (de Waal & Gavrilets, 2013; Dixson, 2013; Lukas & Clutton-Brock, 2013; Opie, Atkinson, Dunbar, & Shultz, 2013b), and there is likely some merit for both in accounting for the multiple cases of independent evolution of

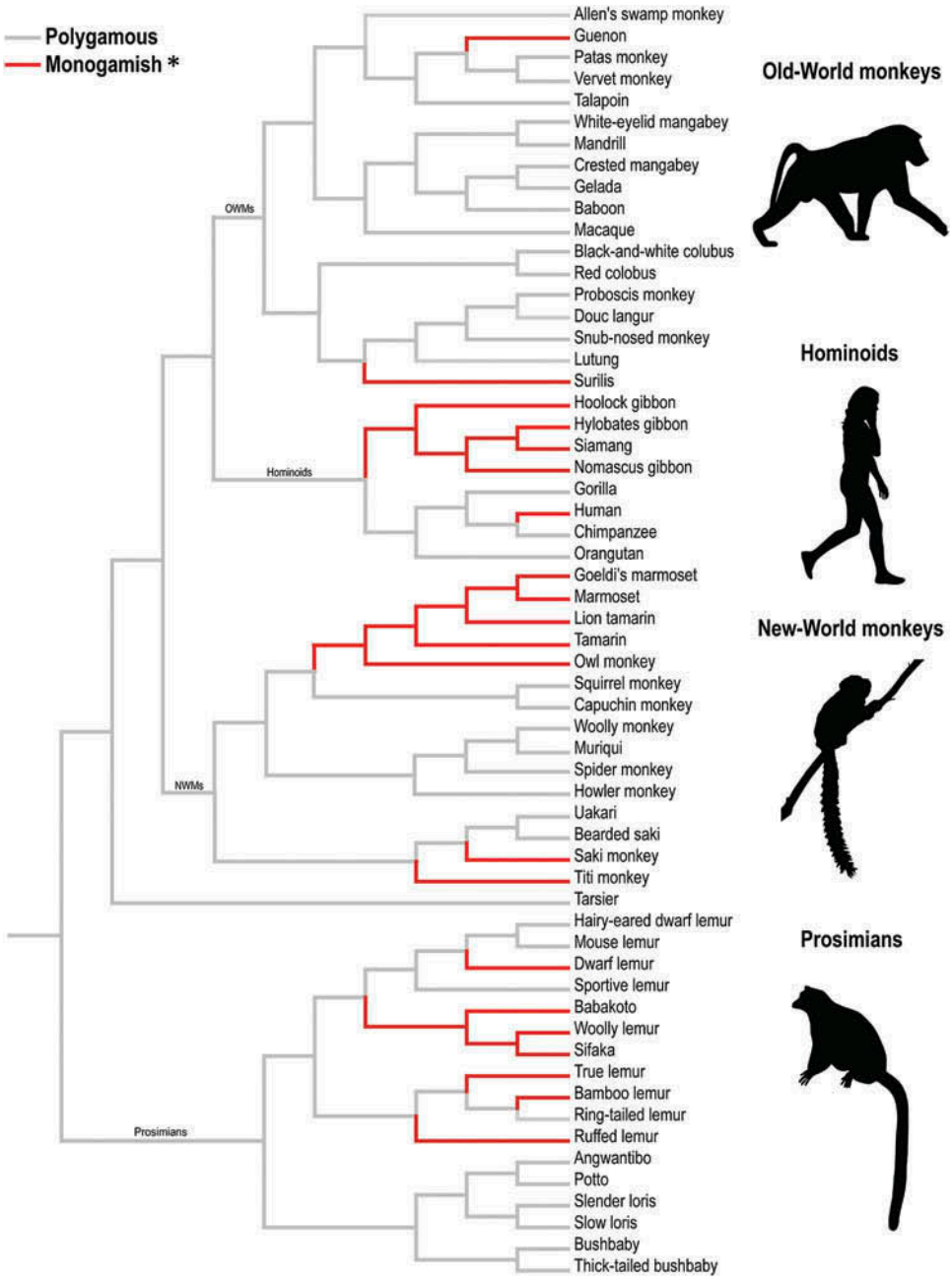

Figure 1. Distribution of social systems across primates with classifications derived from Lukas and Clutton-Brock (2013). Gray lines represent polygamous taxa; red lines represent taxa that show one or more social features associated with monogamy; i.e., "monogamish" *(tip of the hat to Dan Savage). This primate phylogeny was assembled using data from 10kTrees (Arnold, Matthews, & Nunn, 2010) and visualized using Mesquite (Maddison & Maddison, 2001). Representative genera from Old-World monkeys (OWMs), Hominoids, New-World monkeys (NWMs), and Prosimians are presented.

monogamy in primates. The multiple forces that "select" for monogamy across species and across contexts would be expected to generate variants of the behavioral phenotypes that are displayed among monogamous primates, as well as the neurobiology that regulates these phenotypes.

The term *monogamy* has been used as a catchall for describing social organizations (i.e., pair-living), social relationships (i.e., male–female attachment), and mating systems (i.e., exclusive monogamous mating). While these components are often overlapping, they do not necessarily always covary (Tecot, Singletary, & Eadie, 2016). Here, they serve as an illustration of "monogamy as a menu." Some monogamous species cohabit as a male–female pair but do not form an enduring emotional bond (Schülke & Kappeler, 2003), while others engage in pair-living and mate monogamously (Huck, Fernandez-Duque, Babb, & Schurr, 2014). There is no single social repertoire that describes all monogamous primates; however, we can examine broad categories of behavior that typically constitute monogamous relationships. There are four broad social

features that are "on the menu" in primate monogamy: (1) pair-bonding, (2) mate guarding, (3) social attachment, and (4) biparental care. By characterizing the behavioral repertoire of various socially monogamous primates, we will be able to assess the regulatory roles of the neurobiological systems that may underlie each behavioral trait associated with monogamy and the social brain.

Neurobiology of Primate Social Monogamy

The ecological and social factors associated with the transition from group living to pair living may have fine-tuned the brain's neuroendocrine systems to maintain strong individual male–female relationships; following the emergence of monogamy, the development of strong social bonds and biparental care has further shaped the social brain and behavior of primates. Given the importance of brain evolution on primate social phenotypes (Dunbar, 2009; Dunbar & Shultz, 2007; Shultz & Dunbar, 2007), one would expect the evolution of unique neurobiological substrates that regulate the different behavioral facets of social monogamy across primates. Despite the high prevalence of monogamy in NHPs and the important translational status of NHP models for human sociality, investigations into the neurobiological substrates that underlie monogamous relationships are still in their infancy and are only beginning to be uncovered (Bales, Mason, Catana, Cherry, & Mendoza, 2007). Much of the spotlight for the biological mechanisms underlying monogamy has rested primarily on sex steroids (i.e., androgens and estrogens) and neuropeptides (e.g., oxytocin [OT] and arginine-vasopressin [AVP]). Notably, the steroid/peptide theory of social bonds provides a conceptual framework for the integration of these neuroendocrine systems (van Anders, Goldey, & Kuo, 2011). While the interaction between sex-steroid and neuropeptide systems is certainly vital to regulation of social features associated with primate monogamy, several other neuroendocrine systems have also been identified as important modulators of monogamous relationships in NHPs, including glucocorticoids, catecholamines (e.g., dopamine), and opioids. Here, we discuss the multiple interacting neuroendocrine systems that regulate essential "menu items" associated with monogamy, including behavioral indicators of pair-bonding, mate guarding, social attachment, and biparental care (Table 2).

Pair-Bonding

The most conspicuous features of an established monogamous relationship in NHPs are the behavioral manifestations of a pair bond between two individuals, which include high levels of *mate-directed sociality* and a *partner preference*. High-quality social interactions with a mate are, not surprisingly, critical to both the development and the preservation of an enduring bond (Carter et al., 2006). In NHPs, mate-directed sociality is characterized by high rates of physical contact, affiliative behavior (e.g., grooming, food sharing), and sexual behavior (Ågmo, Smith, Birnie, & French, 2012; Kleiman, 1977; Mason & Mendoza, 1998; Schaffner, Shepherd, Santos, & French, 1995; Smith, Ågmo, Birnie, & French, 2010), not unlike human relationships. A pervasive and reciprocal preference for a long-term partner over an opposite-sex stranger (i.e., partner preference) is the second hallmark of a pair bond (Buchanan-Smith & Jordan, 1992; Carp et al., 2016; Fernandez-Duque, Valeggia, & Mason, 2000). Sexual exclusivity to a long-term mate is threatened when one or both members of a pair spend time with an opposite-sex stranger, especially if it is at the expense of spending time with a long-term mate (Digby, 1999; Garber, Porter, Spross, & Di Fiore, 2016; Huck et al., 2014).

While a robust partner preference is important for monogamy, it is not necessarily required. Some NHPs (e.g., titi monkeys) consistently show a preference for their long-term mate over an opposite-sex stranger (and even over individuals they were formerly bonded with) (Carp et al., 2016), while other NHPs (e.g., marmosets, tamarins) have more flexible partner preferences. Marmosets and tamarins are notorious for their expression of high levels of sociality within their family unit, yet, unlike the rigid partner preference in titi monkeys, marmosets and tamarins will engage in affiliative and sociosexual behavior with opposite-sex strangers in some contexts (Baker, Bales, & Dietz, 2002; Baker, Dietz, & Kleiman, 1993; Dietz & Baker, 1993; Epple, 1990; Garber et al., 2016; Goldizen, 1988; Schaffner & French, 2004; Sussman & Garber, 1987). Both males and females will opportunistically interact with an opposite-sex stranger (e.g., when their mate is absent or their visual access is occluded; Inglett, French, & Dethlefs, 1990), yet there are also sex and species differences in the expression of affiliative, sexual, and aggressive behavior as a result of social status, social context, and duration of pair bond (Anzenberger, 1985; Evans, 1983; Smith et al., 2010). Thus, marmosets and tamarins engage in both monogamous and facultative polyandrous mating strategies, suggesting that a categorization of either monogamous or nonmonogamous oversimplifies their complex behavioral repertoires.

Sex Steroids. The hypothalamic–pituitary–gonadal (HPG) axis has important physiological functions, including the regulation of growth and reproductive processes (Mooradian, Morley, & Korenman, 1987), as well as the acquisition and maintenance of sexually dimorphic traits in males and females (Cooke, Hegstrom, Villeneuve, & Breedlove, 1998; MacLusky & Naftolin, 1981). Thus, the HPG axis has the potential to regulate some of the key behavioral traits associated with monogamy. In particular, the class of steroid hormones that includes estrogens and androgens (i.e., sex steroids) has potent effects on brain and behavior, notably on competition and aggression in the context of male reproduction, as well as on female reproductive behaviors

Table 2. *Neurobiological Substrates of Monogamy in Primates*

Measure	Behavioral Trait				References
	Pair-Bonding	Mate Guarding	Social Attachment	Paternal Care	
Sex steroids					
Testosterone[c]	↑	↑		↓	(Nunes et al., 2000; Nunes et al., 2001; Prudom et al., 2008; Ross & French, 2011; Ross et al., 2004; Ziegler et al., 2011; Zeigler et al., 2005; Ziegler & Snowdon, 2000)
Testosterone agonist	↑/↓			0	(Kendrick & Dixson, 1985)
Estradiol[c]	↑				(Digby, 1999; Kendrick & Dixson, 1983; Ziegler et al., 2005)
Estradiol agonist				↑	(Kendrick & Dixson, 1985)
Glucocorticoids					
Cortisol[c]	↑	↑/0	↓	↓	(Fisher-Phelps et al., 2015; Hennessy et al., 1995; Nunes et al., 2001; Ross & French, 2011; Ross et al., 2004; Rukstalis & French, 2005; Smith et al., 2011)
CRH-1 antagonist			↑		(French et al., 2007)
Neuropeptides					
Oxytocin[c]	↑	0			(Finkenwirth et al., 2015; Fisher-Phelps et al., 2016; Snowdon et al., 2010)
Oxytocin agonist	↑		0	↑	(Cavanaugh et al., 2015; Cavanaugh et al., 2014; Mustoe et al., 2015; Saito & Nakamura, 2011; Taylor & French, 2015)
Oxytocin antagonist	↓/0		↓	0	(Cavanaugh et al., 2016; Cavanaugh et al., 2014; Mustoe et al., 2015; Smith et al., 2010)
Vasopressin[c]		↑			(Fisher-Phelps et al., 2016)
Vasopressin agonist	↑			↑	(Jarcho et al., 2011; Taylor & French, 2015)
Dopamine					
Neural activity in the reward system	↓				(Bales et al., 2007)
Opioids					
MOR agonist	↓				(Ragen et al., 2015; Ragen et al., 2013)
KOR agonist			0		(Ragen et al., 2015)
KOR antagonist			↓		(Ragen et al., 2015)
Nonspecific antagonist	↓		↑		(Ragen et al., 2013)

Note. [c] = correlation of measured hormone concentration with social feature. ↑ = increases social feature; ↓ = decreases social feature; 0 = no effect on social feature. Cells without an entry indicate no data have been published.

(Hau, 2007; Wallen, 2001, 2005). In human males, there is a wealth of literature showing the reductions in testosterone in pair-bonded men and fathers compared to single men (Burnham et al., 2003; Gettler, McDade, Agustin, Feranil, & Kuzawa, 2013; Gettler, McDade, & Kuzawa, 2011; Gray, 2003; Gray, Ellison, & Campbell, 2007; Kuzawa, Gettler, Muller, McDade, & Feranil, 2009; McIntyre et al., 2006; van Anders & Goldey, 2010; van Anders & Watson, 2006, 2007). Given the importance of androgenic steroid hormones to both the organization of neural structures underlying sex-typical behavior in primates (Smith, Birnie, & French, 2013) and the activation of aggressive and reproductive behaviors in males and females (Muller & Wrangham, 2004; Wallen, 2005), this section focuses on the impact of estrogens and androgens on pair-bonding behavior in NHPs.

In the wild, marmosets are known to form male–female monogamous pairs as well as multiple-male:single-female polyandrous groups (Ferrari & Digby, 1996), but they rarely exist in groups composed of two breeding females (Digby, 1995a). In a naturalistic lab study, marmosets were housed in both male–female and multiple-male:single-female groups (only groups consisting of two related males were tolerated; Schaffner & French, 2004). While male marmosets in polyandrous groups were less frequently in proximity with the female and copulated more frequently with the female than monogamous males did, there were no differences in testosterone concentrations between polyandrous males and monogamous males (Schaffner & French, 2004). This suggests that marmosets engage in both monogamous and facultative polyandrous mating strategies, that males do not monopolize the female in polyandrous groups and show remarkably low aggression, and that testosterone levels do not explain the behavioral differences between monogamous males and polyandrous males (Baker et al., 1993; Goldizen, 1988).

In NHP species that engage in pair-bonding and biparental care, there is a clear trade-off for males during the postpartum period. Because some NHP females experience a relatively quick postpartum ovulation, changes in males' testosterone levels in response to a postpartum ovulation provide a crucial test of this trade-off hypothesis. If a partner ovulates shortly after parturition, there is a clear and direct benefit to allocating reproductive effort toward mating. Yet if a female's ovulation occurs later after parturition, there is a significant advantage to allocating reproductive effort toward offspring care, and it appears that testosterone may mediate this differential allocation of reproduction effort in male NHPs. Male tamarins whose partner ovulated within two weeks postpartum had a greater concentration of testosterone than males whose partner ovulated more than two weeks postpartum (Nunes, Fite, Patera, & French, 2001), suggesting that variation in testosterone during the paternal care period may be associated with a partner's fertile period rather than response to infants.

While male marmosets have a natural behavioral sensitivity to ovulatory cues from their female partners (i.e., increased sexual behavior during their partner's periovulatory period; Kendrick & Dixson, 1983), there is mixed evidence that male marmosets experience changes in testosterone secretion in response to a females' reproductive cycles (Schaffner & French, 2004; Ziegler, Schultz-Darken, Scott, Snowdon, & Ferris, 2005). However, it is clear that social condition greatly impacts this response. In both paired and single males, but not fathers, exposure to the scent of a novel ovulatory female increased males' testosterone levels and sexual arousal relative to exposure to a vehicle scent (Ziegler et al., 2005). This suggests that male marmosets are behaviorally sensitive to changes in the scent of their female partners across the reproductive cycle, and that testosterone secretion by the HPG axis may play a significant role in this response. Female marmosets, however, are sensitive to changes in estradiol levels. In ovariectomized females, treatment with preovulatory levels of estradiol increased, while treatment with midluteal levels of progesterone virtually abolished, proceptive and receptive behavior (testosterone had no effect; Kendrick & Dixson, 1985). These results suggest that in pair-living NHPs, both males and females appear to be sensitive to neuroendocrine changes in the female across her ovulatory cycle.

Neuropeptides. The neuropeptides OT and AVP are critical and pervasive regulators of physiological and reproductive processes across the life span (Argiolas & Gessa, 1991; Knobloch & Grinevich, 2014). These two neuropeptide systems are implicated in a host of brain regions involved in attachment, parental care, reward, aggression, and social memory (Gimpl & Fahrenholz, 2001; Ludwig & Leng, 2006; Sofroniew, 1983; Stoop, 2012, 2014), all of which are critical behavioral elements of monogamy. For these reasons, OT and AVP are prime candidates to be unique regulators of mate-directed sociality and partner preference in NHPs. In voles, there is pronounced interspecific variation in the density and distribution of the OT receptor (OTR) and the AVP 1a receptor (V1aR) that reflects differential social organization and mating strategies (i.e., monogamous versus nonmonogamous; Barrett, Keebaugh, et al., 2013; Insel & Shapiro, 1992; Ophir, Gessel, Zheng, & Phelps, 2012). A comprehensive sampling of central neuropeptide circuits in NHPs has yet to be accomplished, although information is available for a few species, including marmosets, titi monkeys, rhesus macaques, and humans. OT and AVP receptors are distributed across several sensory-processing centers, indicating that neuropeptides are important modulators of visual and multimodal processing in primates (Freeman & Young, 2016; French, Taylor, Mustoe, & Cavanaugh, 2016). In all the surveyed primates, the OTR and V1aR are also widely distributed throughout the social decision-making network, yet there are strikingly different profiles for these receptors across species, potentially reflecting both species-level differences in social structures and mating systems (Freeman & Young, 2016; French et al., 2016). This marked interspecific

variation in the expression of OT-ergic and AVP-ergic neurons, their central projections, and the density and distribution of cellular receptors, potentially guides important differences in social phenotype, including monogamy, across primates.

Recent studies have attempted to evaluate whether AVP and OT systems across primates are associated with monogamy. In the gene that codes for V1aR, high interspecific variability has been associated with the presence of monogamy in New World monkeys (Ren, Chin, & French, 2014). New World monkeys show even greater variability in the OT system, not only in the gene that codes for the OTR but also in the gene that codes for the structure of the OT ligand itself (six distinct OT ligand variants have been identified in New World monkeys) (French et al., 2016). The structural differences in the OT ligand in New World monkeys has led to a recent surge of interest in the evolution of these OT/OTR systems in light of the fact that (1) New World monkeys have an especially high proportion of species (60%; Lukas & Clutton-Brock, 2013) that exhibit monogamous characteristics and (2) OT is a crucial neuromodulator of behavioral elements underlying monogamy (e.g., affiliation, social bonding, reproduction, parental care). Two independent studies have demonstrated coevolution between differences in OT ligand structure and variability in the OTR across primates; in turn, this OTR variability has been associated with the occurrence of both social monogamy (Ren et al., 2015) and paternal care (Vargas-Pinilla et al., 2015) in New World monkeys. Moreover, the substantial variation in the OTR across humans, gibbons, and New World monkeys suggests that monogamy may have evolved by independent molecular mechanisms in primates (Babb, Fernandez-Duque, & Schurr, 2015). In humans, polymorphisms in the OTR (SNP rs7632287) and V1aR (RS3 microsatellite) genes have also been linked to the expression of behaviors associated with monogamy, including pair-bonding and marital quality (Walum et al., 2008; Walum et al., 2012). Notably, OT and AVP genes contribute to the expression of behavioral traits that comprise monogamy in humans and NHPs, and the molecular data corroborate the point that the evolution of the OT and AVP systems corresponds, at least in part, to the evolution of the social elements comprising monogamy in primates.

In addition to the association between the genetic makeup of the OT and AVP systems with monogamous characteristics among primates, the activity of these neuropeptides has been directly associated with the behavioral features of pair-bonding in NHPs. OT synthesis and release appear to be interwoven with the expression of mate-directed sociality in NHPs. In cotton-top tamarin pairs, basal OT levels are positively correlated among paired males and females; moreover, the pairs with the highest basal OT also displayed the greatest amount of affiliative and sexual behavior (Snowdon et al., 2010), suggesting that the magnitude of mate-directed sociality is highly associated with OT synchrony across time. However, it is still not known whether or how quickly OT levels change following individual behavioral interactions, or whether OT is a cause or consequence of social interactions. These findings also parallel what is known about OT and human relationships, where high levels of circulating OT are positively related to the tendency to express/share feelings with a partner (Tops, van Peer, & Korf, 2007), and warm physical and emotional partner contact (Grewen, Girdler, Amico, & Light, 2005), but have also been linked to relationship quality (Holt-Lunstad, Birmingham, & Light, 2015) and relationship distress (Tabak, McCullough, Szeto, Mendez, & McCabe, 2011; Taylor, Saphire-Bernstein, & Seeman, 2010). While OT synthesis and release are clearly associated with the expression of mate-directed sociality, the role of OT in social behavior is not necessarily limited to pair-living NHPs. In nonmonogamous chimpanzees, the quality of kin and nonkin relationships has been associated with OT fluctuations (Crockford et al., 2013; Finkenwirth, van Schaik, Ziegler, & Burkart, 2015; Wittig et al., 2014). These data suggest dyads that engage in greater levels of affiliative behavior are most likely to share stronger social bonds and show the most similar OT responses, and this may be true for monogamous and nonmonogamous primate alike.

The use of selective OT and AVP agonists and antagonists strengthens our interpretations that the OT and AVP systems are intricately involved in the regulation of behavioral traits that comprise monogamy. In newly formed marmoset pairs, blocking endogenous OT activity reduces mate-directed sociality, while administration of intranasal OT increases a partner preference (Smith et al., 2010). The OT system also appears to regulate mate-directed sociality in well-established marmoset pairs. When male and female marmosets receive intranasal OT they attract more social interest from their untreated pair-mate (Cavanaugh, Huffman, Harnisch, & French, 2015), which suggests that OT induced changes in the stimulus properties of marmosets, rendering them more attractive as social partners. Thus, OT treatment may be a means to enhance social interest in long-term relationships, not only by enhancing motivation to engage in affiliative behavior with a partner but also by enhancing the attractiveness of a social partner.

In addition to enhancing the quantity and quality of interactions with a mate, reducing the level of sociosexual interest in opposite-sex strangers is obviously important for maintaining a monogamous relationship. In marmosets, intranasal OT facilitated fidelity by reducing time spent in proximity with, the expression of sexual solicitation toward, and the expression of food-sharing behavior with an opposite-sex stranger (Cavanaugh, Mustoe, Taylor, & French, 2014; Mustoe, Cavanaugh, Harnisch, Thompson, & French, 2015), thus preserving mate exclusivity and promoting a partner preference. Thus, in social contexts when marmosets have the choice to interact with either their long-term mate or an opposite-sex stranger, administration of OT appears to diminish the motivation to interact with an opposite-sex stranger (Cavanaugh et al., 2014; Mustoe et al., 2015), potentially reducing the likelihood of extrapair

sexual encounters and the formation of a new bond. Together, these findings demonstrate that pair-bonding can be accomplished not only by augmenting affiliation with a mate but also by reducing interactions with opposite-sex strangers.

The role of the AVP system in the regulation of behavioral features associated with monogamous relationships in NHPs has been surprisingly understudied given its relative importance in prairie vole pair-bonding (Barrett, Keebaugh, et al., 2013; Lim et al., 2004; Lim & Young, 2004; Pitkow et al., 2001), but existing data suggest that AVP may enhance both male titi monkeys' motivation to interact with their long-term mate, as well as reduce their motivation to interact with an opposite-sex stranger (Jarcho, Mendoza, Mason, Yang, & Bales, 2011). The role of AVP in female titi monkey social behavior has not been examined.

The OT and AVP systems appear to have an integral role in pair-bond formation and development, as well as in the regulation of behavioral traits that are critical for pair-bond maintenance in well-established pairs. While these two neuropeptides have well-known roles in reproduction and physiology (Blanks & Thornton, 2003; Caruolo, 1971; Landgraf & Neumann, 2004), there is growing support that they are critical regulators of social behavior. It is clear that OT and AVP have pervasive roles in social, emotional, and cognitive processes, regardless of mating system. However, it is also abundantly clear that the two neuropeptides are intricately linked to the expression of mate-directed sociality and a partner preference in NHPs, suggesting that they may have a unique role in pair-bonding.

Dopamine and Opioids. The development and continued persistence of social attraction and affiliation among pair-mates is predicated on the notion that interactions among long-term partners constitute socially rewarding events. As a consequence, attention among neuroscientists has turned to the study of brain reward mechanisms that may be relevant for explaining these relationships. Two systems in particular have been explored in this context: dopamine (DA) circuits, which mediate reward processes in the mesolimbic and cortical regions of the brain, and the endogenous opioid system, which mediates pain processing and reward valence throughout the brain. These brain regions have clear implications for the expression of pair-bonding behavior (monogamous mating may even be partially responsible for connecting the brain's reward system with the brain's social systems) (Aragona, Liu, Curtis, Stephan, & Wang, 2003). This section reviews the crucial roles of DA in several behavioral characteristics that underlie monogamy, including mating, partner-preference formation, and motivational behavior.

There are notable behavioral similarities between drug-seeking behavior in addiction and social-seeking behavior in animals that display strong social ties (Insel, 2003; Machin & Dunbar, 2011). Periods of euphoria, habituation, and withdrawal have been described in both addiction and romantic attachments (Machin & Dunbar, 2011). In the same way that drug addiction occurs through the hijacking of neural systems in place to mediate natural reward, both aversive and rewarding social interactions may likewise be influenced by the brain's complex reward mechanisms (Curtis, Liu, Aragona, & Wang, 2006; Eisenberger, 2012; Insel, 2003). It has therefore been hypothesized that the reward system in the brain, mediated by DA and opioids, may have been co-opted for social purposes (Anderson, 2007; Curtis et al., 2006; Fuxe et al., 2012; Insel, 2003; Jacob, 1977). This "tinkering" of existing neural machinery has produced more diverse and complicated social behaviors, including the expression of the behavioral characteristics underlying monogamy (Anderson, 2007, 2010; Fuxe et al., 2012; Insel, 2003; Jacob, 1977).

Research in prairie voles has informed us that both DA and OT activation in the nucleus accumbens (a key region of the mesolimbic reward system) is critical for the formation of a partner preference (Aragona et al., 2003; Aragona et al., 2006). Administration of DA antagonists directly into the nucleus accumbens of prairie voles can block the formation of partner preference, while administration of a DA agonist can elicit a partner preference in situations where it would be not expected (Aragona et al., 2006). These findings suggest that DA activity in the nucleus accumbens is necessary for the formation and maintenance of pair bonds. Monogamous voles have higher levels of OTRs in the nucleus accumbens than do a closely related polygynous species (Insel & Shapiro, 1992), and there is evidence that OT and DA may also communicate in the medial prefrontal cortex to regulate social attachment (Smeltzer, Curtis, Aragona, & Wang, 2006). Thus, receptor-level connections between the OT and DA system provide a clear pathway for the convergence of social-related stimuli (via the use of the OT system) with reward (via the use of the DA system).

Surprisingly little is known about the roles of DA in NHP behavior. However, the similarities in DA receptor distribution between prairie voles and primates, and the proposed links between neuroendocrine systems of known importance in NHP social behavior (i.e., OT) and DA, indicate that these chemical messengers likely play an important role in the regulation of pair-bonding. Brain imaging studies in NHPs have revealed regions of interest that are activated in response to social cues. Male marmosets exhibit altered brain activation patterns when exposed to the odors of sexually receptive females compared to exposure to nonreceptive female scents (Ferris et al., 2004). Because these brain regions are intimately linked with the DA system, their activation in response to a sexual cue provides indirect evidence that the DA system mediates sexual behavior in pair-living NHPs.

To date, two neuroimaging studies have assessed changes in the brains of NHPs in response to pair-bonding. Male titi monkeys had *decreased* glucose uptake in the nucleus accumbens and the ventral pallidum (but not the lateral septum) within 48 hours of pairing with a female after social isolation (Bales et al., 2007), suggesting that the process of

heterosexual bonding in titi monkeys is associated with functional changes in DA-related circuits within as little as two days following pairing. More direct evidence for the role of the DA system in titi monkey pair-bonding has been unearthed more recently. The expression of D1 receptors in the lateral septum (but not the nucleus accumbens or the ventral pallidum) was increased in male titi monkeys one to two months after pairing with a female compared to a period of social isolation (Hostetler et al., 2017). These results point to one of two potential conclusions: (1) male titi monkeys' mesolimbic reward system is sensitive to changes in their social environment broadly or (2) there is a unique dopaminergic signature that contributes to NHP pair-bonding, much in the same way that the DA system regulates pair-bonding in prairie voles.

There is also evidence DA plays a role in human social and romantic behavior. Humans in romantic relationships show brain activation of the reward system in response to viewing a picture of their long-term partner (Aron, 2005; Fisher, Aron, & Brown, 2005; Scheele et al., 2013), and men treated with OT show enhanced activation in response to this stimulus relative to pictures of familiar and unfamiliar women (Scheele et al., 2013). This suggests that the rewarding properties associated with interacting with a romantic partner may be mediated by neural signaling that is specific to partner-specific cognitive processing. Furthermore, the connections between OT and DA observed in voles may also be expressed in humans, as treatment with OT influences brain activity in DA-rich brain areas, potentially by enhancing the social salience of one's partner (Scheele et al., 2013).

While much of the support for the role of the DA system in partner-specific cognitive processing and mate-directed sociality comes from neuroimaging studies, genetic studies have also indicated that the DA system is influential in human pair-bonding. Polymorphisms in the *DRD4* gene are associated with individual differences in measures of sexual promiscuity and infidelity (Garcia et al., 2010). Additional studies have suggested while polymorphisms in serotonin-signaling genes are associated with differences in possessive or dependent love in human couples, *DRD4* polymorphisms significantly predict differences in intense love, physical attraction, and emotional attachment to a romantic partner (Emanuele, Brondino, Pesenti, Re, & Geroldi, 2007). Together these findings suggest the role of DA in pair-bonding may be conserved among monogamous primates, including humans, and highlight the potential importance of the reward system both in processing social stimuli and in the expression of pair-bonding behavior. Furthermore, these studies also indicate that there may be differences in how social interactions with a romantic partner are processed, relative to nonromantic social companions. Finally, the overlap between DA and OT signaling systems in the primate brain hint at the complex and interwoven roles of these systems in shaping social predispositions with romantic partners (Skuse & Gallagher, 2009).

There are complex interactions at the neuronal and brain circuit level between OT, DA, and the opioids (Kovacs et al., 1987; Machin & Dunbar, 2011). Thus, these three systems may work in concert to produce positive, rewarding effects in response to social cues, while preventing the body from habituating to this effect, as is seen in opioid addiction (Machin & Dunbar, 2011). The role of opioid signaling in social behavior may have been co-opted from its functions in regulating pain relief and negative affect. Opioid system activation may elicit behaviors to reduce social pain and isolation, thereby encouraging social interactions (Machin & Dunbar, 2011; Panksepp, Nelson, & Bekkedal, 1997). This hypothesis, referred to as the brain opioid theory of social attachment (BOTSA), is bolstered by behavioral and emotional similarities observed between narcotic addiction and social relationships (Insel, 2003; Machin & Dunbar, 2011; Panksepp, 1998).

The opioid system appears to be involved in the maintenance of social behavior in NHPs in a variety of contexts beyond pair living. Endogenous levels of opioids (specifically β-endorphin) increase in response to social grooming in peer groups (Keverne, Martensz, & Tuite, 1989), a critical component of NHP social relationships. Pharmacologically blocking the endogenous opioid system results in enhanced levels of grooming solicitations, while activating μ -opioid receptors decreases grooming solicitations (Fabre-Nys, Meller, & Keverne, 1982; Martelle et al., 2007; Meller, Keverne, & Herbert, 1980). These findings suggest that the brain attempts to maintain an optimum balance in opioid tone, thereby (a) increasing social behavior (accompanied by endogenous release of opioids) when the system is blocked and (b) decreasing social behavior (and opioid release) when the system is artificially activated (Nelson & Panksepp, 1998). Opioids influence infant behavior directed toward the mother in a similar manner to peer–peer interactions. Blocking endogenous opioids in infant monkeys increases mother-directed social behaviors, including contact calling and physical contact, while activating μ -opioidreceptors reduces these vocalizations (Kalin, Shelton, & Barksdale, 1988; Kalin, Shelton, & Lynn, 1995). Opioids may play a particularly important role in social behaviors involving touch as a way to facilitate and maintain bonds (Dunbar, 2010; Machin & Dunbar, 2011).

The role of opioids in touch-based interactions in NHPs, coupled with its importance in mother–infant attachment, highlights the potential for opioids to facilitate social behaviors associated with monogamy. In monogamous prairie voles, blocking the opioid system generally, or μ -opioid receptors specifically, in the dorsal striatum, prevents the formation of a partner preference (Burkett, Spiegel, Inoue, Murphy, & Young, 2011). In male titi monkeys, treatment with a nonspecific opioid antagonist decreases levels of grooming between established pair-mates. This reduction in affiliative behavior is also observed when titi monkeys were administered a μ -opioid receptor agonist (Ragen, Maninger, Mendoza, Jarcho, & Bales, 2013). Blockade of the opioid system appears to differentially affect monogamous species

compared to nonmonogamous primates, as it does not increase the amount of affiliation between pair-mates in NHPs (titi monkeys) or rodents (prairie voles), unlike its effect on grooming behavior in nonmonogamous primates (Burkett et al., 2011; Ragen et al., 2013; Resendez, Kuhnmuench, Krzywosinski, & Aragona, 2012; Shapiro, Meyer, & Dewsbury, 1989). This finding suggests that differences in the opioid system may reflect differences in social structure and mating system rather than phylogenetic relatedness.

While treatment of male titi monkeys with a μ -opioid receptor agonist did not affect total amount of contact between pair-mates, it did alter mate-directed sociality. μ -opioid receptor stimulation was associated with a decrease in males initiating contact with their partners and a decrease in females breaking contact with their partners (Ragen, Maninger, Mendoza, & Bales, 2015). This suggests coordination of behaviors between pair-mates may potentially underlie some of the differences observed in the effects of μ -opioid receptors activation on social behavior between monogamous and nonmonogamous species.

Mate Guarding

As monogamous NHPs transition from the formation period to a more well-established relationship, they begin to use behavioral strategies aimed at preserving and strengthening their pair bond. One such strategy is mate guarding, which includes the expression of *selective aggression* toward same-sex strangers, and/or maintaining close proximity with the mate and expressing *mate-directed sociality* during social intrusions. Mate-guarding behavior is an important reproductive strategy to avoid cuckoldry by a sexual rival (or "mate poaching"; Schmitt & Buss, 2001). Pair-living, affiliation, and fidelity are essential outcomes that characterize socially monogamous relationships, and mate guarding plays an important role in facilitating the preservation of these relationships.

Mate guarding is a prevalent trait across many primate social relationships, as both nonmonogamous and monogamous primates exhibit mate-guarding behaviors. For example, in nonmonogamous primates, including many Old World monkeys and hominoids, male aggression toward other adult males is quite prevalent. This behavior facilitates polyandry by enabling males to maintain and defend access to multiple mates, which in many primates is often determined by exhibiting dominance and aggression to maintain position in a social hierarchy (Alberts, Buchan, & Altmann, 2006; Arlet, Molleman, & Chapman, 2008; Boesch, Kohou, Néné, & Vigilant, 2006; Setchell, Charpentier, & Wickings, 2005; Watts, 1998; Weingrill, Lycett, Barrett, Hill, & Henzi, 2003). Likewise, monogamous primates also engage in aggression toward same-sex adults to maintain sexual exclusivity with their long-term partners (Baker et al., 1993; Dietz & Baker, 1993; Digby, 1995b; Rangel-Negrín, Dias, Chavira, & Canales-Espinosa, 2011). The distinct behavioral responses to a same-sex rival (i.e., selective aggression or mate-directed sociality) may be regulated by independent neurobiological mechanisms.

Sex Steroids. Given that one of the most prevalent mate-guarding behaviors is the expression of selective aggression toward same-sex strangers (i.e., protection against "threats to monogamy"), it is unsurprising that one of the key neurobiological modulators of mate guarding is the HPG axis, particularly the secretion of androgens. The importance of testosterone in mate guarding has been conceptualized in two primary hypotheses: The *trade-off hypothesis* suggests that the role of testosterone in mate guarding would depend on the presence of offspring. While increased testosterone is associated with enhanced motivation to seek sexual encounters, the presence of offspring leads to a reduction in testosterone and an increase in parental effort in most primates (Clark & Galef, 1999). The *challenge hypothesis* predicts that monogamous males that engage in paternal care will show greater testosterone responsiveness to social challenges (e.g., intrasexual competition, territory establishment, mate guarding) than nonmonogamous, nonpaternal males (Wingfield, Lynn, & Soma, 2001; Wingfield, Hegner, Dufty, & Ball, 1990). Taken together, these hypotheses predict that testosterone secretion should be transitory and responsive to social and environmental factors. In essence, the neurobiological regulation of mate guarding can both precede or initiate behavior, or be a consequence of behavioral or social changes.

The presence of mate-guarding behavior can depend on the degree of within-species competition, and there are clear associations between these behaviors and changes in androgens. For instance, marmosets and tamarins engage in both monogamous and polyandrous mating strategies, depending on a variety of environmental factors (Baker et al., 1993; Dietz & Baker, 1993; Digby, 1995b; Rangel-Negrín et al., 2011). As a result, their behavioral repertoires and underlying hormonal status needs to be flexible to adapt to different types of group composition and variable probability of intra- and extragroup competition. Specifically, dominant male tamarins in a polyandrous group had significantly higher androgen levels compared to unrelated subordinate males, but not related subordinate males (Bales, French, McWilliams, Lake, & Dietz, 2006). These differences in androgens based on group relatedness and mating strategy suggest that changes in androgens may regulate social cohesion among the group and competition toward nonkin. In marmosets, there aren't observed differences in testosterone levels between males in monogamous groups and polyandrous groups, although male marmosets in polyandrous groups copulate with the females significantly more than males in monogamous groups (Schaffner & French, 2004). These observations are limited, and more work is needed to examine these changes experimentally in both males and females.

Androgens are also important for regulating mate-guarding behavior in primates that do not live in family groups.

For example, depending on environmental conditions, howler monkeys may live in male–female pairs or multiple-male groups. Male howler monkeys that live in single-male groups and have exclusive access to a female are much more likely to be challenged by extragroup males and thus are more likely to engage in mate-guarding behavior. Unlike in marmoset and tamarins, male howler monkeys living in male–female pairs have significantly *higher* testosterone levels than males living in multiple-male groups (Rangel-Negrín et al., 2011) and transiently increase their testosterone levels when solitary males are in close vicinity (Cristóbal-Azkarate, Chavira, Boeck, Rodríguez-Luna, & Veàl, 2006). This suggests that testosterone secretion in males may be an anticipatory response to guard against reproductive conflict. Overall, these changes in androgen levels and behavior depend on both social status and group composition in species that engage in varying mating strategies.

Researchers have also attempted to elucidate the neurobiological underpinnings of mate-guarding behavior via experimental manipulations called "intruder tests." In these paradigms, a stranger is presented to a male–female pair and behavioral and endocrine responses are observed. The notion is that males will behave aggressively toward a male intruder, while females will behave aggressively toward a female intruder. For instance, both male and female marmosets display high levels of intrasexual aggression toward same-sex, unfamiliar intruders (Ross & French, 2011). Moreover, the frequency and intensity of the aggressive encounter is positively associated with testosterone levels after the encounter in both males (Ross, French, & Patera, 2004) and females (Ross & French, 2011) (up to 24 hours later). These studies suggest that the degree of responsiveness is conditional upon the intensity of the aggressive encounter among pair-bonded partners.

Neuropeptides. Much of the research on mate guarding has focused primarily on the role of aggression during conflicts with potential sexual or social competition. However, mate guarding is multifaceted and encompasses affiliative and reconciliation-like behaviors both during and following encounters. To the best of our knowledge, there have yet to be any studies in NHPs that have specifically examined the role of neuropeptides in this mate-directed sociality component of mate guarding, but it is likely that the neuropeptide mechanisms underlying social bonding would be involved in mate guarding as well. OT and AVP have surprisingly received little attention in this area in NHPs despite AVP's roles in intruder aggression in monogamous rodent species (Bester-Meredith & Marler, 2001; Gobrogge, Liu, Young, & Wang, 2009; Winslow, Hastings, Carter, Harbaugh, & Insel, 1993; Young, Winslow, Nilson, & Insel, 1997) and OT's role in regulating human ethnocentrism (De Dreu, Greer, van Kleef, Shalvi, & Handgraaf, 2011) and aggression during social conflict in monogamous rodent species (Bales & Carter, 2003; Trainor, Takahashi, Silva, Crean, & Hostetler, 2010), in addition to the profound impact of OT and AVP on attachment, parental care, reward, and social cognition (Carter, 2013; Gaustella & MacLeod, 2012; Lee, Macbeth, Pagani, & Young, 2009; MacDonald & MacDonald, 2010).

One study in titi monkeys has shown that a laboratory simulation of an intruder (with the use of a mirror instead of a live animal) elicited typical behavioral responses but did not alter concentrations of neuropeptides; however, neuropeptides were correlated with specific behaviors that are involved in the maintenance of pair bonds, including aggressive body postures and increased approaches toward their mate during these "intrusions" (Fisher-Phelps et al., 2016). This affiliative mate guarding (e.g., increased social proximity and prosocial behavior toward mates) is likely to be especially important for pair-living and may be an important distinction between mate guarding in monogamous and nonmonogamous species. Examining the role of neuropeptides and their integration with other neurobiological systems during and following a variety of major social conflicts is an area of growing importance and interest (de Dreu & Kret,, 2016; van Anders et al., 2011).

Social Attachment

High-quality social bonds provide advantages to health and well-being, including providing "protection" against predation, aggression, disease, and environmental stressors (Ditzen & Heinrichs, 2014) and improving survival and reproductive success (Hazan & Diamond, 2000). Attachments underlying monogamous relationships might similarly provide both reproductive and individual health benefits. Behavioral and physiological responses to mate separation have been used as measures of social attachment between mates (Mason & Mendoza, 1998; Mendoza & Mason, 1997), much like measures of the attachment of an infant to its mother (Hoffman, Mendoza, Hennessy, & Mason, 1995). Individuals separated from their pair-mate generally display increased vocalization rate, heart rate, hypothalamic–pituitary–adrenal (HPA) axis activity, and locomotor activity (Mendoza & Mason, 1986). These behavioral and physiological indicators of separation distress are indicative of an attachment between mates. The presence of a long-term mate can also serve as a powerful buffer against environmental stressors (i.e., social buffering). In NHPs that display social buffering, the benefits of social support may occur either through passive presence of a pair-mate or active intervention by a pair-mate (e.g., vocal reassurance, physical contact) during a stressor, mitigating the physiological and behavioral stress response (Cohen & Willis, 1985; Levine, 1993; Smith, McGreer-Whitworth, & French, 1998). Partners in a monogamous relationship can therefore utilize each other to minimize the negative impacts of stressors and can benefit from the widespread social advantages associated with social attachments.

Glucocorticoids. Social support produces social buffering through attenuation of the glucocorticoid HPA axis response and to a stressor as well as reductions in anxiety. Marmosets and titi monkeys exhibit attenuated cortisol levels in response to a novel stressor when in the presence of their pair-mate compared to when alone (Hennessy, Mendoza, Mason, & Moberg, 1995; Smith & French, 1997). This reduction in cortisol response does not occur when nonmonogamous NHPs experience a stressor with a conspecific (Hennessy et al., 1995). Stimuli associated with the pair-mate can also serve the same stress-buffering function: Marmosets that are exposed to environmental novelty but hear recorded vocalizations from their pair-mate during this stressor have reduced cortisol relative to stressor exposure without the partner's vocalizations (Rukstalis & French, 2005). This "vocal buffering" effect is specific to the pair-mate's vocalizations, because marmosets undergoing the stress paradigm that heard vocalizations from an unfamiliar opposite-sex marmoset conversely exhibited *augmented* cortisol responses relative to the silent condition (Rukstalis & French, 2005). These findings suggest that the neural mechanisms that mediate social buffering may have been shaped to reflect species-specific social structure and mating systems, and that in species exhibiting monogamous traits social buffering is uniquely induced by a pair-mate.

In addition, glucocorticoid levels prior to pairing may influence the development of a pair bond. Marmosets that were socially isolated prior to pairing had higher cortisol levels relative to marmosets housed socially prior to pairing, and these cortisol differences persisted throughout the first three months of cohabitation with a pair-mate (Smith, Birnie, & French, 2011). These glucocorticoid differences were associated with alterations in the time course of pair-bond formation: Previously isolated marmosets spent more time in close proximity to their pair-mate than did nonisolated marmosets (Smith et al., 2011), indicating the potential for glucocorticoid levels to alter interactions between partners. These data suggest not only that changes in glucocorticoid levels are a consequence of exposure to a stressor, and that the presence of a pair-mate can serve as a potent social buffer, but that glucocorticoid levels may influence the social interactions with a new partner.

Neuropeptides. While there are a number of neurobiological pathways that contribute to the stress-buffering effect of social support, including the sympathetic nervous system, limbic and cortical regions (e.g., amygdala, hippocampus, prefrontal cortex), and the HPA axis (Ditzen & Heinrichs, 2014; Hostinar, Sullivan, & Gunnar, 2014), the OT system has been identified as a leading candidate for the regulation of social buffering. In titi monkeys, both short- and long-term isolations from a pair-mate led to increases in OT levels in cerebral spinal fluid, potentially as a motivational signal to seek out their pair-mate. Moreover, reunion with their pair-mate stimulated release of OT both centrally and peripherally in male, but not female, titi monkeys (Hinde et al., 2016). Thus, OT synthesis and release is related to both separation distress and reunion with a long-term pair-mate.

The OT system may have HPA-axis-reducing properties independent of social interactions. In nonmonogamous NHPs, OT administration is associated with decreased plasma ACTH (but not cortisol) after social isolation (Parker, Buckmaster, Schatzberg, & Lyons, 2005), indicating a potential for OT to attenuate physiological stress responses to social cues. Alternatively, OT's effects on social motivation may moderate OT's stress-attenuating properties. In pair-living marmosets, blocking the OT system with antagonists results in increased HPA axis activity during a stressor, as well as reduced time spent in proximity to a pair-mate, compared to treatment with a control (Cavanaugh, Carp, Rock, & French, 2016). However, treatment with an OT agonist did not alter either the behavioral or physiological stress response during social separation (Cavanaugh et al., 2016). These results suggest that the OT system may be important for the expression of mate-seeking behavior and social buffering during stress in marmosets.

OT has also been implicated in social support in humans. Individuals allowed to recover from a stressor with a long-term partner show central and peripheral OT release that facilitates the attenuation of the HPA axis and the associated psychosocial stress (Grewen et al., 2005; Heinrichs, Baumgartner, Kirschbaum, & Ehlert, 2003), and positive interactions between romantic partners have a stress-buffering effect on cortisol levels (Ditzen, Hoppmann, & Klumb, 2008). When OT was administered intranasally during couple conflict, positive communication between partners increased, circulating cortisol levels decreased (Ditzen et al., 2009), and small blister wounds healed more quickly in marital couples (Gouin et al., 2010), relative to individuals that received a control. Thus, the HPA axis and OT system appear to be intricately linked in the regulation of social buffering.

Dopamine and Opioids. The reward system also plays a role in the expression of separation distress and social buffering, both independently and through interactions with the glucocorticoid system. There have been a limited number of studies conducted on the effect of both the dopamine and opioid systems on pair behavior generally and social buffering specifically. Blocking κ-opioid receptors in male titi monkeys reduces some behavioral expressions of separation distress (e.g., locomotion) when temporarily separated from a pair-mate; however, this treatment had no effect on isolation vocalizations or the hormonal response (cortisol) to the stressor (Ragen et al., 2015). Though activating κ-opioid receptors in the presence of a social partner facilitates a separation distress response in rat pups, it does not have this effect in titi monkeys (Carden, Hernandez, & Hofer,

1996; Ragen et al., 2015). Thus, the presence of a pair-mate may have the potential to buffer the negative emotional effects of the κ-opioid receptor agonist (Ragen et al., 2015).

The opioid system has effects on other neural systems as well, including the HPA axis. Activation of κ-opioid receptors increases levels of stress hormones, including glucocorticoids (Calogero et al., 1996; Pascoe et al., 2008), while activating μ -opioid receptors decreases cortisol concentrations (Broadbear, Winger, & Woods, 2004). Social context may also influence the effect of opioid manipulation on HPA axis functioning. Male titi monkeys treated with an opioid antagonist displayed increased cortisol responses to a stressor when alone compared to when their pair-mates were present (Ragen et al., 2013). Opioid effects on the stress response are not limited to cortisol. AVP concentrations in male titi monkeys, another neurohormone released as part of the response to a stressor (Ring, 2005), were higher in socially separated males that had also been treated with an opioid antagonist than in similarly treated males that were not separated from partners (Ragen et al., 2013). Taken together, these findings suggest that the presence of a pair-mate alleviates the negative behavioral and hormonal effects of opioid antagonism, providing support for the role of the opioid system in social buffering.

Biparental Care

In primates, monogamy and biparental care often go hand in hand, as there is significant overlap between species characterized as monogamous and those that engage in biparental care (Lukas & Clutton-Brock, 2013). Unlike most nonmonogamous species, monogamous fathers are bonded to mothers and maintain that social relationship across the development of the offspring. Paternal care in primates varies in both form and intensity between and within species, but is generally defined as any form of care selectively directed toward offspring that results in improved fitness (Kleiman & Malcolm, 1981). Paternal care in primates includes but is not necessarily limited to (1) carrying preambulatory young, (2) grooming, (3) food sharing, (4) support during agonistic interactions with peers, (5) protection against infanticide or predation, (6) playing, (7) huddling, and (8) teaching behavioral skills. Only a few primate genera display direct, conspicuous, and sustained levels of paternal care, most notably marmosets, tamarins, titi monkeys, and owl monkeys (Fernandez-Duque, Valeggia, & Mendoza, 2009; French, Fite, & Ross, 2008; Spence-Aizenberg, Di Fiore, & Fernandez-Duque, 2016), but also lemurs (Overdorff & Tecot, 2006). Paternal care in New World monkeys is so vital to the survival and well-being of offspring that the fathers' biology changes (e.g., decreased testosterone) during their mates' pregnancies to prime fathers for the arrival of offspring (Ziegler, Prudom, Schultz-Darken, Kurian, & Snowdon, 2006; Ziegler, Washabaugh, & Snowdon, 2004).

Several other primate species show less extensive and overt paternal investment, including gibbons (Lappan, 2008; Rafacz, Margulis, & Santymire, 2012), and to a lesser extent some Old World monkeys that are generally categorized as neither monogamous nor paternal (Bolin, 1981; Buchan, Alberts, Silk, & Altmann, 2003; Burton, 1972; Rangel-Negrín et al., 2011; Small, 1990). While a high proportion of primates compared to all other mammals display paternal care, the majority of primates do not engage in any form of direct or indirect paternal care and will typically show only tolerance of offspring or occasionally affiliation, but the vast majority of these species are nonmonogamous.

Neuropeptides. The OT and AVP systems have also been implicated in parenthood and the modulation of offspring care patterns in biparental species (Bosch & Neumann, 2012; Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Rilling & Young, 2014). Female mammals are primed for motherhood by hormonal and neural changes associated with pregnancy and lactation, including alterations in circulation of steroid hormones, prolactin, and OT (Bosch & Neumann, 2012). Males in biparental species also experience changes in hormonal status during the period of intense offspring care. Further, parental experience profoundly influences both the expression of parental care behavior, including responsiveness to offspring, and the underlying neurobiology (French et al., 2008). Paternally experienced marmoset fathers that are not currently caring for dependent offspring have significantly higher levels of OT and prolactin, and reduced levels of DA in hypothalamic explants, than paternally inexperienced fathers (Woller et al., 2012). Because males were not currently caring for dependent offspring at the time of sampling, these results suggest that male brains undergo long-term changes associated with previous paternal experience. Further, primiparous and multiparous marmoset fathers have a higher density of dendritic spines on pyramidal AVP neurons in the prefrontal cortex than nulliparous adult males. Fatherhood also enhances the overall abundance of V1aR in the prefrontal cortex, but does not alter the density and distribution of V1b, OTR, or the prolactin receptor (Kozorovitskiy, Hughes, Lee, & Gould, 2006). These results suggest that engaging in paternal care serves as a potent stimulus for neuropeptide release and receptor expression in the forebrain, and provides evidence for structural organization of the parental brain as a result of offspring care experience.

For many NHPs, the most intense and energy-demanding period of offspring care is during the first postpartum month, when young wholly depend on caregivers for warmth, protection, transportation, and nutrition. During this early period of offspring care, infant-licking behavior is positively related to postpartum OT level in mothers, fathers, and even alloparents (Finkenwirth, Martins, Deschner, & Burkart, 2016). Postweaning, marmoset offspring still depend on caregivers for nutrition. Proactive food sharing, a relatively rare behavior that is characterized both by caregiver willingness to share solid food and the absence of offspring begging, is positively related to

caregivers urinary OT levels during the late period of offspring care (Finkenwirth et al., 2016). Marmoset fathers receiving a high dose of intracerebroventricular OT express higher rates of food sharing with older offspring, while fathers receiving a low dose of OT express higher rates of food sharing with younger offspring, each made manifest by a reduction in fathers' propensity to refuse offspring in a food transfer test (Saito & Nakamura, 2011). These results suggest that the OT system regulates maternal, paternal, and alloparental caregiver motivation and promotes paternal tolerance of offspring.

In biparental rodents, stimulation of the AVP system typically increases, while inhibition of the AVP system decreases, the expression of parental behavior (Bester-Meredith & Marler, 2001; Bosch & Neumann, 2012; Wang, Ferris, & De Vries, 1994); however, this line of research has also shown us that AVP's effects are sex specific and are contingent upon patterns of species-typical offspring care. In marmosets, intranasal AVP reduces the latency to respond to infant cues in females, and intranasal OT quickens responsiveness to infant cues in males (Taylor & French, 2015). However, neither intranasal AVP or OT affect sustained interest in infant stimuli, and OT or AVP antagonist treatments did not alter either measure of parental responsiveness (Taylor & French, 2015). These findings suggest that both the OT and AVP systems regulate parental responsiveness in a pair-living NHP.

These results are in line with what we know about the relationship between peripheral OT levels and social interactions between caregivers and offspring in humans. Peripheral measures of OT have been linked to touch and gaze synchrony between caregivers and infant (Feldman et al., 2012). Children that experience a social stressor and receive maternal vocal comfort show reduced salivary cortisol and increased salivary OT, compared to children that receive no maternal comfort (Seltzer, Ziegler, & Pollak, 2010), suggesting that the OT system may mediate the attenuation of the physiological stress response from positive comfort from a caregiver.

Sex Steroids. Monogamous males that engage in paternal care must determine the proportion of energy to allocate to intrasexual competition and mate attraction versus the energy devoted to offspring care. In species that exhibit paternal care, testosterone levels are typically increased during courtship and mating, and relatively lower during periods where paternal care is required, potentially due to high levels of testosterone interfering with paternal investment (French et al., 2008; Saltzman & Ziegler, 2014; compare Trainor & Marler, 2001). If one of the functions of testosterone variation is to modulate mating and paternal effort, then it is expected that HPG axis activity will vary during the differential allocation of reproductive effort (i.e., mating and parenting). Male golden lion tamarins have significantly higher androgen levels during the mating season than during the birth/infant care season (Bales et al., 2006). The period of time when marmoset fathers engage in maximal infant-carrying behavior coincides with significant declines in testosterone titers (Nunes, Fite, & French, 2000), suggesting that testosterone secretion differs as a function of the level of investment. Moreover, males that engage in high levels of paternal effort have consistently lower levels of testosterone across the postpartum period than males that engage in low levels of paternal effort (Nunes et al., 2001), indicating that testosterone appears to vary as a function of both the active expression of paternal care and paternal experience in monogamous marmosets. This increased investment in paternal care, during the period of low testosterone secretion, may be a corollary with a decrease in mating effort with either a pair-mate or an opposite-sex stranger. In male siamangs, androgen titers rise during the prepartum period and subsequently decrease as parturition approaches (Rafacz et al., 2012), potentially as a result of signals gleaned from their pregnant mates. Thus, androgens appear to mediate the trade-off between mating effort and paternal effort in monogamous NHPs.

This pattern of testosterone secretion and mating/paternal effort is also seen in humans, as pair-bonded men (Kuzawa et al., 2009) and fathers (Berg & Wynne-Edwards, 2001; Gettler et al., 2011; Muller, Marlowe, Bugumba, & Ellison, 2009; Storey, Noseworthy, Delahunty, Halfyard, & McKay, 2011) have lower levels of bioavailable testosterone compared to single men and nonfathers, respectively. However, there is notable overlap between fatherhood and relationship status (i.e., unmarried men are *typically* nonfathers and fathers are *often* married) that partially confounds this comparison. Examination of cultural differences in mating systems, as well as norms for offspring care, has allowed researchers to begin to tease apart the relative contributions of each (see Alvergne, Faurie, & Raymond, 2009; Gettler, McDade, Feranil, & Kuzawa, 2011; Gray, Jeffrey Yang, & Pope, 2006; Muller et al., 2009), with parental status and relationship status contributing independently. There is also growing evidence that testosterone may modulate a trade-off between mating and parenting effort in women, with both marriage and motherhood being associated with lower testosterone levels (Barrett, Tran, et al., 2013; Kuzawa, Gettler, Huang, & McDade, 2010).

A decrease in testosterone concentration during periods of high paternal effort may be mediated by cues from the infants. In humans, fathers with lower testosterone levels displayed more sympathetic and alert responses to infant cries (Fleming, Corter, Stallings, & Steiner, 2002). Moreover, exposure to infant cries elicits rapid changes in testosterone secretion, but the response is modulated by father's responses. Fathers that exhibited nurturant responses also had a decline in testosterone, while fathers that were prevented from expressing nurturant responses displayed an increase in testosterone (van Anders, Tolman, & Volling, 2012). In marmosets, paternally experienced fathers had lower testosterone levels after exposure to their own offspring's scent but not to a novel infant's scent. Importantly, testosterone reductions (concurrent with

elevated estrogens) occurred only when scents were from two-week-old infants and not when scents were from three-month-old infants. These results suggest the olfactory cues from related dependent offspring may be signals for HPG axis regulation and testosterone decline during the period of maximal paternal care in marmoset fathers. However, paired but paternally inexperienced males did not experience declines in testosterone concentrations (Prudom et al., 2008). Thus, testosterone secretion appears to be contingent on the relatedness of the infant, whether the infant is of a dependent age, and paternal experience. Interestingly, in families with stillborn infants or in families that experience postpartum infant mortality, fathers' postpartum reduction in testosterone levels occurs irrespective of whether infants are present (Nunes et al., 2000; Ziegler, Wegner, Carlson, Lazaro-Perea, & Snowdon, 2000). This suggests that direct exposure to infants may not necessarily be required to down-regulate testosterone secretion during the postpartum period, and that male hormonal responses may be related to other environmental cues.

Testosterone levels are also influenced by other factors during the postpartum period, including signals from a mate. In particular, if a female ovulates shortly after parturition, males have a very clear choice to allocate reproductive effort to mating behavior or to offspring care. Furthermore, the biological response to these opposing cues is a good test of the trade-off between mating effort and paternal effort. Testosterone levels were significantly greater in tamarin fathers whose partners ovulated within two weeks postpartum than in fathers whose partners ovulated more than two weeks postpartum (Ziegler et al., 2000). Despite an increase in androgens that coincided with their mates' postpartum ovulation, tamarin fathers did not express diminished caregiving effort during the period of offspring dependence (Ziegler, Jacoris, & Snowdon, 2004). Thus, it does not appear that short-term increases in testosterone and mating behavior in response to their mates' postpartum ovulation interrupts the expression of paternal care (Storey & Ziegler, 2016). These results suggest that variation in testosterone during the paternal care period may be associated with a partner's fertile period rather than in response to infants. Yet single and paired male marmosets with no dependent offspring had increased plasma testosterone titers in response to novel scent secretions of ovulatory females, while marmoset fathers showed no change in testosterone levels (Ziegler et al., 2005). This indicates that experienced fathers may be less responsive to ovulatory cues from unfamiliar females when they are committed to paternal care. Furthermore, these results suggest that male primates that engage in significant offspring care need to have flexible hormonal responses to olfactory and multimodal signals from their mates and offspring, and it appears that testosterone may mediate this differential allocation of reproduction effort.

Paternal experience may modulate the influence of testosterone on the expression of paternal care. The increase in testosterone levels during late gestation is typically followed by a decrease in testosterone levels postpartum and may be due to mate guarding or territorial defense (Ziegler & Snowdon, 2000). Male marmosets with offspring care experience had significantly lower testosterone levels across the postpartum period than did males without prior offspring care experience (Nunes et al., 2001). In male marmosets without paternal care experience, urinary testosterone levels tended to be lowest during the period of maximal infant care, while males with offspring care experience had consistently low levels of testosterone during times of paternal care (Cavanaugh & French, 2013), suggesting the role of testosterone in paternal care may diminish as males gain offspring care experience.

Overall, these studies suggest that in pair-living NHPs the period of elevated paternal effort is associated with decreases in testosterone concentrations. Moreover, males that engage in high levels of paternal care have lower levels of testosterone than males that engage in low levels of paternal effort. This hormone–behavior relationship is analogous to the pattern seen in human fathers (Alvergne et al., 2009; Fleming et al., 2002; Gettler, McDade, Feranil, & Kuzawa, 2011; Storey et al., 2011). Thus, testosterone appears to mediate a trade-off between mating effort and paternal effort in monogamous primates that engage in extensive paternal care.

Concluding Remarks

It is clear that primate monogamy is not simply a unitary trait but is instead an amalgam of numerous social components, including pair-living, selective partner preference, distress following mate separation, maintaining social and sexual exclusivity, and biparental care of offspring. We have shown that monogamous relationships in primates commonly share many behavioral features. In some cases, species show the full spectrum of behavioral traits that comprise monogamy (e.g., titi monkeys); in other cases, species exhibit variable expression of the "menu items" associated with social monogamy (e.g., marmosets, tamarins). Thus, our proposition that social monogamy is not a unitary construct, either at the individual level or at the species level, appears to be a worthy heuristic approach for both human and nonhuman primates. Primate monogamous relationships are a product of a diverse collection of elemental social features—hence, monogamy à la carte.

The neurobiological mechanisms regulating these behavioral features are critical puzzle pieces toward revealing the underpinnings of monogamy in nonhuman primates. As mentioned at the outset (and borne out in the blank cells in Table 1), there are many missing pieces of the puzzle regarding the impact of the endocrine, neuroendocrine, and neurotransmitters that mediate and modulate social phenotypes in marmosets. Several themes, however, emerge from this review, most obviously with regard to neuropeptides.

First, both oxytocin and vasopressin have been demonstrated to influence all component elements of social monogamy. Experimental and correlational studies reveal that elevated neuropeptide activity enhances pair-bonding, mate guarding, social

attachment, and paternal care. The few studies that have blocked neuropeptide action in the brain pharmacologically have yielded evidence consistent with this hypothesis. Second, sex steroids appear to have differential effects on separate components of social monogamy. Elevated estrogens are associated with the pair-bonding process in females, and elevated androgens are also associated with bond formation in males. The role of androgens in paternal care, in contrast, appears to be inhibitory. Males that engage in high rates of contact with dependent infants have lower androgen levels, and androgen levels are lower in paternally experienced males than in first-time fathers or offspring-naive males. Because neurons expressing steroid receptors are present in many locations in the brain, it must be the case that androgens in particular have differential effects on neural circuits regulating partner-directed versus offspring-directed behavior. Third, the few studies that have tested dopamine or opioid modulation of social behavior in monogamous primates suggest complexity in the influence of these systems on the traits associated with social monogamy. Given the wide variety of receptor subtypes for these two classes of neural signals, this is not surprising.

In summary, our review has highlighted the folly of defining a monogamous relationship or classifying a species as monogamous based on a single social phenotype. No careful observer of human sociosexual relationships would attempt to classify the species *Homo sapiens* as monogamous or nonmonogamous, given the diverse array of both romantic and sexual relationships both among and within cultures. Likewise, it would appear to be a similar fool's errand to hypothesize that a single biological mechanism can account for behavioral traits that lead to all components of a socially monogamous lifestyle or life history. Monogamy is clearly a multivariate trait that is regulated by complex brain chemistry, and we are just beginning to scratch the surface of the nature of the causal links among neurobiological systems and monogamy.

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References

Ågmo, A., Smith, A. S., Birnie, A. K., & French, J. A. (2012). Behavioral characteristics of pair bonding in the black tufted-ear marmoset (*Callithrix penicillata*). *Behaviour*, *149*, 407–440. doi:10.1163/156853912X638454

Alberts, S. C., Buchan, J. C., & Altmann, J. (2006). Sexual selection in wild baboons: From mating opportunities to paternity success. *Animal Behaviour*, *72*(5), 1177–1196. doi:10.1016/j.anbehav.2006.05.001

Alvergne, A., Faurie, C., & Raymond, M. (2009). Variation in testosterone levels and male reproductive effort: Insight from a polygynous human population. *Hormones and Behavior*, *56*(5), 491–497. doi:10.1016/j.yhbeh.2009.07.013

Anderson, M. L. (2007). Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist*, *13*(1), 13–21. doi:10.1177/1073858406294706

Anderson, M. L. (2010). Neural reuse: A fundamental organizational principle of the brain. *Behavioral and Brain Sciences*, *33*(4), 245–313. doi:10.1017/S0140525X10000853

Anzenberger, G. (1985). How stranger encounters of common marmosets (*Cllithrix jacchus jacchus*) are influenced by family members: The quality of behavior. *Folia Primatologica*, *45*(3–4), 204–224. doi:10.1159/000156229

Aragona, B. J., Liu, Y., Curtis, J. T., Stephan, F. K., & Wang, Z. (2003). A critical role for nucleus accumbens dopamine in partner-preference formation in male prairie voles. *Journal of Neuroscience*, *23*(8), 3483–3490.

Aragona, B. J., Liu, Y., Yu, Y. J., Curtis, J. T., Detwiler, J. M., Insel, T. R., & Wang, Z. (2006). Nucleus accumbens dopamine differentially mediates the formation and maintenance of monogamous pair bonds. *Nature Neuroscience*, *9*(1), 133–139. doi:10.1038/nn1613

Argiolas, A., & Gessa, G. L. (1991). Central functions of oxytocin. *Neuroscience and Biobehavioral Reviews*, *15*(2), 217–231. doi:10.1016/S0149-7634(05)80002-8

Arlet, M. E., Molleman, F., & Chapman, C. A. (2008). Mating tactics in male grey-cheeked mangabeys (*Lophocebus albigena*). *Ethology*, *114*(9), 851–862. doi:10.1111/j.1439-0310.2008.01533.x

Arnqvist, G., & Kirkpatrick, M. (2005). The evolution of infidelity in socially monogamous passerines: The strength of direct and indirect selection on extrapair copulation behavior in females. *American Naturalist*, *165*(Suppl. 5), S26–S37. doi:10.1086/429350

Aron, A. (2005). Reward, motivation, and emotion systems associated with early-stage intense romantic love. *Journal of Neurophysiology*, *94*(1), 327–337. doi:10.1152/jn.00838.2004

Babb, P. L., Fernandez-Duque, E., & Schurr, T. G. (2015). Oxytocin receptor gene sequences in owl monkeys and other primates show remarkable interspecific regulatory and protein coding variation. *Molecular Phylogenetics and Evolution*, *91*, 160–177. doi:10.1016/j.ympev.2015.05.006

Baker, A., Bales, K. L., & Dietz, J. M. (2002). Mating system and group dynamics in golden lion tamarins (*Leontopithecus rosalia*). In D. G. Kleiman & A. B. Rylands (Eds.), *Lion tamarins: Biology and conservation* (pp. 188–212). Washington, DC: Smithsonian Institution Press.

Baker, A. J., Dietz, J. M., & Kleiman, D. G. (1993). Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour*, *46*, 1091–1103. doi:10.1006/anbe.1993.1299

Bales, K. L., & Carter, C. S. (2003). Developmental exposure to oxytocin facilitates partner preferences in male prairie voles (*Microtus ochrogaster*). *Behavioral Neuroscience*, *117*(4), 854–859. doi:10.1037/0735-7044.117.4.854

Bales, K. L., French, J. A., McWilliams, J., Lake, R. A., & Dietz, J. M. (2006). Effects of social status, age, and season on androgen and cortisol levels in wild male golden lion tamarins (*Leontopithecus rosalia*). *Hormones and Behavior*, *49*(1), 88–95. doi:10.1016/j.yhbeh.2005.05.006

Bales, K. L., Mason, W. A., Catana, C., Cherry, S. R., & Mendoza, S. P. (2007). Neural correlates of pair-bonding in a monogamous primate. *Brain Research*, *1184*, 245–253. doi:10.1016/j.brainres.2007.09.087

Barrett, C. E., Keebaugh, A. C., Ahern, T. H., Bass, C. E., Terwilliger, E. F., & Young, L. J. (2013). Variation in vasopressin receptor (*Avpr1a*) expression creates diversity in behaviors related to monogamy in prairie voles. *Hormones and Behavior*, *63*(3), 518–526. doi:10.1016/j.yhbeh.2013.01.005

Barrett, E. S., Tran, V., Thurston, S., Jasienska, G., Furberg, A.-S., Ellison, P. T., & Thune, I. (2013). Marriage and motherhood are associated with lower testosterone concentrations in women. *Hormones and Behavior*, *63*(1), 72–79. doi:10.1016/j.yhbeh.2012.10.012

Berg, S. J., & Wynne-Edwards, K. E. (2001). Changes in testosterone, cortisol, and estradiol levels in men becoming fathers. *Mayo Clinic Proceedings*, *76*, 582–592. doi:10.1016/S0025-6196(11)62407-5

Bester-Meredith, J. K., & Marler, C. A. (2001). Vasopressin and aggression in cross-fostered California mice (*Peromyscus californicus*) and white-footed mice (*Peromyscus leucopus*). *Hormones and Behavior*, *40*(1), 51–64. doi:10.1006/hbeh.2001.1666

Blanks, A., & Thornton, S. (2003). The role of oxytocin in parturition. *BJOG: An International Journal of Obstetrics and Gynaecology*, *110*, 46–51. doi:10.1016/S1470-0328(03)00024-7

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï Forest. *American Journal of Physical Anthropology*, *130*(1), 103–115. doi:10.1002/ajpa.20341

Bolin, I. (1981). Male parental behavior in black howler monkeys (*Alouatta palliata pigra*) in Belize and Guatemala. *Primates*, *22*(3), 349–360. doi:10.1007/BF02381575

Bosch, O. J., & Neumann, I. D. (2012). Both oxytocin and vasopressin are mediators of maternal care and aggression in rodents: From central release to sites of action. *Hormones and Behavior*, *61*(3), 293–303. doi:10.1016/j.yhbeh.2011.11.002

Brandon, M. E. (2013). Marriage in America. *Tulsa Law Review*, *49*(2), 327–344. Retrieved from http://digitalcommons.law.utulsa.edu/tlr/vol49/iss2/9

Broadbear, J. H., Winger, G., & Woods, J. H. (2004). Self-administration of fentanyl, cocaine, and ketamine: Effects on the pituitary–adrenal axis in rhesus monkeys. *Psychopharmacology*, *176*(3–4), 398–406. doi:10.1007/s00213-004-1891-x

Buchan, J. C., Alberts, S. C., Silk, J. B., & Altmann, J. (2003). True paternal care in a multi-male primate society. *Nature*, *425*, 179–181. doi:10.1038/nature01866

Buchanan-Smith, H. M., & Jordan, T. R. (1992). An experimental investigation of the pair bond in the callitrichid monkey, *Saguinus Labiatus*. *International Journal of Primatology*, *13*(1), 51–72. doi:10.1007/BF02547727

Burkett, J. P., Spiegel, L. L., Inoue, K., Murphy, A. Z., & Young, L. J. (2011). Activation of μ-opioid receptors in the dorsal striatum is necessary for adult social attachment in monogamous prairie voles. *Neuropsychopharmacology*, *36*(11), 2200–2210. doi:10.1038/npp.2011.117

Burnham, T., Chapman, J. F., Gray, P., McIntyre, M., Lipson, S., & Ellison, P. (2003). Men in committed, romantic relationships have lower testosterone. *Hormones and Behavior*, *44*(2), 119–122. doi:10.1016/S0018-506X(03)00125-9

Burton, F. D. (1972). The integration of biology and behavior in the socialization of *Macaca sylvan* of Gibraltar. In F. Poirier (Ed.), *Primate socialization* (pp. 29–62). New York, NY: Random House.

Calogero, A. E., Scaccianoce, S., Burrello, N., Nicolai, R., Muscolo, L. A. A., Kling, M. A., … D'Agata, R. (1996). The kappa-opioid receptor agonist MR-2034 stimulates the rat hypothalamic-pituitary-adrenal axis: Studies in vivo and in vitro. *Journal of Neuroendocrinology*, *8*(8), 579–585. doi:10.1111/j.1365-2826.1996.tb00691.x

Carden, S. E., Hernandez, N., & Hofer, M. A. (1996). The isolation and companion comfort responses of 7- and 3-day-old rat pups are modulated by drugs active at the opioid receptor. *Behavioral Neuroscience*, *110*(2), 324–330. doi:10.1037/0735-7044.110.2.324

Carp, S. B., Rothwell, E. S., Bourdon, A., Freeman, S. M., Ferrer, E., & Bales, K. L. (2016). Development of a partner preference test that differentiates between established pair bonds and other relationships in socially monogamous titi monkeys (*Callicebus cupreus*). *American Journal of Primatology*, *78*(3), 326–339. doi:10.1002/ajp.22450

Carter, C. (2013). Oxytocin pathways and the evolution of human behavior. *Annual Review of Psychology*, *65*(1), 17–39. doi:10.1146/annurev-psych-010213-115110

Carter, C., Devries, A. C., & Getz, L. L. (1995). Physiological substrates of mammalian monogamy: The prairie vole model. *Neuroscience and Biobehavioral Reviews*, *19*(2), 303–314. doi:10.1016/0149-7634(94)00070-H

Carter, C., Devries, A. C., Taymans, S. E., Roberts, R. L., Williams, J. R., & Getz, L. L. (2006). Peptides, steroids, and pair bonding. *Annals of the New York Academy of Sciences*, *807*(1), 260–272. doi:10.1111/j.1749-6632.1997.tb51925.x

Caruolo, E. V. (1971). Exogenous oxytocin and lactation in the mouse. *Journal of Dairy Science*, *54*(8), 1207–1211. doi:10.3168/jds.S0022-0302(71)86001-0

Cavanaugh, J., Carp, S. B., Rock, C. M., & French, J. A. (2016). Oxytocin modulates behavioral and physiological responses to a stressor in marmoset monkeys. *Psychoneuroendocrinology*, *66*, 22–30. doi:10.1016/j.psyneuen.2015.12.027

Cavanaugh, J., & French, J. A. (2013). Post-partum variation in the expression of paternal care is unrelated to urinary steroid metabolites in marmoset fathers. *Hormones and Behavior*, *63*(4), 551–558. doi:10.1016/j.yhbeh.2013.02.006

Cavanaugh, J., Huffman, M. C., Harnisch, A. M., & French, J. A. (2015). Marmosets treated with oxytocin are more socially attractive to their long-term mate. *Frontiers in Behavioral Neuroscience*, *9*, 251. doi:10.3389/fnbeh.2015.00251

Cavanaugh, J., Mustoe, A. C., Taylor, J. H., & French, J. A. (2014). Oxytocin facilitates fidelity in well-established marmoset pairs by reducing sociosexual behavior toward opposite-sex strangers. *Psychoneuroendocrinology*, *49*, 1–10. doi:10.1016/j.psyneuen.2014.06.020

Clark, M. M., & Galef, B. G., Jr. (1999). A testosterone-mediated trade-off between parental and sexual effort in male Mongolian gerbils (*Meriones unguiculatus*). *Journal of Comparative Psychology*, *113*(4), 388. doi:10.1037/0735-7036.113.4.388

Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, *29*, 141–177. doi:10.1146/annurev.ecolsys.29.1.141

Cohen, S., & Willis, T. A. (1985). Stress, social support, and the buffering hypothesis. *Psychological Bulletin*, *98*(2), 310–357. doi:10.1037/0033-2909.98.2.310

Conley, T. D., Moors, A. C., Matsick, J. L., & Ziegler, A. (2013). The fewer the merrier? Assessing stigma surrounding consensually non-monogamous romantic relationships. *Analyses of Social Issues and Public Policy*, *13*(1), 1–30. doi:10.1111/j.1530-2415.2012.01286.x

Conley, T. D., Ziegler, A., Moors, A. C., Matsick, J. L., & Valentine, B. (2013). A critical examination of popular assumptions about the benefits and outcomes of monogamous relationships. *Personality and Social Psychology Review*, *17*(2), 124–141. doi:10.1177/1088868312467087

Cooke, B., Hegstrom, C. D., Villeneuve, L. S., & Breedlove, S. M. (1998). Sexual differentiation of the vertebrate brain: Principles and mechanisms. *Frontiers in Neuroendocrinology*, *19*, 323–362. doi:10.1006/frne.1998.0171

Cristóbal-Azkarate, J., Chavira, R., Boeck, L., Rodríguez-Luna, E., & Veàl, J. J. (2006). Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: A test of the challenge hypothesis. *Hormones and Behavior*, *49*(2), 261–267. doi:10.1016/j.yhbeh.2005.07.015

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbuhler, K., & Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1755), 20122765. doi:10.1098/rspb.2012.2765

Curtis, J. T., Liu, Y., Aragona, B. J., & Wang, Z. (2006). Dopamine and monogamy. *Brain Research*, *1126*(1), 76–90. doi:10.1016/j.brainres.2006.07.126

de Dreu, C. K., & Kret, M. E. (2016). Oxytocin conditions intergroup relations through upregulated in-group empathy, cooperation, conformity, and defense. *Biological Psychiatry*, *79*(3), 165–173. doi:10.1016/j.biopsych.2015.03.020

de Dreu, C. K. W., Greer, L. L., van Kleef, G. A., Shalvi, S., & Handgraaf, M. J. J. (2011). Oxytocin promotes human ethnocentrism. *Proceedings of the National Academy of Sciences*, *108*(4), 1262–1266. doi:10.1073/pnas.1015316108

de Waal, F. B., & Gavrilets, S. (2013). Monogamy with a purpose. *Proceedings of the National Academy of Sciences*, *110*(38), 15167–15168. doi:10.1073/pnas.1315839110

Díaz-Muñoz, S. L., & Bales, K. L. (2016). "Monogamy" in primates: Variability, trends, and synthesis. *American Journal of Primatology*, *78*, 283–287. doi:10.1002/ajp.22463

Dietz, J. M., & Baker, A. J. (1993). Polygyny and female reproductive success in golden lion tamarins. *Leontopithecus Rosalia. Animal Behaviour*, *46*, 1067–1078. doi:10.1006/anbe.1993.1297

Digby, L. J. (1995a). Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*.) *Behavioral Ecology and Sociobiology*, *37*(1), 51–61. doi:10.1007/BF00173899

Digby, L. J. (1995b). Social organization in a wild population of *Callithrix jacchus*: II. Intragroup social behavior. *Primates*, *36*(3), 361–375. doi:10.1007/BF02382859

Digby, L. J. (1999). Sexual behavior and extragroup copulations in a wild population of common marmosets (*Callithrix jacchus*). *Folia Primatologica*, *70*(3), 136–145. doi:10.1159/000021686

Ditzen, B., & Heinrichs, M. (2014). Psychobiology of social support: The social dimension of stress buffering. *Restorative Neurology and Neuroscience*, *32*(1), 149–162. doi:10.3233/RNN-139008

Ditzen, B., Hoppmann, C., & Klumb, P. (2008). Positive couple interactions and daily cortisol: On the stress-protecting role of intimacy. *Psychosomatic Medicine*, *70*, 883–889. doi:10.1097/PSY.0b013e318185c4fc

Ditzen, B., Schaer, M., Gabriel, B., Bodenmann, G., Ehlert, U., & Heinrichs, M. (2009). Intranasal oxytocin increases positive communication and reduces cortisol levels during couple conflict. *Biological Psychiatry*, *65*, 728–731. doi:10.1016/j.biopsych.2008.10.011

Dixson, A. F. (2013). Male infanticide and primate monogamy. *Proceedings National Academic Sciences USA*, *110*, E4937. doi:10.1073/pnas.1318645110

Dow, M. M., & Eff, E. A. (2013). When one wife is enough: A cross-cultural study of the determinants of monogamy. *Journal of Social, Evolutionary, and Cultural Psychology*, *7*(3), 211. doi:10.1037/h0099200

Dunbar, R. I. (2009). The social brain hypothesis and its implications for social evolution. *Annals of Human Biology*, *36*(5), 562–572. doi:10.1080/03014460902960289

Dunbar, R. I. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience and Biobehavioral Reviews*, *34*(2), 260–268. doi:10.1016/j.neubiorev.2008.07.001

Dunbar, R. I., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344–1347. doi:10.1126/science.1145463

Eisenberger, N. I. (2012). The pain of social disconnection: Examining the shared neural underpinnings of physical and social pain. *Nature Reviews: Neuroscience*, *13*(6), 421–434. doi:10.1038/nrn3231

Emanuele, E., Brondino, N., Pesenti, S., Re, S., & Geroldi, D. (2007). Genetic loading on human loving styles. *Neuroendocrinology Letters*, *28*(6), 815–821.

Epple, G. (1990). Sex differences in partner preference in mated pairs of saddle-back tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, *27*, 455–459. doi:10.1007/BF00164073

Evans, S. (1983). The pair-bond of the common marmoset, *Callithrix jacchus jacchus*: An experimental investigation. *Animal Behaviour*, *31*(3), 651–658. doi:10.1016/S0003-3472(83)80220-6

Fabre-Nys, C., Meller, R. E., & Keverne, E. B. (1982). Opiate antagonists stimulate affiliative behaviour in monkeys. *Pharmacology Biochemistry and Behavior*, *16*(4), 653–659. doi:10.1016/0091-3057(82)90432-4

Feldman, R., Weller, A., Zagoory-Sharon, O., & Levine, A. (2007). Evidence for a neuroendocrinological foundation of human affiliation: Plasma oxytocin levels across pregnancy and the postpartum period predict mother–infant bonding. *Psychological Science*, *18*(11), 965–970. doi:10.1111/j.1467-9280.2007.02010.x

Feldman, R., Zagoory-Sharon, O., Weisman, O., Schneiderman, I., Gordon, I., Maoz, R., … Ebstein, R. P. (2012). Sensitive parenting is associated with plasma oxytocin and polymorphisms in the OXTR and CD38 genes. *Biological Psychiatry*, *72*(3), 175–181. doi:10.1016/j.biopsych.2011.12.025

Fernandez-Duque, E., Valeggia, C. R., & Mason, W. A. (2000). Effects of pair-bond and social context on male-female interactions in captive titi monkeys (*Callicebus moloch*, primates: Cebidae). *Ethology*, *106*, 1067–1082. doi:10.1046/j.1439-0310.2000.00629.x

Fernandez-Duque, E., Valeggia, C. R., & Mendoza, S. P. (2009). The biology of paternal care in human and nonhuman primates. *Annual Review of Anthropology*, *38*(1), 115–130. doi:10.1146/annurev-anthro-091908-164334

Ferrari, S. F., & Digby, L. J. (1996). Wild *Callithrix* groups: Stable extended families? *American Journal of Primatology*, *38*(1), 19–27. doi:10.1002/(SICI)1098-2345

Ferris, C. F., Snowdon, C. T., King, J. A., Sullivan, J. M., Ziegler, T. E., Olson, D. P., … Duong, T. Q. (2004). Activation of neural pathways associated with sexual arousal in non-human primates. *Journal of Magnetic Resonance Imaging*, *19*(2), 168–175. doi:10.1002/jmri.10456

Fincham, F. D., & May, R. W. (2017). Infidelity in romantic relationships. *Current Opinion in Psychology*, *13*, 70–74. doi:10.1016/j.copsyc.2016.03.008

Finkenwirth, C., Martins, E., Deschner, T., & Burkart, J. M. (2016). Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys. *Hormones and Behavior*, *80*, 10–18. doi:10.1016/j.yhbeh.2016.01.008

Finkenwirth, C., van Schaik, C., Ziegler, T. E., & Burkart, J. M. (2015). Strongly bonded family members in common marmosets show synchronized fluctuations in oxytocin. *Physiology and Behavior*, *151*, 246–251. doi:10.1016/j.physbeh.2015.07.034

Fisher, H., Aron, A., & Brown, L. L. (2005). Romantic love: An fMRI study of a neural mechanism for mate choice. *Journal of Comparative Neurology*, *493*(1), 58–62. doi:10.1002/cne.20772

Fisher-Phelps, M.L., Mendoza, S.P., Serna, S., Griffin, L.L., Schaefer, T.J., Jarcho, M.R., … & Bales, K. L. (2016). Laboratory simulations of mate-guarding as a component of the pair-bond in male titi monkeys, Callicebus cupreus. *American Journal of Primatology*, *78*(5), 573–582. doi: 10.1002/ajp.22483

Fleming, A. S., Corter, C., Stallings, J., & Steiner, M. (2002). Testosterone and prolactin are associated with emotional responses to infant cries in new fathers. *Hormones and Behavior*, *42*(4), 399–413. doi:10.1006/hbeh.2002.1840

Freeman, S. M., & Young, L. J. (2013). Oxytocin, vasopressin, and the evolution of mating systems in mammals. In E. Choleris, D. W. Pfaff, & M. Kavaliers (Eds.), *Oxytocin, vasopressin, and related peptides in the regulation of behavior* (pp. 128–147). Cambridge, United Kingdom: Cambridge University Press.

Freeman, S. M., & Young, L. J. (2016). Comparative perspectives on oxytocin and vasopressin receptor research in rodents and primates: Translational implications. *Journal of Neuroendocrinology*, *28*(4). Advance online publication. doi:10.1111/jne.12382

French, J. A., Fite, J.E., Jensen, H., Oparowski, K., Rukstalis, M.R., Fix, H., … & Schulkin, J. (2007). Treatment with CRH-1 antagonist antalarmin reduces behavioral and endocrine responses to social stressors in marmosets (Callithrix kuhlii). *American Journal of Primatology*, *69*(8), 877–889. doi: 10.1002/ajp.20385

French, J., Fite, J., & Ross, C. (2008). Family life in marmosets: Causes and consequences of variation in caregiving. In R. S. Bridges (Ed.), *Neurobiology of the parental brain* (pp. 461–477). Burlington, MA: Academic Press.

French, J. A., Taylor, J. H., Mustoe, A. C., & Cavanaugh, J. (2016). Neuropeptide diversity and the regulation of social behavior in New World primates. *Frontiers in Neuroendocrinology*, *42*, 18–39. doi:10.1016/j.yfrne.2016.03.004

Fuxe, K., Borroto-Escuela, D. O., Romero-Fernandez, W., Ciruela, F., Manger, P., Leo, G., … Agnati, L. F. (2012). On the role of volume transmission and receptor–receptor interactions in social behaviour: Focus on central catecholamine and oxytocin neurons. *Brain Research*, *1476*, 119–131. doi:10.1016/j.brainres.2012.01.062

Garber, P. A., Porter, L. M., Spross, J., & Di Fiore, A. (2016). Tamarins: Insights into monogamous and non-monogamous single female social and breeding systems. *American Journal of Primatology*, *78*(3), 298–314. doi:10.1002/ajp.22370

Garcia, J. R., MacKillop, J., Aller, E. L., Merriwether, A. M., Wilson, D. S., & Lum, J. K. (2010). Associations between dopamine D4 receptor gene variation with both infidelity and sexual promiscuity. *PLoS One*, *5*(11), e14162. doi:10.1371/journal.pone.0014162

Gaustella, A. J., & MacLeod, C. (2012). A critical review of the influence of oxytocin nasal spray on social cognition in humans: Evidence and future directions. *Hormones and Behavior*, *61*(3), 410–418. doi:10.1016/j.yhbeh.2012.01.002

Gettler, L. T., McDade, T. W., Agustin, S. S., Feranil, A. B., & Kuzawa, C. W. (2013). Do testosterone declines during the transition to marriage and fatherhood relate to men's sexual behavior? Evidence from the Philippines. *Hormones and Behavior*, *64*(5), 755–763. doi:10.1016/j.yhbeh.2013.08.019

Gettler, L. T., McDade, T. W., Feranil, A. B., & Kuzawa, C. W. (2011). Longitudinal evidence that fatherhood decreases testosterone in human males. *Proceedings of the National Academy of Sciences*, *108*(39), 16194–16199. doi:10.1073/pnas.1105403108

Gettler, L. T., McDade, T. W., & Kuzawa, C. W. (2011). Cortisol and testosterone in Filipino young adult men: Evidence for co-regulation of both hormones by fatherhood and relationship status. *American Journal of Human Biology*, *23*(5), 609–620. doi:10.1002/ajhb.21187

Gimpl, G., & Fahrenholz, F. (2001). The oxytocin receptor system: Structure, function, and regulation. *Physiological Reviews*, *81*(2), 629–683.

Gobrogge, K. L., Liu, Y., Young, L. J., & Wang, Z. (2009). Anterior hypothalamic vasopressin regulates pair-bonding and drug-induced aggression in a monogamous rodent. *Proceedings of the National Academy of Sciences*, *106*(45), 19144–19149. doi:10.1073/pnas.0908620106

Goldizen, A. W. (1988). Tamarin and marmoset mating systems: Unusual flexibility. *Trends in Ecology and Evolution*, *3*(2), 36–40. doi:10.1016/0169-5347(88)90045-6

Gouin, J.-P., Carter, C. S., Pournajafi-Nazarloo, H., Glaser, R., Malarkey, W. B., Loving, T. J., … Kiecolt-Glaser, J. K. (2010). Marital behavior, oxytocin, vasopressin, and wound healing. *Psychoneuroendocrinology*, *35*(7), 1082–1090. doi:10.1016/j.psyneuen.2010.01.009

Gowaty, P. A. (1996). Battles of the sexes and origins of monogamy. In J. M. Black (Ed.), *Partnerships in birds: The study of monogamy* (pp. 21–52). New York, NY: Oxford University Press.

Gray, P. B. (2003). Marriage, parenting, and testosterone variation among Kenyan Swahili men. *American Journal of Physical Anthropology*, *122*(3), 279–286. doi:10.1002/ajpa.10293

Gray, P. B., Ellison, P. T., & Campbell, B. C. (2007). Testosterone and marriage among Ariaal men of Northern Kenya. *Current Anthropology*, *48*(5), 750–755. doi:10.1086/522061

Gray, P. B., Jeffrey Yang, C. F., & Pope, H. G. (2006). Fathers have lower salivary testosterone levels than unmarried men and married non-fathers in Beijing, China. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1584), 333–339. doi:10.1098/rspb.2005.3311

Grewen, K. M., Girdler, S. S., Amico, J. A., & Light, K. C. (2005). Effects of partner support on resting oxytocin, cortisol, norepinephrine, and blood pressure before and after warm partner contact. *Psychosomatic Medicine*, *67*(4), 531–538. doi:10.1097/01.psy.0000170341.88395.47

Griffith, S. C., Owens, I. P., & Thuman, K. A. (2002). Extra pair paternity in birds: A review of interspecific variation and adaptive function. *Molecular Ecology*, *11*(11), 2195–2212. doi:10.1046/j.1365-294X.2002.01613.x

Hau, M. (2007). Regulation of male traits by testosterone: Implications for the evolution of vertebrate life histories. *BioEssays*, *29*(2), 133–144. doi:10.1002/bies.20524

Hazan, C., & Diamond, L. M. (2000). The place of attachment in human mating. *Review of General Psychology*, *4*, 186–204. doi:10.1037/1089-2680.4.2.186

Heinrichs, M., Baumgartner, T., Kirschbaum, C., & Ehlert, U. (2003). Social support and oxytocin interact to suppress cortisol and subjective responses to psychosocial stress. *Biological Psychiatry*, *54*(12), 1389–1398. doi:10.1016/S0006-3223(03)00465-7

Hennessy, M. B., Mendoza, S. P., Mason, W. A., & Moberg, G. P. (1995). Endocrine sensitivity to novelty in squirrel monkeys and titi monkeys: Species differences in characteristic modes of responding to the environment. *Physiology and Behavior*, *57*(2), 331–338. doi:10.1016/0031-9384(94)00250-9

Hinde, K., Muth, C., Maninger, N., Ragen, B. J., Larke, R. H., Jarcho, M. R., … Bales, K. L. (2016). Challenges to the pair bond: Neural and hormonal effects of separation and reunion in a monogamous primate. *Frontiers in Behavioral Neuroscience*, 10, 221. doi:10.3389/fnbeh.2016.00221

Hoffman, K. A., Mendoza, S. P., Hennessy, M. B., & Mason, W. A. (1995). Responses of infant titi monkeys, *Callicebus moloch*, to removal of one or both parents: Evidence for paternal attachment. *Developmental Psychobiology*, *28*(7), 399–407. doi:10.1002/(ISSN)1098-2302

Holt-Lunstad, J., Birmingham, W. C., & Light, K. C. (2015). Relationship quality and oxytocin: Influence of stable and modifiable aspects of relationships. *Journal of Social and Personal Relationships*, *32*(4), 472–490. doi:10.1177/0265407514536294

Hostetler, C. M., Hinde, K., Maninger, N., Mendoza, S. P., Mason, W. A., Rowland, D. J., … Bales, K. L. (2017). Effects of pair bonding on dopamine D1 receptors in monogamous male titi monkeys (*Callicebus cupreus*). *American Journal of Primatology*, *79*(3), e22612. doi:10.1002/ajp.22612

Hostinar, C. E., Sullivan, R. M., & Gunnar, M. R. (2014). Psychobiological mechanisms underlying the social buffering of the hypothalamic–pituitary–adrenocortical axis: A review of animal models and human studies across development. *Psychological Bulletin*, *140*(1), 256–282. doi:10.1037/a0032671

Huck, M., Fernandez-Duque, E., Babb, P., & Schurr, T. (2014). Correlates of genetic monogamy in socially monogamous mammals: Insights from Azara's owl monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1782), 20140195. doi:10.1098/rspb.2014.0195

Inglett, B., French, J. A., & Dethlefs, T. M. (1990). Patterns of social preference across different contexts in golden lion tamarins (*Leontopithecus rosalia*). *Journal of Comparative Psychology*, *104*(2), 131–139. doi:10.1037/0735-7036.104.2.131

Insel, T. (2003). Is social attachment an addictive disorder? *Physiology and Behavior*, *79*(3), 351–357. doi:10.1016/S0031-9384(03)00148-3

Insel, T. (2014). The NIMH Research Domain Criteria (RDoC) Project: Precision medicine for psychiatry. *American Journal of Psychiatry*, *171*(4), 395–397. doi:10.1176/appi.ajp.2014.14020138

Insel, T., Cuthbert, B., Garvey, M., Heinssen, R., Pine, D. S., Quinn, K., … Wang, P. (2010). Research domain criteria (RDoC): Toward a new classification framework for research on mental disorders. *American Journal of Psychiatry*, *167*(7), 748–751. doi:10.1176/appi.ajp.2010.09091379

Insel, T., & Shapiro, L. E. (1992). Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proceedings of the National Academy of Sciences*, *89*(13), 5981–5985. doi:10.1073/pnas.89.13.5981

Jacob, F. (1977). Evolution and tinkering. *Science*, *196*(4295), 1161–1166. doi:10.1126/science.860134

Jarcho, M. R., Mendoza, S. P., Mason, W. A., Yang, X., & Bales, K. L. (2011). Intranasal vasopressin affects pair bonding and peripheral gene expression in male *Callicebus cupreus*. *Genes, Brain, and Behavior*, *10*(3), 375–383. doi:10.1111/j.1601-183X.2010.00677.x

Johnson, Z. V., & Young, L. J. (2015). Neurobiological mechanisms of social attachment and pair bonding. *Current Opinion in Behavioral Sciences*, *3*, 38–44. doi:10.1016/j.cobeha.2015.01.009

Kalin, N. H., Shelton, S. E., & Barksdale, C. M. (1988). Opiate modulation of separation-induced distress in non-human primates. *Brain Research*, *440*(2), 285–292. doi:10.1016/0006-8993(88)90997-3

Kalin, N. H., Shelton, S. E., & Lynn, D. E. (1995). Opiate systems in mother and infant primates coordinate intimate contact during reunion. *Psychoneuroendocrinology*, *20*(7), 735–742. doi:10.1016/0306-4530(95)00023-2

Kendrick, K. M., & Dixson, A. F. (1983). The effect of the ovarian cycle on the sexual behavior of the common marmoset (*Callithrix jacchus*). *Physiology and Behavior*, *30*(5), 735–742. doi:10.1016/0031-9384(83)90171-3

Kendrick, K. M., & Dixson, A. F. (1985). Effects of oestradiol 17B, progesterone, and testosterone upon proceptivity and receptivity in ovariectomized common marmosets (*Callithrix jacchus*). *Physiology and Behavior*, *34*(1), 123–128. doi:10.1016/0031-9384(85)90089-7

Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, *14*(1–2), 155–161. doi:10.1016/0306-4530(89)90065-6

Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, *52*, 39–69. doi:10.1086/409721

Kleiman, D. G., & Malcolm, J. R. (1981). The evolution of male parental investment. In D. J. Gubernick & P. H. Klopfer (Eds.), *Parental care in mammals* (pp. 347–387). New York, NY: Plenum Press.

Knobloch, H. S., & Grinevich, V. (2014). Evolution of oxytocin pathways in the brain of vertebrates. *Frontiers in Behavioral Neuroscience*, 8, 31. doi:10.3389/fnbeh.2014.00031

Kovacs, G. L., Sarnyai, Z., Izbeki, F., Szabo, G., Telegdy, G., Barth, T., … Brtnik, F. (1987). Effects of oxytocin-related peptides on acute morphine tolerance: Opposite actions by oxytocin and its receptor antagonists. *Journal of Pharmacology and Experimental Therapeutics*, *241*(2), 569–574.

Kozorovitskiy, Y., Hughes, M., Lee, K., & Gould, E. (2006). Fatherhood affects dendritic spines and vasopressin V1a receptors in the primate prefrontal cortex. *Nature Neuroscience*, *9*(9), 1094–1095. doi:10.1038/nn1753

Kuzawa, C. W., Gettler, L. T., Huang, Y., & McDade, T. W. (2010). Mothers have lower testosterone than non-mothers: Evidence from the Philippines. *Hormones and Behavior*, *57*(4–5), 441–447. doi:10.1016/j.yhbeh.2010.01.014

Kuzawa, C. W., Gettler, L. T., Muller, M. N., McDade, T. W., & Feranil, A. B. (2009). Fatherhood, pairbonding, and testosterone in the Philippines. *Hormones and Behavior*, *56*(4), 429–435. doi:10.1016/j.yhbeh.2009.07.010

Landgraf, R., & Neumann, I. D. (2004). Vasopressin and oxytocin release within the brain: A dynamic concept of multiple and variable modes of neuropeptide communication. *Frontiers in Neuroendocrinology*, *25*(3–4), 150–176. doi:10.1016/j.yfrne.2004.05.001

Lappan, S. (2008). Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology*, *62*(8), 1307–1317. doi:10.1007/s00265-008-0559-7

Larmuseau, M. H., Matthijs, K., & Wenseleers, T. (2016). Cuckolded fathers rare in human populations. *Trends in Ecology and Evolution*, *31*(5), 327–329. doi:10.1016/j.tree.2016.03.004

Lee, H.-J., Macbeth, A. H., Pagani, J., & Young, W. S. (2009). Oxytocin: The great facilitator of life. *Progress in Neurobiology*, *88*(2), 127–151. doi:10.1016/j.pneurobio.2009.04.001

Levine, S. (1993). The influence of social factors on the response to stress. *Psychotherapy and Psychosomatics*, *60*(1), 33–38. doi:10.1159/000288677

Lim, M., Wang, Z., Olazábal, D. E., Ren, X., Terwilliger, E. F., & Young, L. J. (2004). Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene. *Nature*, *429*(6993), 754–757. doi:10.1038/nature02539

Lim, M., & Young, L. (2004). Vasopressin-dependent neural circuits underlying pair bond formation in the monogamous prairie vole. *Neuroscience*, *125*(1), 35–45. doi:10.1016/j.neuroscience.2003.12.008

Ludwig, M., & Leng, G. (2006). Dendritic peptide release and peptide-dependent behaviours. *Nature Reviews Neuroscience*, *7*(2), 126–136. doi:10.1038/nrn1845

Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, *341*(6145), 526–530. doi:10.1126/science.1238677

MacDonald, K., & MacDonald, T. M. (2010). The peptide that binds: A systematic review of oxytocin and its prosocial effects in humans. *Harvard Review of Psychiatry*, *18*(1), 1–21. doi:10.3109/10673220903523615

Macedo, S. (2015). *Just married: Same-sex couples, monogamy, and the future of marriage*. Princeton, NJ: Princeton University Press.

Machin, A. J., & Dunbar, R. I. (2011). The brain opioid theory of social attachment: A review of the evidence. *Behaviour*, *148*(9), 985–1025. doi:10.1163/000579511X596624

MacLusky, N. J., & Naftolin, F. (1981). Sexual differentiation of the central nervous system. *Science*, *211*(4488), 1294–1302. doi:10.1126/science.6163211

Marlowe, F. (2000). Paternal investment and the human mating system. *Behavioural Processes*, *51*(1), 45–61. doi:10.1016/S0376-6357(00)00118-2

Martelle, J. L., Claytor, R., Ross, J. T., Reboussin, B. A., Newman, A. H., & Nader, M. A. (2007). Effects of two novel D3-selective compounds, NGB 2904 [N-(4-(4-(2,3-dichlorophenyl)piperazin-1-yl)butyl)-9H-fluorene-2-carboxamide] and CJB 090 [N-(4-(4-(2,3-dichlorophenyl) piperazin-1-yl)butyl)-4-(pyridin-2-yl)benzamide], on the reinforcing and discriminative stimulus effects of cocaine in rhesus monkeys. *Journal of Pharmacology and Experimental Therapeutics*, *321*(2), 573–582. doi:10.1124/jpet.106.113571

Mason, W. A., & Mendoza, S. P. (1998). Generic aspects of primate attachments: Parents, offspring, and mates. *Psychoneuroendocrinology*, *23*(8), 765–778. doi:10.1016/S0306-4530(98)00054-7

McIntyre, M., Gangestad, S. W., Gray, P. B., Chapman, J. F., Burnham, T. C., M. T., & Thornhill, R. (2006). Romantic involvement often reduces men's testosterone levels–But not always: The moderating role of extrapair sexual interest. *Journal of Personality and Social Psychology*, *91*(4), 642–651. doi:10.1037/0022-3514.91.4.642

Meller, R. E., Keverne, E. B., & Herbert, J. (1980). Behavioural and endocrine effects of naltrexone in male talapoin monkeys. *Pharmacology Biochemistry and Behavior*, *13*(5), 663–672. doi:10.1016/0091-3057(80)90010-6

Mendoza, S. P., & Mason, W. A. (1986). Contrasting responses to intruders and to involuntary separation by monogamous and polygynous New World monkeys. *Physiology and Behavior*, *38*(6), 795–801. doi:10.1016/0031-9384(86)90045-4

Mendoza, S. P., & Mason, W. A. (1997). Attachment relationships in new world primates. *Annals of the New York Academy of Sciences*, *807*(1), 203–209. doi:10.1111/j.1749-6632.1997.tb51921.x

Mendoza, S. P., Reeder, D. M., & Mason, W. A. (2002). Nature of proximate mechanisms underlying primate social systems: Simplicity and redundancy. *Evolutionary Anthropology: Issues, News, and Reviews*, *11*(Suppl. 1), 112–116. doi:10.1002/evan.10071

Mooradian, A. D., Morley, J. E., & Korenman, S. G. (1987). Biological actions of androgens. *Endocrine Reviews*, *8*(1), 1–28. doi:10.1210/edrv-8-1-1

Muller, M. N., Marlowe, F. W., Bugumba, R., & Ellison, P. T. (2009). Testosterone and paternal care in East African foragers and pastoralists. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 347–354. doi:10.1098/rspb.2008.1028

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression, and testosterone in wild chimpanzees: A test of the "challenge hypothesis." *Animal Behaviour*, *67*(1), 113–123. doi:10.1016/j.anbehav.2003.03.013

Mustoe, A. C., Cavanaugh, J., Harnisch, A. M., Thompson, B. E., & French, J. A. (2015). Do marmosets care to share? Oxytocin treatment reduces prosocial behavior toward strangers. *Hormones and Behavior*, *71*, 83–90. doi:10.1016/j.yhbeh.2015.04.015

Nelson, E. E., & Panksepp, J. (1998). Brain substrates of infant–mother attachment: Contributions of opioids, oxytocin, and norepinephrine.

Neuroscience and Biobehavioral Reviews, *22*(3), 437–452. doi:10.1016/S0149-7634(97)00052-3

Nunes, S., Fite, J. E., & French, J. A. (2000). Variation in steroid hormones associated with infant care behaviour and experience in male marmosets (*Callithrix kuhlii*). *Animal Behaviour*, *60*(6), 857–865. doi:10.1006/anbe.2000.1524

Nunes, S., Fite, J. E., Patera, K. J., & French, J. A. (2001). Interactions among paternal behavior, steroid hormones, and parental experience in male marmosets (*Callithrix kuhlii*). *Hormones and Behavior*, *39*(1), 70–82. doi:10.1006/hbeh.2000.1631

Ophir, A. G., Gessel, A., Zheng, D.-J., & Phelps, S. M. (2012). Oxytocin receptor density is associated with male mating tactics and social monogamy. *Hormones and Behavior*, *61*(3), 445–453. doi:10.1016/j.yhbeh.2012.01.007

Opie, C., Atkinson, Q. D., Dunbar, R. I., & Shultz, S. (2013a). Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences*, *110*(33), 13328–13332. doi:10.1073/pnas.1307903110

Opie, C., Atkinson, Q. D., Dunbar, R. I., & Shultz, S. (2013b). Reply to Dixson: Infanticide triggers primate monogamy. *Proceedings of the National Academy of Sciences*, *110*(51), E4938. doi:10.1073/pnas.1319662110

Opie, C., Atkinson, Q. D., & Shultz, S. (2012). The evolutionary history of primate mating systems. *Communicative and Integrative Biology*, *5*(5), 458–461. doi:10.4161/cib.20821

Overdorff, D. J., & Tecot, S. R. (2006). Social pair-bonding and resource defense in wild red-bellied lemurs (*Eulemur rubriventer*). In L. Gould & M. L. Sauther (Eds.), *Lemurs: Ecology and adaptation* (pp. 235–254). New York, NY: Springer.

Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. New York, NY: Oxford University Press.

Panksepp, J., Nelson, E., & Bekkedal, M. (1997). Brain systems for the mediation of social separation-distress and social-reward evolutionary antecedents and neuropeptide intermediaries. *Annals of the New York Academy of Sciences*, *807*(1), 78–100. doi:10.1111/j.1749-6632.1997.tb51914.x

Parker, K. J., Buckmaster, C. L., Schatzberg, A. F., & Lyons, D. M. (2005). Intranasal oxytocin administration attenuates the ACTH stress response in monkeys. *Psychoneuroendocrinology*, *30*(9), 924–929. doi:10.1016/j.psyneuen.2005.04.002

Pascoe, J. E., Williams, K. L., Mukhopadhyay, P., Rice, K. C., Woods, J. H., & Ko, M.-C. (2008). Effects of mu, kappa, and delta opioid receptor agonists on the function of hypothalamic–pituitary–adrenal axis in monkeys. *Psychoneuroendocrinology*, *33*(4), 478–486. doi:10.1016/j.psyneuen.2008.01.006

Pitkow, L. J., Sharer, C. A., Ren, X., Insel, T. R., Terwilliger, E. F., & Young, L. J. (2001). Facilitation of affiliation and pair-bond formation by vasopressin receptor gene transfer into the ventral forebrain of a monogamous vole. *Journal of Neuroscience*, *21*(18), 7392–7396.

Platt, M. L., Seyfarth, R. M., & Cheney, D. L. (2016). Adaptations for social cognition in the primate brain. *Philosophical Transactions of the Royal Society B*, *371*(1687), 20150096. doi:10.1098/rstb.2015.0096

Prudom, S. L., Broz, C. A., Schultz-Darken, N., Ferris, C. T., Snowdon, C., & Ziegler, T. E. (2008). Exposure to infant scent lowers serum testosterone in father common marmosets (*Callithrix jacchus*). *Biology Letters*, *4*(6), 603–605. doi:10.1098/rsbl.2008.0358

Rafacz, M. L., Margulis, S., & Santymire, R. M. (2012). Hormonal correlates of paternal care differences in the Hylobatidae. *American Journal of Primatology*, *74*(3), 247–260. doi:10.1002/ajp.21994

Ragen, B. J., Maninger, N., Mendoza, S. P., & Bales, K. L. (2015). The effects of morphine, naloxone, and κ-opioid manipulation on endocrine functioning and social behavior in monogamous titi monkeys (*Callicebus cupreus*). *Neuroscience*, *287*, 32–42. doi:10.1016/j.neuroscience.2014.11.053

Ragen, B. J., Maninger, N., Mendoza, S. P., Jarcho, M. R., & Bales, K. L. (2013). Presence of a pair-mate regulates the behavioral and physiological effects of opioid manipulation in the monogamous titi monkey (*Callicebus cupreus*). *Psychoneuroendocrinology*, *38*(11), 2448–2461. doi:10.1016/j.psyneuen.2013.05.009

Rangel-Negrín, A., Dias, P. A. D., Chavira, R., & Canales-Espinosa, D. (2011). Social modulation of testosterone levels in male black howlers (*Alouatta pigra*). *Hormones and Behavior*, *59*(1), 159–166. doi:10.1016/j.yhbeh.2010.11.005

Ren, D., Chin, K. R., & French, J. A. (2014). Molecular variation in AVP and AVPR1a in New World monkeys (Primates, Platyrrhini): Evolution and implications for social monogamy. *PLoS One*, *9*(10), e111638. doi:10.1371/journal.pone.0111638

Ren, D., Lu, G., Moriyama, H., Mustoe, A. C., Harrison, E. B., & French, J. A. (2015). Genetic diversity in oxytocin ligands and receptors in New World monkeys. *PLoS One*, *10*(5), e0125775. doi:10.1371/journal.pone.0125775

Resendez, S. L., Kuhnmuench, M., Krzywosinski, T., & Aragona, B. J. (2012). κ-opioid receptors within the nucleus accumbens shell mediate pair bond maintenance. *Journal of Neuroscience*, *32*(20), 6771–6784. doi:10.1523/JNEUROSCI.5779-11.2012

Rilling, J. K., & Young, L. J. (2014). The biology of mammalian parenting and its effect on offspring social development. *Science*, *345*(6198), 771–776. doi:10.1126/science.1252723

Ring, R. (2005). The central vasopressinergic system: Examining the opportunities for psychiatric drug development. *Current Pharmaceutical Design*, *11*(2), 205–225. doi:10.2174/1381612053382241

Ross, C. N., & French, J. (2011). Female marmosets' behavioral and hormonal responses to unfamiliar intruders. *American Journal of Primatology*, *73*, 1072–1081. doi:10.1002/ajp.20975

Ross, C. N., French, J., & Patera, K. (2004). Intensity of aggressive interactions modulates testosterone in male marmosets. *Physiology and Behavior*, *83*(3), 437–445. doi:10.1016/j.physbeh.2004.08.036

Rukstalis, M., & French, J. A. (2005). Vocal buffering of the stress response: Exposure to conspecific vocalizations moderates urinary cortisol excretion in isolated marmosets. *Hormones and Behavior*, *47*(1), 1–7. doi:10.1016/j.yhbeh.2004.09.004

Saito, A., & Nakamura, K. (2011). Oxytocin changes primate paternal tolerance to offspring in food transfer. *Journal of Comparative Physiology A*, *197*(4), 329–337. doi:10.1007/s00359-010-0617-2

Saltzman, W., & Ziegler, T. E. (2014). Functional significance of hormonal changes in mammalian fathers. *Journal of Neuroendocrinology*, *26*(10), 685–696. doi:10.1111/jne.12176

Schaffner, C. M., & French, J. A. (2004). Behavioral and endocrine responses in male marmosets to the establishment of multimale breeding groups: Evidence for non-monopolizing facultative polyandry. *International Journal of Primatology*, *25*(3), 709–732. doi:10.1023/B:IJOP.0000023582.34854.43

Schaffner, C. M., Shepherd, R. E., Santos, C. V., & French, J. A. (1995). Development of heterosexual relationships in Wied's black tufted-ear marmosets (*Callithrix kuhli*). *American Journal of Primatology*, *36*(3), 185–200. doi:10.1002/(ISSN)1098-2345

Scheele, D., Wille, A., Kendrick, K. M., Stoffel-Wagner, B., Becker, B., Gunturkun, O., … Hurlemann, R. (2013). Oxytocin enhances brain reward system responses in men viewing the face of their female partner. *Proceedings of the National Academy of Sciences*, *110*(50), 20308–20313. doi:10.1073/pnas.1314190110

Schmitt, D. P., & Buss, D. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology*, *80*(6), 917–984. doi:10.1037/0022-3514.80.6.894

Schülke, O., & Kappeler, P. M. (2003). So near and yet so far: Territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. *Animal Behaviour*, *65*(2), 331–343. doi:10.1006/anbe.2003.2018

Seltzer, L. J., Ziegler, T. E., & Pollak, S. D. (2010). Social vocalizations can release oxytocin in humans. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1694), 2661–2666. doi:10.1098/rspb.2010.0567

Setchell, J. M., Charpentier, M., & Wickings, E. J. (2005). Mate guarding and paternity in mandrills: Factors influencing alpha male monopoly. *Animal Behaviour*, *70*(5), 1105–1120. doi:10.1016/j.anbehav.2005.02.021

Seyfarth, R. M., & Cheney, D. L. (2002). What are big brains for?. *Proceedings of the National Academy of Sciences*, *99*(7), 4141–4142. doi:10.1073/pnas.082105099

Shapiro, L. E., Meyer, M. E., & Dewsbury, D. A. (1989). Affiliative behavior in voles: Effects of morphine, naloxone, and cross-fostering. *Physiology and Behavior*, *46*(4), 719–723. doi:10.1016/0031-9384(89)90357-0

Shultz, S., & Dunbar, R. I. (2007). The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*(1624), 2429–2436. doi:10.1098/rspb.2007.0693

Shultz, S., Opie, C., & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. *Nature*, *479*(7372), 219–222. doi:10.1038/nature10601

Skuse, D. H., & Gallagher, L. (2009). Dopaminergic-neuropeptide interactions in the social brain. *Trends in Cognitive Sciences*, *13*(1), 27–35. doi:10.1016/j.tics.2008.09.007

Small, M. F. (1990). Alloparental behaviour in Barbary macaques. *Macaca Sylvanus*. *Animal Behaviour*, *39*(2), 297–306. doi:10.1016/S0003-3472(05)80874-7

Smeltzer, M. D., Curtis, J. T., Aragona, B. J., & Wang, Z. (2006). Dopamine, oxytocin, and vasopressin receptor binding in the medial prefrontal cortex of monogamous and promiscuous voles. *Neuroscience Letters*, *394*(2), 146–151. doi:10.1016/j.neulet.2005.10.019

Smith, A. S., Ågmo, A., Birnie, A. K., & French, J. A. (2010). Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, *Callithrix Penicillata*. *Hormones and Behavior*, *57*(2), 255–262. doi:10.1016/j.yhbeh.2009.12.004

Smith, A. S., Birnie, A. K., & French, J. A. (2011). Social isolation affects partner-directed social behavior and cortisol during pair formation in marmosets, *Callithrix Geoffroyi*. *Physiology and Behavior*, *104*(5), 955–961. doi:10.1016/j.physbeh.2011.06.014

Smith, A. S., Birnie, A. K., & French, J. A. (2013). Prenatal androgens affect development and behavior in primates. In K. B. H. Clancy, K. Hinde, & J. N. Rutherford (Eds.), *Building babies* (pp. 103–131). New York, NY: Springer.

Smith, T. E., & French, J. A. (1997). Psychosocial stress and urinary cortisol excretion in marmoset monkeys. *Physiology and Behavior*, *62*(2), 225–232. doi:10.1016/S0031-9384(97)00103-0

Smith, T. E., McGreer-Whitworth, B., & French, J. A. (1998). Close proximity of the heterosexual partner reduces the physiological and behavioral consequences of novel-cage housing in black tufted-ear marmosets (*Callithrix kuhli*). *Hormones and Behavior*, *34*(3), 211–222. doi:10.1006/hbeh.1998.1469

Snowdon, C. T., Pieper, B. A., Boe, C. Y., Cronin, K. A., Kurian, A. V., & Ziegler, T. E. (2010). Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. *Hormones and Behavior*, *58*(4), 614–618. doi:10.1016/j.yhbeh.2010.06.014

Sofroniew, M. V. (1983). Morphology of vasopressin and oxytocin neurons and their central and vascular projections. *Progress in Brain Research*, *60*, 101–114. doi:10.1016/S0079-6123(08)64378-2

Spence-Aizenberg, A., Di Fiore, A., & Fernandez-Duque, E. (2016). Social monogamy, male–female relationships, and biparental care in wild titi monkeys (*Callicebus discolor*). *Primates*, *57*(1), 103–112. doi:10.1007/s10329-015-0489-8

Stoop, R. (2012). Neuromodulation by oxytocin and vasopressin. *Neuron*, *76*(1), 142–159. doi:10.1016/j.neuron.2012.09.025

Stoop, R. (2014). Neuromodulation by oxytocin and vasopressin in the central nervous system as a basis for their rapid behavioral effects. *Current Opinion in Neurobiology*, *29*, 187–193. doi:10.1016/j.conb.2014.09.012

Storey, A. E., Noseworthy, D. E., Delahunty, K. M., Halfyard, S. J., & McKay, D. W. (2011). The effects of social context on the hormonal and behavioral responsiveness of human fathers. *Hormones and Behavior*, *60*(4), 353–361. doi:10.1016/j.yhbeh.2011.07.001

Storey, A. E., & Ziegler, T. E. (2016). Primate paternal care: Interactions between biology and social experience. *Hormones and Behavior*, *77*, 260–271. doi:10.1016/j.yhbeh.2015.07.024

Sussman, R. W., & Garber, P. A. (1987). A new interpretation of the social organization and mating system of the Callitrichidae. *International Journal of Primatology*, *8*(1), 73–92. doi:10.1007/BF02737114

Tabak, B. A., McCullough, M. E., Szeto, A., Mendez, A. J., & McCabe, P. M. (2011). Oxytocin indexes relational distress following interpersonal harms in women. *Psychoneuroendocrinology*, *36*(1), 115–122. doi:10.1016/j.psyneuen.2010.07.004

Taylor, J. H., & French, J. A. (2015). Oxytocin and vasopressin enhance responsiveness to infant stimuli in adult marmosets. *Hormones and Behavior*, *75*, 154–159. doi:10.1016/j.yhbeh.2015.10.002

Taylor, S. E., Saphire-Bernstein, S., & Seeman, T. E. (2010). Are plasma oxytocin in women and plasma vasopressin in men biomarkers of distressed pair-bond relationships? *Psychological Science*, *21*(1), 3–7. doi:10.1177/0956797609356507

Tecot, S. R., Singletary, B., & Eadie, E. (2016). Why "monogamy" isn't good enough. *American Journal of Primatology*, *78*(3), 340–354. doi:10.1002/ajp.22412

Tops, M., van Peer, J. M., & Korf, J. (2007). Individual differences in emotional expressivity predict oxytocin responses to cortisol administration: Relevance to breast cancer? *Biological Psychology*, *75*(2), 119–123. doi:10.1016/j.biopsycho.2007.01.001

Trainor, B. C., & Marler, C. A. (2001). Testosterone, paternal behavior, and aggression in the monogamous California mouse (*Peromyscus californicus*). *Hormones and Behavior*, *40*(1), 32–42. doi:10.1006/hbeh.2001.1652

Trainor, B. C., Takahashi, E. Y., Silva, A. L., Crean, K. K., & Hostetler, C. (2010). Sex differences in hormonal responses to social conflict in the monogamous California mouse. *Hormones and Behavior*, *58*(3), 506–512. doi:10.1016/j.yhbeh.2010.04.008

van Anders, S. M., & Goldey, K. L. (2010). Testosterone and partnering are linked via relationship status for women and "relationship orientation" for men. *Hormones and Behavior*, *58*(5), 820–826. doi:10.1016/j.yhbeh.2010.08.005

van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The steroid/peptide theory of social bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology*, *36*(9), 1265–1275. doi:10.1016/j.psyneuen.2011.06.001

van Anders, S. M., Tolman, R. M., & Volling, B. L. (2012). Baby cries and nurturance affect testosterone in men. *Hormones and Behavior*, *61*(1), 31–36. doi:10.1016/j.yhbeh.2011.09.012

van Anders, S. M., & Watson, N. V. (2006). Relationship status and testosterone in North American heterosexual and non-heterosexual men and women: Cross-sectional and longitudinal data. *Psychoneuroendocrinology*, *31*(6), 715–723. doi:10.1016/j.psyneuen.2006.01.008

van Anders, S. M., & Watson, N. V. (2007). Testosterone levels in women and men who are single, in long-distance relationships, or same-city relationships. *Hormones and Behavior*, *51*(2), 286–291. doi:10.1016/j.yhbeh.2006.11.005

Vargas-Pinilla, P., Paixão-Côrtes, V. R., Paré, P., Tovo-Rodrigues, L., Vieira, C. M. D. A. G., Xavier, A., … Bortolini, M. C. (2015). Evolutionary pattern in the OXT-OXTR system in primates: Coevolution and positive selection footprints. *Proceedings of the National Academy of Sciences*, *112*(1), 88–93. doi:10.1073/pnas.1419399112

Wallen, K. (2001). Sex and context: Hormones and primate sexual motivation. *Hormones and Behavior*, *40*(2), 339–357. doi:10.1006/hbeh.2001.1696

Wallen, K. (2005). Hormonal influences on sexually differentiated behavior in nonhuman primates. *Frontiers in Neuroendocrinology*, *26*(1), 7–26. doi:10.1016/j.yfrne.2005.02.001

Walum, H., Lichtenstein, P., Neiderhiser, J. M., Reiss, D., Ganiban, J. M., Spotts, E. L., … Westberg, L. (2012). Variation in the oxytocin receptor gene is associated with pair-bonding and social behavior. *Biological Psychiatry*, *71*(5), 419–426. doi:10.1016/j.biopsych.2011.09.002

Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J. M., Reiss, D., Igl, W., … Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor *1a* gene (AVPR1A) associates with pair-bonding behavior in humans. *Proceedings of the National Academy of Sciences*, *105*(37), 14153–14156. doi:10.1073/pnas.0803081105

Wang, Z., Ferris, C. F., & De Vries, G. J. (1994). Role of septal vasopressin innervation in paternal behavior in prairie voles (*Microtus ochrogaster*). *Proceedings of the National Academy of Sciences*, *91*, 400–404. doi:10.1073/pnas.91.1.400

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioral Ecology and Sociobiology*, *44*(1), 43–55. doi:10.1007/s002650050513

Weingrill, T., Lycett, J. E., Barrett, L., Hill, R. A., & Henzi, S. P. (2003). Male consortship behaviour in chacma baboons: The role of demographic factors and female conceptive probabilities. *Behaviour*, *140* (3), 405–427. doi:10.1163/156853903321826701

Whitton, S. W., Weitbrecht, E. M., & Kuryluk, A. D. (2015). Monogamy agreements in male same-sex couples: Associations with relationship quality and individual well-being. *Journal of Couple and Relationship Therapy*, *14*(1), 39–63. doi:10.1080/15332691.2014.953649

Wingfield, J. C., Hegner, R. E., Dufty Jr, A. M., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, *136*(6), 829–846.

Wingfield, J. C., Lynn, S. E., & Soma, K. K. (2001). Avoiding the "costs" of testosterone: Ecological bases of hormone-behavior interactions. *Brain, Behavior, and Evolution*, *57*, 239–251. doi:10.1159/000047243

Winslow, J. T., Hastings, N., Carter, C. S., Harbaugh, C. R., & Insel, T. R. (1993). A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature*, *365*, 545–548. doi:10.1038/365545a0

Wittig, R. M., Crockford, C., Deschner, T., Langergraber, K. E., Ziegler, T. E., & Zuberbuhler, K. (2014). Food sharing is linked to urinary oxytocin levels and bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133096. doi:10.1098/rspb.2013.3096

Woller, M. J., Sosa, M. E., Chiang, Y., Prudom, S. L., Keelty, P., Moore, J. E., & Ziegler, T. E. (2012). Differential hypothalamic secretion of neurocrines in male common marmosets: Parental experience effects? *Journal of Neuroendocrinology*, *24*(3), 413–421. doi:10.1111/j.1365-2826.2011.02252.x

Young, L. J., Winslow, J. T., Nilson, R., & Insel, T. R. (1997). Species differences in *V□a* receptor gene expression in monogamous and nonmonogamous voles: Behavioral consequences. *Behavioral Neuroscience*, *111*(3), 599–605. doi:10.1037/0735-7044.111.3.599

Ziegler, T., Jacoris, S., & Snowdon, C. T. (2004). Sexual communication between breeding male and female cotton-top tamarins (*Saguinus oedipus*) and its relationship to infant care. *American Journal of Primatology*, *64*(1), 57–69. doi:10.1002/ajp.20061

Ziegler, T. E., Peterson, L. J., Sosa, M. E., & Barnard, A. M. (2011). Differential endocrine responses to infant odors in common marmoset (Callithrix jacchus) fathers. *Hormones and Behavior*, *59*(2), 265–270. doi: 10.1016/j.yhbeh.2010.12.001

Ziegler, T., Prudom, S. L., Schultz-Darken, N. J., Kurian, A. V., & Snowdon, C. T. (2006). Pregnancy weight gain: Marmoset and tamarin dads show it too. *Biology Letters*, *2*(2), 181–183. doi:10.1098/rsbl.2005.0426

Ziegler, T., Schultz-Darken, N. J., Scott, J. J., Snowdon, C. T., & Ferris, C. F. (2005). Neuroendocrine response to female ovulatory odors depends upon social condition in male common marmosets, *Callithrix jacchus*. *Hormones and Behavior*, *47*(1), 56–64. doi:10.1016/j.yhbeh.2004.08.009

Ziegler, T., & Snowdon, C. T. (2000). Preparental hormone levels and parenting experience in male cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*, *38*(3), 159–167. doi:10.1006/hbeh.2000.1617

Ziegler, T., Washabaugh, K. F., & Snowdon, C. T. (2004). Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*, *45*(2), 84–92. doi:10.1016/j.yhbeh.2003.09.003

Ziegler, T., Wegner, F. H., Carlson, A. A., Lazaro-Perea, C., & Snowdon, C. T. (2000). Prolactin levels during the periparturitional period in the biparental cotton-top tamarin (*Saguinus oedipus*): Interactions with gender, androgen levels, and parenting. *Hormones and Behavior*, *38* (2), 111–122. doi:10.1006/hbeh.2000.1606