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Abstract

Hormones, and hormone responses to social contexts, are the proximate mechanisms of evolutionary pathways to pair bonds and other social bonds. Testosterone (T) is implicated in tradeoffs relevant to pair bonding, and oxytocin (OT) and arginine vasopressin (AVP) are positively tied to social bonding in a variety of species. Here, we present the Steroid/Peptide Theory of Social Bonds (S/P Theory), which integrates T and peptides to provide a model, set of predictions, and classification system for social behavioral contexts related to social bonds. The S/P Theory also resolves several paradoxes apparent in the literature on social bonds and hormones: the Offspring Defense Paradox, Aggression Paradox, and Intimacy Paradox. In the S/P Theory, we partition aggression into antagonistic and protective aggression, which both increase T but exert distinct effects on AVP and thus social bonds. Similarly, we partition intimacy into sexual and nurturant intimacy, both of which increase OT and facilitate social bonds, but exert distinct effects on T. We describe the utility of the S/P Theory for classifying "tricky" behavioral contexts on the basis of their hormonal responses using partner cuddling, a behavior which is assumed to be nurturant but increases T, as a test case of the S/P Theory. The S/P Theory provides a comparative basis for conceptualizing and testing evolved hormonal

pathways to pair bonds with attention to species, context, and gender/sex specificities and convergences.

Keywords: androgen, sexual, nurturant, close relationships, romantic, women, men, parenting, competition, challenge, child aggression

1. Introduction

The close ties between hormones and pair bonds have been studied in a variety of species, with most research focusing on the peptides oxytocin (OT) and arginine vasopressin (AVP). A parallel literature focuses on the steroid testosterone (T) and social behaviors, and this work has provided similarly important insights into social neuroendocrinology. However, few studies have incorporated both T and peptides, and the theoretical framing of these fields are similarly distinct, though a recent review jointly describes T and peptide administration (Bos et al., 2011). Our goal is to bring T and peptides together to better understand their joint evolutionary significance in pair bonds and other social bonds via the Steroid/Peptide Theory of Social Bonds (S/P Theory). In the S/P Theory, we integrate T and peptides to provide a model, set of predictions, and classification system for social behavioral contexts related to bonds.

We first briefly discuss ultimate and proximate considerations for pair bonds, highlighting how they overlap with and diverge from other social bonds and systems. Next, we discuss paradoxes that arise in hormonal approaches to social bonds, illustrating how aspects of the S/P Theory resolve these paradoxes. We then further detail aspects of the S/P Theory, articulating the value of incorporating both classes of hormones, and also making a set of predictions. Using partner cuddling as a test case, we next detail the utility of the S/P Theory for classifying "tricky" behavioral contexts whose "kind" is not immediately apparent or can be misleading. We also address the importance of gender/sex and conclude with a discussion of the S/P Theory and its gaps.

A major goal of this paper is to discuss how neuroendocrine responses provide a proximate means for addressing evolutionary questions about pair bonds and other social bonds. Our model is comparative and relies on the nonhuman animal literature to a large extent but also is intended to be especially relevant for human research, given that we focus largely on social modulation of hormones, a useful and potentially noninvasive experimental approach for human or other studies where more invasive approaches are less likely to be employed.

2. Pair bonds: ultimate and proximate considerations

2.1. Evolutionary significance of pair bonds
Why do pair bonds exist when they limit reproductive opportunity? Pair bonds are cross-culturally ubiquitous among humans (Hawkes, 2004) and are common in some species like birds and other primates. They are generally defined by social and sexual "monogamy," and though extra-pair sexual contacts occur, pair bonds still limit sexual access to others. Like others, we define pair bonds as long-lasting affiliations involving intimacy, sexual

contact, preferential proximity, and emotional attachment with relative exclusivity (Hawkes, 2004).

Pair bonds may be evolutionarily adaptive, enhancing biparental care and parent—offspring bonds when they promote parent or offspring fitness in some way (Snowdon, 2001; Fernandez-Duque et al., 2009). For example, in marmosets and tamarins, pair bonding and paternal care enhance offspring survival (Snowdon, 1996). Pair bonds also appear to carry fitness benefits to mothers, as pair bonded women and female owl monkeys receive higher caloric provisioning during lactation, a time characterized by increased energetic needs (Marlowe, 2003; Wolovich et al., 2008).

Pair bonds are typically understood to exist between one female and one male. However, a large body of research demonstrates that pair bonds exist between individuals of the *same* gender/sex in a number of pair bonding species, and this obviously includes humans. The exclusive "two-point" nature of pair bonds is assumed but not well studied, i.e. that pair bonds can exist only between two people, and any one person can be a part of only one pair bond. The two-point assumption is undertheorized, however, as the presence of a pair bond between two individuals does not necessarily preclude additional pair bonds (see Fig. 1). For example, there are a host of species in which multiple females appear to bond with one male. In humans, a relationship approach known as polyamory involves multiple committed romantic/sexual relationships, which might be characterized by "polyfidelity" or a type of multiple monogamy. And, most species with pair bonds can develop sequential or serial monogamous pair bonds. However, evidence does suggest that two-point pair bonds differ hormonally from multi-point or embedded two-point pair bonds (Fig. 1 defines these terms further) (van Anders et al., 2007b).
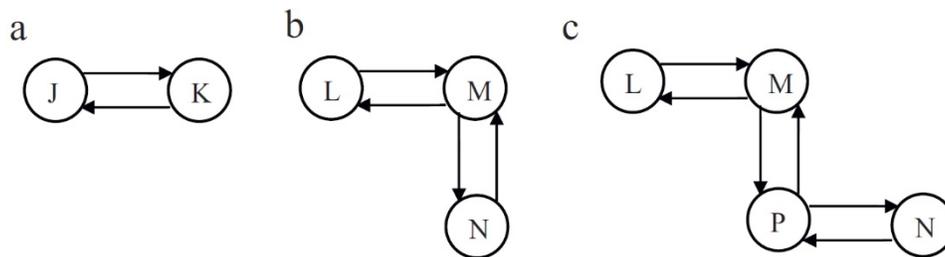
Figure 1. Examples of pair bonds in multiple configurations: (a) "two-point," as is typically conceptualized, where each individual is in only one pair bond; (b) "embedded two-point" for L and N, where L and N are in only one pair bond each, but their partner is not exclusively bonded to them; "multi-point" for M, where M has two pair bonds, and each of these pair bond partners is pair bonded only with M; and (c) "embedded two-point" for L and N; "embedded multi-point" for M and P, where M and P have two pair bonds each, which include a mixture of partners exclusively bonded with them and bonded with others. Letters represent separate individuals, and arrows represent the direction of the bond. An example of (b) is polygyny or polyandry, and of (c) is polyamory for individuals M and P (and potentially L and N, depending on definitions).

2.2. Proximate mechanisms for pair bonds

Hormones often are the proximate mechanisms by which social traits critical to life-history trade-offs are expressed and can be helpful in gaining insights into ultimate function. Moreover, researchers have shown that hormone responsivity, specifically, is notably important in studying the comparative evolution of mating systems (McGlothlin et al., 2010). Hormones, and hormone responsiveness, therefore provide an important method for investigating the evolution of pair bonding.

Evolutionary theories of pair bonds highlight the similarity of these types of bonds and those that exist between parents and offspring; both include attachment, intimacy, and overlapping hormonal mechanisms (Carter, 1998). Given that parent-offspring bonds are likely to be evolutionarily older, pair bonds may be predicated upon a neuroendocrine system that evolved to support parent-offspring bonds but in general promotes nurturance (Fisher, 1992; Carter, 1998; Fernandez-Duque et al., 2009).

Pair and parent-offspring bonds may overlap evolutionarily in aspects of function and mechanism, but also clearly diverge as pair bonds additionally facilitate sexual contact and reproductive potential: How could the same physiological system promote nurturance within pair and parent-offspring bonds but also facilitate sexual contact *exclusively* within pairs? Given this need for bifurcation, researchers have theorized a separate physiological system that promotes sexual contact (Diamond, 2003), and evolved to facilitate reproduction directly and indirectly via pair bonds. In support, sexual activity does enhance pair bonds in a variety of species (Carter, 1998; Snowdon, 2001; van Anders et al., 2007a). Pair bonds may thus rely on two physiological systems: a nurturant system evolved to support parent-offspring bonds and infant survival, and a sexual system evolved to support reproduction (Fig. 2). T is a favorable candidate for testing these distinct evolutionary functions, since it is positively linked to sexuality but negatively linked to nurturance (van Anders and Watson, 2006b; Ziegler et al., 2009), and because it is so strongly implicated in trade-offs relevant to pair bonding (Wingfield et al., 1990; Ketterson et al., 2005; Bales et al., 2006; van Anders and Watson, 2006b).
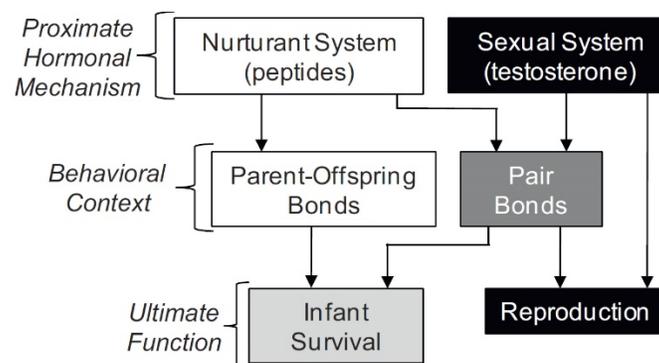

Figure 2. Ultimate functions and proximate mechanisms of pair and parent-offspring bonds. Predictions based on this model would be (1) if pair and parent-offspring bonds elicit similar hormonal responses, then a shared evolutionary history is supported and (2) if sexual and nurturant intimacy within pair bonds elicit divergent hormonal responses,

then the existence of two systems underlying/contributing to pair bonds is supported. Note that sexual activity can occur within and outside a pair bond context, even in pair bonding species; this removes any evolutionary imperative for sexuality to occur only within pair bonds. As far as we know, only humans engage in sexual activity with the intent to reproduce, but most human sexuality is not oriented around reproduction and instead around sexual pleasure, power, relationship maintenance, intimacy, displays of gender, or resource acquisition.

3. The Steroid/Peptide Theory of Social Bonds

In this paper, we put forth an overarching conceptual umbrella we call the Steroid/Peptide Theory of Social Bonds (S/P Theory). In the S/P Theory, we integrate hormonal pathways to social bonds that include T, OT, and AVP, and reference other steroids and peptides. The S/P Theory has two major aspects and one minor feature, which we introduce briefly here but are best examined in the forthcoming sections when noted. The first major aspect of the S/P Theory is the S/P Model (Fig. 3), which details how a specifically defined set of behavioral contexts affect T, OT, and AVP, and how these in turn facilitate or inhibit social bonds. The second major aspect to the S/P Theory is the S/P Framework (Fig. 4), which is a conceptual map of T and OT that labels the *kinds* of behavioral contexts linked to high and low levels of both hormones. The S/P Framework is useful for conceptualizing what T or OT "mean" in terms of social bonds, that is, their "role" or manifestation as relevant to social bonds. In contrast, the S/P Model is useful for delineating how two sets of behavioral contexts can affect T and peptides, to either facilitate or inhibit social bonds.
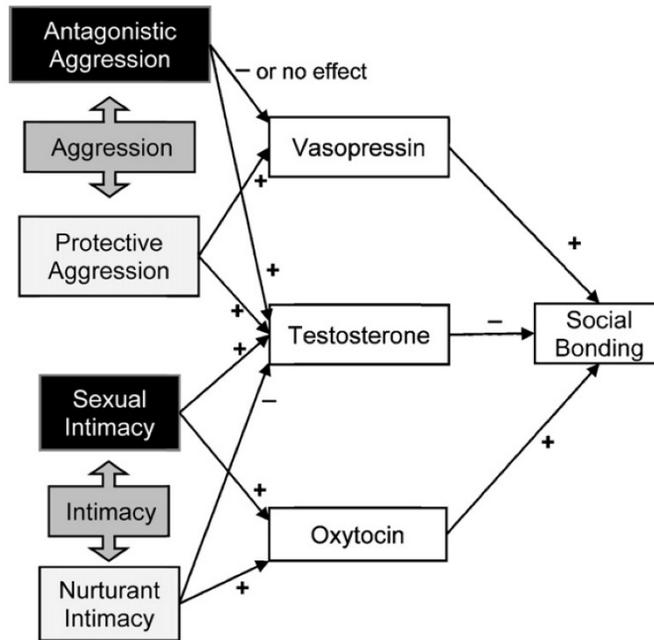
Figure 3. The Steroid/Peptide Model of Social Bonds. This model demonstrates pathways from aggression and intimacy to T, AVP, and OT and how these hormones in turn affect social bonding. We partition aggression into *antagonistic* and *protective* aggression; both types increase testosterone (T), but only protective aggression increases vasopressin (AVP), while antagonistic aggression decreases or has no effect on AVP. We partition intimacy into *sexual* and *nurturant* intimacy; both types increase oxytocin (OT), but only sexual intimacy increases T, while nurturant intimacy decreases T. OT and AVP promote, while T inhibits, social bonding. Aggression involves direct conflict that is instigated to be (1) *antagonistic:* obtaining new territory, status, mates, dominance, etc.; (2) *protective:* protecting or safeguarding social bonds, e.g. infant defense, partner/mate guarding or defense, etc. Only AVP can be used to distinguish aggression types, since both increase T. Intimacy involves direct close physical contact that is (1) *sexual:* sexual contact between individuals that may be oriented around pleasure, reproduction, power, etc.; (2) *nurturant:* warm loving contact between individuals that enhances social bonds. Only T can be used to distinguish intimacy types, since both increase OT. AVP and OT are represented separately for visual purposes, but likely overlap with each other to a large extent (also possibly with PRL); estradiol may also work similarly to OT, and progesterone to AVP. "+" indicates a positive effect; "−" indicates a negative effect.
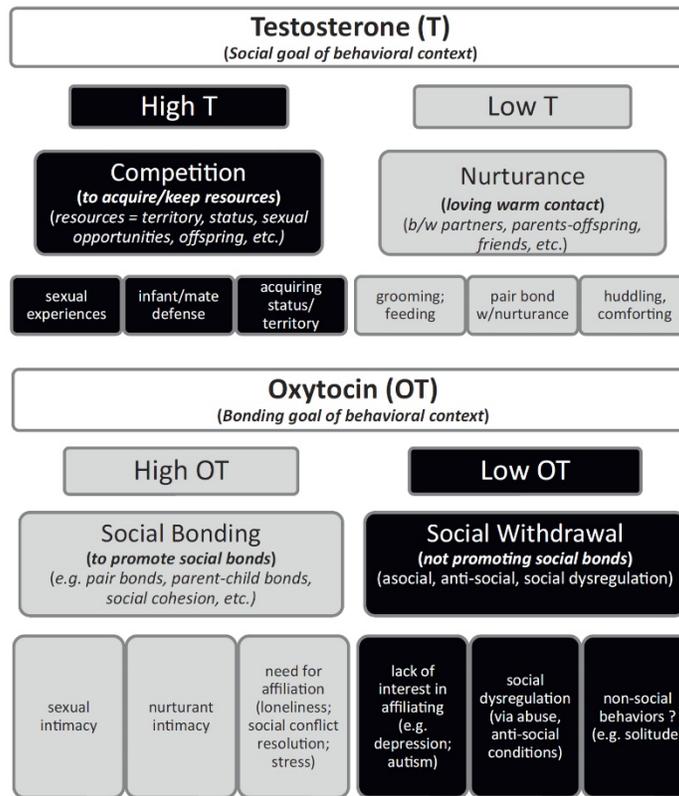
Figure 4. Steroid/Peptide Framework of Social Bonds. This framework lays out a conceptual map of behavioral contexts relevant to social bonds linked to high and low T and OT. The lighter boxes are associated with social bond facilitation/promotion; the darker boxes are associated with the inhibition/dysregulation of social bonds. The framework is divided into a top section for T (social goals) and a bottom section for OT (bonding goals), with the left column for high levels and the right column for low levels of each hormone. The boxes immediately below the high/low T/OT represent the "kind" of behavioral context, or role, for that level of that hormone. Below, at the lowest level for each hormone, are smaller boxes representing a nonexhaustive list of examples of each kind/role.

The S/P Theory has as additional but less central aspect, which is the S/P Matrix (Table 1). The S/P Matrix is useful for considering how high and/or low T and peptides combine to result in specific behavioral contexts related to social bonds or their obverse (e.g., bond dysregulation). The S/P Matrix thus provides a synthesis, a reference "cheat sheet" of sorts, that integrates points made in both the S/P Framework and the S/P Model but differs from each because it provides predictions that synthesize both OT and T. The S/P Theory is in part built upon concepts put forth in the Challenge Hypothesis (Wingfield et al., 1990) and our prior theoretical work with T (van Anders and Watson, 2006b). The Challenge Hypothesis posits a trade-off between low T and parenting (including pair bonds) versus high T and challenges (including mating/sexuality). Findings from a variety of species support the Challenge Hypothesis (Hirschenhauser and Oliveira, 2006), but there are specific predictions that have failed to garner support, and these revolve around behavioral classifications. In these next sections, we describe three major paradoxes that the S/P Theory and its features help to resolve.

Table 1. The steroid/peptide matrix of social bonds. Up and down arrows are relative to population norms but could relate to individual norms as well. "T" indicates testosterone.

		Oxytocin		Vasopressin	
		↑	↓	↑	↓
T	↑	Sexual intimacy	Antagonistic aggression; social dysfunction	Protective aggression	Antagonistic aggression; social dysfunction
	↓	Nurturant intimacy (need or presence)	Depression? Withdrawal?	Nurturant intimacy (need or presence)	Depression? Withdrawal?

3.1. Paradoxes and the S/P Theory

3.1.1. The Offspring Defense Paradox

The Challenge Hypothesis positions all parental behaviors in a low T category (Wingfield et al., 1990), but offspring defense has been linked to high T (Teichroeb and Sicotte, 2008), leading to what we call the "Offspring Defense Paradox" (i.e., that parental behaviors are linked to low T, but infant defense increases T). Adding to this paradox is that infant cues like cries increase T in men (Storey et al., 2000; Fleming et al., 2002) and exogenous T enhances neural responses to infant cries in women (Bos et al., 2010). Accordingly, in the S/P Theory, we hypothesize that low T is linked only to parental contexts that are perceived/experienced as *nurturant*, and high T is implicated in those parental contexts that invoke the need for defensive or *protective* responses. Infant cries with no opportunity for intervention might therefore be tied to high T because there is no possibility for nurturant response and they might invoke the need for infant defense. In contrast, nurturing infants in response to cries would be tied to low T. Data from our lab actually support this, in that we have found that men who hear infant cries but have no opportunity for nurturant response demonstrate increased T, while men who do engage in a nurturant response demonstrate decreased T (van Anders et al., in preparation).

In the S/P Framework (Fig. 4), we classify behaviors on the basis of their apparent or evolutionary motivation, and any behavioral context linked to competition, including defending resources (and offspring certainly represent resources), is linked to high T. In contrast, any behavioral context linked to nurturance is tied to low T. The S/P Model thus resolves the Offspring Defense Paradox, that is, that low T is linked to "all" parental behaviors but offspring defense increases T, because the S/P Model links nurturant parental behaviors to low T, and competitive parental behaviors to high T. The Offspring Defense Paradox that arises via the target-based classification of the Challenge Hypothesis is thus resolved by the "kind" based classification of the S/P Theory.

3.1.2. The Aggression Paradox

As the Offspring Defense Paradox (i.e., that all parental behaviors are linked to low T, but offspring defense increases T) exposes a conceptual gap in the social role for T, aggression exposes a similar conceptual gap in the social role of peptides. Peptides are most generally tied to intimacy within social bonds (Carter, 1998), yet they also contribute to certain types of aggression. For example, AVP and OT are linked to both infant defense and attacks of other-sex intruders (e.g. Bosch, 2011). How can peptides be associated both with intimacy and aggression if aggression and intimacy are mutually exclusive?

In what we call the "Aggression Paradox," peptides are linked to social bonds and aggression, even though these are thought to be mutually exclusive. Partitioning aggression into antagonistic aggression and protective aggression (see Fig. 3 for model and definitions of these kinds of aggression) resolves this paradox because the bifurcated aggressive pathways can differentially affect T and AVP, and thus either promote (via AVP) or inhibit (via T) social bonding. In other words, some types of aggression can increase peptides and thus facilitate social bonds, and other types of aggression can increase T and inhibit social bonds. Those types of aggression aimed at protecting others follow the peptidergic route, and those types of aggression that are antagonistic follow the androgenic route.

However, the above is somewhat simplified, as both types of aggression increase T, while only protective aggression additionally increases peptides. In this case, how can peptides promote social bonds more than T inhibits them? We speculate that peptides are more salient than T for social bonds, and that this could be reflected via a number of mechanisms. These might include a higher density of peptide than androgen receptors (AR) (or downregulation of AR) in neural substrates for social bonds (Lynn, 2008). Or, there may be stronger affinity for peptides than T within social bond-related nuclei. Permissive effects of T on AVP (Carter, 2007) also might be at play such that stimuli that increase both T and AVP lead to an androgenic upregulation of AVP (and thus higher AVP).

3.1.3. The Intimacy Paradox

The Challenge Hypothesis holds that sexual activity should be tied to high T and pair bonds to low T (Wingfield et al., 1990), and does not address links between sexuality and pair bonds directly. However, sexual activity actually facilitates pair bonds and very often occurs within a pair bond context (Carter, 1998; Snowdon et al., 2006; van Anders et al., 2007a). The "Intimacy Paradox" thus arises because sexual activity is tied to high T and

facilitates pair bonds, but T inhibits pair bonds (van Anders and Watson, 2006a; van Anders et al., 2007a). Partitioning intimacy into sexual intimacy and nurturant intimacy (see Fig. 3 for the model and definitions of these kinds of intimacies) resolves the Intimacy Paradox (i.e., that sexual activity increases T, T inhibits pair bonds, but sexual activity *facilitates* pair bonds) because each of these types of intimacies differentially affects T even as both increase OT to thus facilitate (via OT) or inhibit (via T) social bonding.

Consensual sexual activity could be conceptualized as involving both nurturant and sexual intimacy, so why should sexual activity *increase* T? After all, the nurturant aspects of sexual activity could decrease T. We speculate that sexual intimacy is a more salient stimulus for *T* than nurturant intimacy. In other words, there have been stronger selective pressures for a T response to sexual intimacy because of its importance in reproduction. So, though both nurturant intimacy and sexual intimacy pathways respond to sexual activity, sexual intimacy should exert a stronger facilitatory pressure on T release than nurturant intimacy exerts a reductive effect.

3.2. The Steroid/Peptide Framework of Social Bonds

The S/P Framework lays out a more general conceptual hypothesis for the role that T and OT play in social bonds (Fig. 4). Both T and OT are related to goals of behavioral contexts, but T is specifically implicated in *social* and OT in *bonding* goals. Though we focus on OT, we expect that other peptides and estradiol will fulfill similar roles (Lynch and Wilczynski, 2006; Heinrichs et al., 2009). The S/P Matrix (Table 1) makes a set of predictions specifically about the interactions between T, OT, and AVP for behavioral contexts related both to social bonds and their obverse (e.g., missing or dysfunctional bonds). The S/P Theory details specific kinds of behavioral contexts that might fall into each category; though we expect convergent evolution across species for the social role of high/ low T and OT (Carter, 1998; Gleason et al., 2009), we also espouse the need for context- and species-specificity (and this may include gender/sex).[1] For example, the same behavior may fulfill different evolutionary functions by context (e.g., cuddling between partners vs. parents and infants).

The S/P Framework is useful for identifying and classifying behavioral contexts and providing a comprehensive conceptualization of the spectrum of high and low T and OT. However, an additional major function of the S/P Framework is to explore hormonal responses to untested behavioral contexts in order to classify their evolutionary or neuroendocrine role. There are some "tricky" behaviors that are either difficult to categorize or easy to miscategorize based on cultural (mis)-conceptions, and the S/P Framework can be used to make hypotheses about the evolutionary role of these behaviors based on the hormonal response they elicit. Below (in Section 3.3), we discuss cuddling as a test case for this use of the S/P Framework.

3.2.1. Testosterone and social goals

High T is related to *competition*, that is, social behavioral contexts that involve acquiring or keeping resources. Resources are broadly defined and include traditionally conceptualized resources like territory, status, etc., but also sexual/mating opportunities and offspring. Actual examples of competitive behavioral contexts could include sexual activity, offspring

defense, mate/partner guarding including jealousy, acts designed to acquire status or territory (e.g., fights and status-oriented maneuvering), etc. This in many ways overlaps with Wingfield et al.'s (1990) concept of challenge, and recent reviews provide support for links between these behavioral contexts and high T (Hirschenhauser and Oliveira, 2006; van Anders and Watson, 2006b). Our model specifically adds to previous conceptualizations by incorporating infant and partner-related behaviors that are tied to competition, rather than nurturance, since these "competitive" parental contexts have been empirically tied to higher T (Storey et al., 2000; Fleming et al., 2002; Goymann et al., 2003; Teichroeb and Sicotte, 2008; Bos et al., 2010) in contrast to theoretical links between a general "parental" category and low T as in Wingfield et al. (1990). In addition, our model makes clear that sexual intimacy is tied to higher T, and evidence does link sexual contexts to higher T in humans (Rupp and Wallen, 2007; van Anders et al., 2007a; van Anders, 2010; Goldey and van Anders, 2011) and other species (Bales et al., 2006; Snowdon et al., 2006; Gleason et al., 2009). So, high T is linked to competitive behavioral contexts—those that involve acquiring or keeping resources.

Low T is related to *nurturance*, i.e. social behavioral contexts that involve loving warm contact with others (e.g. partners/mates, offspring, friends, etc.) (and this may possibly transpire via conversation of T to estradiol, and estrogenic facilitation of peptides).[2] Actual examples of nurturant behavioral contexts could include grooming, feeding, pair bond existence, huddling, and other close warm contact. In support of this, pair bonded individuals have lower T than singles, but only if the bonds involve nurturant intimacy and are two-point pair bonds (van Anders and Gray, 2007; van Anders, 2009; van Anders and Goldey, 2010). Links between T and other types of nurturance (i.e., beyond simply relationship status) are less well characterized, especially in women, as most research with T has focused on its competitive associations and/or men. Still, lower T is linked to higher parental responsiveness and feelings (Storey et al., 2000; Fleming et al., 2002), and T administration decreases what should be a hallmark of nurturance: empathy (van Honk et al., 2011). There is also evidence that T decreases at parturition in mammalian fathers (Storey et al., 2000; Wynne-Edwards, 2001) and that parents have lower T than nonparents (Gray and Campbell, 2009; Kuzawa et al., 2010). Our model builds on the Challenge Hypothesis but adds to it by clarifying that low T is linked to nurturance in any context rather than parental behaviors in general. As such, low T is linked to nurturant behavioral contexts—those that involve loving warm contact with others.

3.2.2. Oxytocin and bonding goals

High OT is tied to social behavioral contexts that involve *social bonds*, and this can relate to the anticipation of these contexts, the need/desire for these contexts, or their existence (e.g., initiation, development, maintenance). Social bonds can be pair bonds, parent-offspring bonds, friendships, etc. Actual examples of social bonding could include sexual intimacy, nurturant intimacy, loneliness (i.e., the need for social bonding), social conflict resolution (e.g., arguments with loved ones that arise out a of need to strengthen a bond), etc. Consistent with the above, OT facilitates social cognitions and empathy in humans (Bos et al., 2011). The prairie vole model has been a comprehensive source of support for linking OT and pair bonds (Carter, 1998; Young et al., 1998), as has research with callichitrid primates

(Smith et al., 2010; Snowdon et al., 2010). In humans, OT has been linked to greater in-couple communication (Grewen et al., 2005; Holt-Lunstad et al., 2008; Gouin et al., 2010). OT is also implicated in sexual intimacy, including orgasm, satiety, and activity (Carter, 1992; Insel et al., 1998; Young et al., 2008; Snowdon et al., 2010). Finally, OT has been ro-bustly tied to a broad range of nurturantly intimate behavioral contexts (Francis et al., 2000; Light et al., 2000; Feldman et al., 2007). High OT is therefore tied to social bond–related contexts, including the initiation, existence, and maintenance of positive social bonds.

Though findings link high OT with pair bonds and partner closeness, other research demonstrates a complementary role for OT, that is, as tied to the *need* or *desire* for social bonds. Thus, OT has been tied to distressed relationships (Taylor et al., 2010) and has been theorized to be an additional hormonal pathway that responds to stress and promotes the need to affiliate (Taylor, 2006). Recent work shows that OT administration decreases neural responses to infant cries in the amygdala and insula, with the interpretation of associated decreased anxiety and increased nurturant responsivity (Riem et al., 2011). And, as de-scribed in the Aggression Paradox (Section 3.1.2), high OT can be linked to aggression that protects offspring or the pair bond. So, OT can also be a marker for experiencing an unde-sired lack of social bonds, or even "negative" cues like aggression, and thus is not necessarily tied to all things "good." Therefore, high OT is linked to the need/desire for establishing or improving social bonds, in addition to its link with existing positive social bonds.

Low OT is related to social withdrawal or those behavioral contexts that are *not* tied to promoting social bonds. Actual examples of social withdrawal could include an atypical lack of interest in affiliating as might occur with autism (Carter, 2007) or depression, or solitude-related behaviors (though these could also be unrelated to OT at all). This cate-gory might also include social dysregulation that accompanies anti-social psychological conditions and/or that results from abuse/neglect. For example, being raped or sexually abused might dysregulate the OT response to typically desired and consensual sexual con-texts. Being exposed to early abuse and/or neglect might lead to the development of dysregulated social bond-related systems. Perpetrating rape or offenses that hurt others without the concomitant experience of empathy for victims might also lead to or reflect dysregulation (that itself could sometimes have resulted from early abuse/neglect: Peder-sen, 2004). This dysregulation could be at the neural level, that is, that social bond systems have not developed along typical patterns; at the hormonal level, that is, that OT does not respond to bond-related stimuli; or at the perceptual level, that is, that bond-related stimuli are not perceived as such. There is evidence that neglected children have lower OT than controls (Fries et al., 2005) as do adult women abused in childhood (Heim et al., 2009). Accordingly, low OT is linked to the obverse of social bonds—that is, social dysregulation, isolation/solitude, and/or depression possibly. To clarify, high OT is linked to social bonds, even poor ones. Low OT is instead linked to *dysregulated* social bonds, which differs con-ceptually from "poor" social bonds.

Despite our differentiation between high OT (strong or poor social bonds) and low OT (dysregulated social bonds), there are a variety of "tricky" behavioral contexts that could be conceptualized as falling into both high and low OT categories, and depression is one of these. We speculate that depression accompanied by need/desire for social bonds, in-

cluding distressed relationships, should be tied to high OT. However, depression accompanied by a *lack of interest* in social bonds (potentially despite not having social bonds) should be tied to low OT, which might be especially likely to characterize more severe depression, and evidence might be interpreted to support this (Scantamburlo et al., 2007).

3.3. Cuddling: a test case of the S/P framework for "tricky" behavioral contexts

As we have indicated throughout, there are some "tricky" behaviors that are not so easily classified as high or low T. For example, huddling ostensibly should reflect nurturant intimacy, but if it reflects an offspring-defense mechanism, then we would argue that it is a competitive high T behavior, and evidence supports this (Trainor and Marler, 2001). Cuddling between partners is a similarly tricky behavioral context since ostensibly it reflects nurturant intimacy and low T. However, physical closeness can be implicated in both sexual *and* nurturant intimacy (i.e., high and low T). In this section, we thus use partner cuddling as a test case for the S/P Framework to demonstrate its utility at parsing tricky behavioral contexts.

In a study originally designed to test sexual modulation of T, we found that both sexual activity (penis-vagina intercourse) and cuddling increased T over baseline and compared to exercise (a control for physical arousal) (see Fig. 5) (van Anders et al., 2007a). We had included cuddling as a nurturant control based on our and cultural assumptions that it is nonsexual and embodies nurturance. How could cuddling increase T but be nurturant? Here is where the phenomenological value of the S/P Theory becomes apparent.
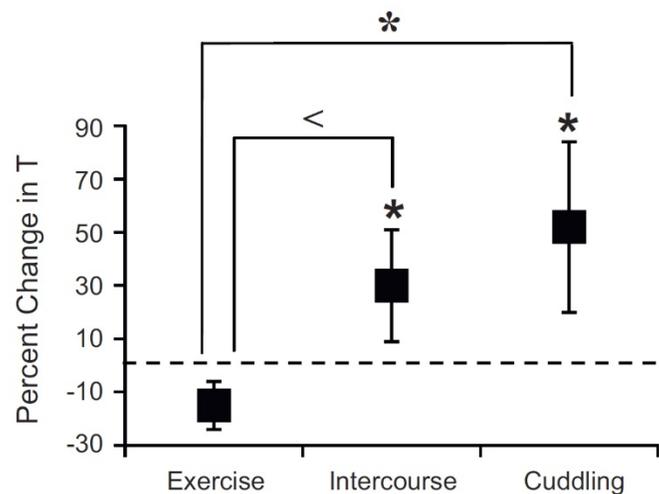

Figure 5. The percent change in testosterone (T) in response to exercise, intercourse, and cuddling, with standard error bars. The dashed line indicates 0% change, or no change; points above this line indicate an increase in T from baseline, while points below this line indicate decreases in T from baseline. "*" indicates a significant difference at $p < .05$; "<" indicates a trend for a statistical difference at $p < .10$. Adapted with permission from van Anders et al. (2007).

We used the S/P Theory to develop a hypothesis about the tricky behavioral context of cuddling, a hypothesis which we tested in a follow-up study. Cuddling is thought to be nurturant and nonsexual but increases T. The S/P Model holds that sexual but not nurturant intimacy increases T. Therefore, we hypothesized that cuddling involves sexual intimacy and is thus a high T competitive behavioral context. The implicit alternative hypothesis is that the S/P Theory is incorrect or needs revision; this example thus highlights the falsifiability of the S/P Theory. Though cuddling increased T, we found that anticipation of sexual activity but *not* cuddling increased T (van Anders et al., 2007a), and this, along with cultural considerations of cuddling as nurturant and nonsexual, led to the specific predictions that cuddling would be perceived as nurturant and nonsexual but *experienced* as sexual. To clarify, anticipation of sexual activity should increase T since it is conscious anticipation of a high T competitive behavioral context, but anticipation of cuddling should not increase T, since it is conscious anticipation of an activity that is not perceived to be sexual. This is what our data showed, that is, that anticipation of sexual activity increased T, while anticipation of cuddling did not. However, *experiencing* an activity that is sexual (via ultimate or conditioned pathways) should increase T regardless of how it is perceived.

In the earlier study, we found that sexual activity and cuddling increased T, but only anticipation of sexual activity increased T whereas anticipation of cuddling did not (van Anders et al., 2007a), and these data fit into the S/P Theory. But the S/P Theory is being articulated in this paper well after these data were collected—so the fit between initial data and subsequent theory cannot be held as clear support for the predictive power of any theory. Instead, in a newer study, we tested predictions based on the S/P Theory and the previous findings. These were supported, as cuddling was perceived as nurturant and nonsexual but experienced as sexual (van Anders et al., submitted for publication). Participants spontaneously reported nurturant themes when asked about cuddling experiences—for example, calmness, love, relaxation, comfort—and very few reported sexual themes. However, our targeted questions showed that cuddling involves high levels of sexual intimacy, as it frequently occurs before or after sexual activity and is reported to be sexually arousing when this is specifically queried. Hence, cuddling can be classified as a sexual behavioral context within the high T competitive category; this does not eliminate its nurturant aspects, but as we argue above, sexual intimacy is a stronger/more salient stimulus for T. This reasoning should apply only to partner cuddling, and we predict that parent-child cuddling should *decrease* T as a low T nurturant behavior (unless it is experienced as infant defense, which should accordingly increase T; a testable viable alternative hypothesis). It is also possible that some partner cuddling contexts, that is, those that could *not* be tied to sexual intimacy in any way, should be linked to low T—this assumes that close bodily contact between partners could be experienced as nonsexual.

Our example with cuddling highlights the importance of incorporating T into research on intimacies, even though intimacy is typically studied only in conjunction with peptides, and T is only studied in conjunction with competition. As we note above and in Fig. 3, sexual *and* nurturant intimacy are linked to high OT. Thus, only by the incorporation of T can these two types of intimacy (i.e., sexual; nurturant) be distinguished for evolutionary or neuroendocrine purposes. We thus used the S/P Model to determine how best to classify

a "tricky" behavioral context—partner cuddling—that increased T despite assumptions of nurturance; based on the S/P Theory, we were able to develop a hypothesis that cuddling involves sexual intimacy, leading to a better classification of partner cuddling, and supporting the S/P Theory. We expect the S/P Theory to be similarly useful for others and for classifying other tricky behavioral contexts along hormonal dimensions.

4. Gender/sex and the S/P Theory of Social Bonds

Though there are increasing exceptions, research on nonhuman species with peptides and T has largely been gendered, with OT measured in females, and AVP in males; in contrast, peptide administration studies in humans are more often conducted with men. And, research with T has mostly been conducted with males. The gendering continues from the gender/sexes of the individuals studied to the topics studied: research with T has mostly been conducted on the competitive side, which neatly fits with cultural attitudes about masculinity and T, and much less attention has been paid to the nurturance side (cf. Storey et al., 2000; Fleming et al., 2002; Trainor and Marler, 2002; van Anders and Watson, 2006a, 2007; van Anders and Gray, 2007). Research with OT in females has focused more on social bonds, while research with AVP in males has focused more on protective aggression, again neatly fitting societal ideas about masculinity and femininity. On one hand, there is evidence for gender/sex-specific effects (Carter, 2007; Taylor et al., 2010; Domes et al., 2010), which validates this approach. On the other hand, this gendering of research subjects and topics has made it difficult to make broader conceptualizations about peptides: are OT and AVP similar or not? Do they act the same in females and males, or not? There is evidence for *overlapping* function (Carter, 2007), as OT *and* AVP facilitate protective aggression (Bosch, 2011), and both peptides seem to function in males and females (Gouin et al., 2010; Snowdon et al., 2010). Moreover, T is meaningfully studied in relation to nurturance in females as well as males (Fleming et al., 1997; Prudom et al., 2008; Kuzawa et al., 2010).

We have found some evidence that there may be nuances about the effects of intimacy on T. We find that sexual stimuli are more likely to increase T in women than men (van Anders et al., 2007a; Goldey and van Anders, 2011, submitted for publication). And, we have pilot data suggesting that cuddling may not affect T in men (unpublished data), perhaps due to gendered experiences of cuddling (van Anders et al., submitted for publication). Similarly, Snowdon et al. (2010) has found nuances by sex about the types of intimacy tied to OT in tamarins. Thus, there may be gender/sex sensitivities in the specificity or type of hormonal response. In humans, gender/ sex specificities of the S/P Theory could relate to evolved functions, social roles, and/or socializations. As an example, certain activities may be high T competitive for men but not women because men have been taught to value those activities as competitive, while women have not (e.g., handshake grip strength); or women have not been encouraged or allowed to engage in those activities, while men have been.

5. Conclusion

We have put forth the Steroid/Peptide Theory of Social Bonds (S/P Theory), highlighting its relevance for understanding evolutionary pathways to pair bonds and other social bonds, as well as its importance in classifying and conceptualizing behavioral contexts. There are assuredly additional behavioral contexts we have not included that are species-, context-, or gender/sex-specific that are also relevant. Still, we have provided specific predictions that may be used to test the S/P Theory, with T and peptides alone or in conjunction. The S/P Theory provides a way to conduct theoretically rooted experimental work with humans (or other species) that does not rely on more invasive approaches, including administration, that is, by testing hormonal *responses* to social behavioral contexts. This may be especially relevant for humans, other primates, and field studies, where ethical and practical concerns preclude many experimental methods (e.g., hormone administration/ blocking).

There are limitations to the S/P Theory as we present it here in that we have not discussed cognitive mechanisms, neural structures, or steroid-peptide interactions at the molecular level; these have been comprehensively reviewed recently (Bos et al., 2011). In addition, the S/P Theory reflects gaps in the literature in that research has largely focused on OT rather than AVP or prolactin (PRL), and T rather than other steroids. However, research with both cortisol and estradiol underscore their potential. Estradiol has been linked to sexual intimacy in females of various species (Zehr et al., 1998; van Anders et al., 2009) and nurturant intimacy in males (Wynne-Edwards, 2001; Trainor and Marler, 2002). Cortisol has also been linked to nurturant intimacy (Storey et al., 2000; Fleming et al., 2002) but negatively with sexual stimuli (van Anders et al., 2009). These distinctions suggest that estradiol is informative for social bonds, and that cortisol might be useful in distinguishing nurturant from sexual systems. Moreover, the aromatization of T to estradiol leads to the possibility of central action being in part mediated by estrogen rather than androgen receptors. Another gap in the S/P Theory is that we have not extensively addressed stress. Perhaps most critically, we have addressed the nonhormonal neurobiological mechanisms by which the S/P Theory operates in only minute detail and instead focused on the behavioral endocrine level of analysis.

Additional gaps also reflect the literature and point to areas open for inquiry. For example, most studies of nurturance focus on parents, and the importance of OT for the offspring side of bonding remains unclear. Friendships have also been under-studied, and it remains unclear if their development is predicated on the same evolutionary systems that underlie parent-offspring and/or pair bonds. Pair bond relationships, and multiple romantic/ sexual relationships, have also been under-studied in humans, despite their prevalence. Finally, nonaffiliative relationships or violations of affiliation have also received little attention, and these include intimate partner violence/abuse, rape, etc. What are the proximate mechanisms of social bonds or close contact that are tied to power or force rather than closeness or warmth?

The S/P Theory provides a set of predictions and hypotheses that integrate T, OT, and AVP for testing evolutionary pathways to social bonds and related behavioral contexts. In the S/P Theory, we partition aggression into antagonistic and protective aggression, which

both increase T but exert distinct effects on AVP and thus social bonds. Similarly, we partition intimacy into sexual and nurturant intimacy, both of which increase OT and facilitate social bonds but exert distinct effects on T. By partitioning intimacy and aggression, the S/P Theory also resolves several paradoxes apparent in the literature on social bonds and hormones: the Offspring Defense Paradox, Aggression Paradox, and Intimacy Paradox. Moreover, the S/P Theory has utility for classifying "tricky" behavioral contexts that are either difficult to categorize prima facie or are easy to miscategorize based on cultural assumptions; the latter are most likely identified via paradoxical findings and, we argue, are amenable to testing via the S/P Theory. We see the integration of steroids and peptides as a powerful way to move the comparative study of intimacy, social bonds, and social behavioral contexts forward.

Notes

1. Catherine Marler helped us crystallize the importance of this point.
2. We are indebted to Charles Snowdon for this suggestion.

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