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From Norway with Love: A Study of Oxytocin, Social Bonding, and Life-history Trade-offs

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**FROM NORWAY WITH LOVE: A STUDY OF OXYTOCIN,
SOCIAL BONDING, AND LIFE-HISTORY TRADE-OFFS**

BY

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DISSERTATION

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DEDICATION

To Bandit.

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This achievement is not mine alone—not by a long shot. Below I name just a few of the people who helped me along the way.

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ABSTRACT

Oxytocin (OT) is a mammalian neuropeptide hormone that has been extensively studied in the field of obstetrics and mother-infant bonding. More recently, animal and human studies have suggested that OT might also have important functions within sexual pair-bonds. While some have advanced the perspective that OT is a ‘bonding’, ‘cuddle’, or ‘trust’ hormone, a number of opposing findings cast doubt on such interpretations. Several research groups have attempted to address this so-called ‘paradox’. I propose a different type of framework that attempts to address this paradox, but perhaps more importantly, also aims to provide additional explanatory power regarding the functions of OT within human romantic relationships—and perhaps other types of close bonds, as well. This theoretical framework has four central properties. First, it considers the adaptive design of the OT system as a central issue; OT should be ‘tagged’ to specific intimate social partners such as offspring or mates, rather than functioning as a general-purpose hormone for prosociality. Second, it builds upon theoretical models in evolutionary biology suggesting that endocrine hormones function as messengers

coordinating biological activity across an organism in an adaptive fashion. Third, it emphasizes the inevitability of trade-offs in an organism's energy allocation decisions, and proposes that hormones evolved, in part, to mediate these trade-offs. Fourth, it also emphasizes the contingency of biological responses on appraisals of environmental conditions, such as current budgets and future resource availability. To test these ideas, I recruited 148 Norwegian participants in committed romantic relationships and assessed how facets of one's romantic relationship, perceptions of assistance from the 'Nordic Welfare State', and investment in social bonding outside the romantic relationship predicted changes in OT across a thought-writing task regarding one's partner. Results were mixed. Replicating a recent finding in American couples (Grebe et al., 2016), participants who were highly involved in their relationships, but felt that their partner was less involved, had the largest OT increases across the task. In other words, OT increases reflected discrepancies between assessments of self and partner relationship involvement. Across multiple measures, there was no consistent indication that perceptions and attitudes regarding state welfare, either alone or interacting with relationship involvement, influenced OT responses. Finally, individuals with stronger OT responses, and who reported greater discrepancies in romantic relationship involvement, reported less interest in certain kinds of social bonding outside the relationship, consistent with a trade-off between classes of social bonding effort. In light of these results, I discuss the value of replication in psychological research, strengths and weaknesses of the proposed theoretical framework, and potential directions for future research.

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Introduction

The mammalian protein hormone oxytocin (OT) has become one of the hottest research topics within biological psychology/psychiatry and social endocrinology in the last twenty years. An ever-growing body of findings has espoused the hormone's potential as a therapeutic substance or a 'hormone of love'—and more generally, as a biological foundation for the diverse classes of intimate social bonds that define us as humans. At the same time, theoretical models have struggled to absorb what many see as inconsistent, even contradictory findings. Findings that associate endogenous OT or OT administration with prosocial bonding behavior appear to be tempered by a growing set of results indicating a 'dark side' (e.g., Bower, 2011) for oxytocin (i.e., its associations with anti-social behaviors such as anxiety and ethnocentrism). Various conceptualizations have been put forth to resolve this apparent paradox. One theoretical perspective, provisionally advanced for some steroid hormones, presents a novel way to understand the overarching role of OT, like other endocrine hormones, as a mediator of life-history trade-offs between various categories of fitness-enhancing activities. Life-history strategies coordinate the activities of varied biological systems into a (flexible) phenotype of cost-benefit optimization; theoretical biology implicates endocrine hormones as important mediators of this process. A review of the literature regarding OT suggests a number of possible trade-offs fostered by oxytocinergic activity. The current project was generated under this theoretical perspective to address the roles of oxytocin within romantic relationships, and how these relationship functions might interact with its roles in other types of social bonds. The study has several goals. First, it seeks to replicate an earlier finding in a sample of American couples (Grebe, Emery Thompson, &

Gangestad, 2016), in which a discrepancy in relationship involvement predicts an OT response generated via thinking about one's partner. Second, the proposed study will be conducted in Norway, where individuals enjoy a high level of state-sponsored support in their life-history decisions; the study therefore asks whether this difference between Norway and the USA is somehow reflected in OT's roles in romantic relationships. Third, this study explicitly seeks to identify a trade-off in which OT allocates psychological resources toward a certain kind of social relationship—in this case, a valued, vulnerable romantic relationship—but might also orient an individual *away* from investing in other social bonds.

The Hormone Oxytocin

OT is a mammalian protein hormone, part of a family of structurally similar peptides (e.g., vasotocin, mesotocin) that exist in birds, reptiles, and invertebrates. These “-tocin” hormones likely debuted between 450 and 700 million years ago (Gwee et al., 2008; Feldman, Monakhov, Pratt, & Ebstein, 2015). OT is well-known within medical circles for its functions in parturition, nursing, and maternal behavior, but has more recently gained notoriety for its roles in social behavior. Since the discovery that OT mediates the formation of sexual pair-bonds (e.g., Williams et al., 1994) much in the way it mediates mother-offspring bonds (Nelson & Panksepp, 1998), scholars have focused on the potential OT might have as a biological basis underlying different types of psychologically impactful ‘close’ relationships.

OT and the Mother-Infant “Biological Prototype”

The evolutionary debut of OT coincides with the emergence of placental mammals approximately 250 million years ago (Donaldson & Young, 2008). Reflecting the generalized function of OT and similar peptides (e.g., vasotocin, mesotocin) in smooth muscle contraction (Altura & Altura, 1977; La Pointe, 1977), some of the most ancient functions for OT are obstetric. Physiologists realized over 100 years ago that extracts from the pituitary gland (containing OT) induced uterine contractions in pregnant humans and non-human mammals (Dale, 1906; Bell, 1909). Similarly, across mammalian species, OT significantly reduces the severity of postpartum hemorrhage (Dogs: Weitzman, Glatz, & Fisher, 1978; Women: Elbourne, Prendiville, & Chalmers, 1988). During mammalian lactation, it activates the milk let-down reflex, itself involving control of smooth muscle contraction (Rats: Wakerley & Lincoln, 1973; Women: McNeilly, Robinson, Houston, & Howie, 1983).

Peripheral reproductive functions facilitating parturition and lactation may have been subsequently coordinated with behavioral aspects of maternal care through OT projections in the central nervous system shaped by natural selection (Crespi, 2015). This coupling of physiological and behavioral aspects of maternity may well be core to an understanding of wider aspects of OT’s functionality. Indeed, Carter (2014) summarizes the literature on OT and social behavior as stemming from the “biological prototype” for mammalian sociality: the mother-infant bond.

Decades of research has demonstrated that OT is a key mediator of maternal bonding to offspring as well as, perhaps, attachment of offspring to mothers, forged during parturition (Carter, 2014), lactation (Crowley & Armstrong, 1992), emotionally

‘warm’ touch (Feldman et al., 2010), and responses to infant’s cries (Riem et al., 2011). Mothers’ self-reports of ‘orienting sensitivity’ toward emotions and physical sensations positively predict OT responses from playing with their infants (Strathearn et al., 2012), perhaps indicating that responsiveness to infants is aided by OT. The success of mother-infant bond formation during the early developmental period may have consequences for the OT system throughout the lifespan. Fries et al. (2005) compared children reared in a typical home environment to children raised in an early environment of severe neglect, and found that neglected children, unlike controls, showed blunted OT responses to interacting with their mothers. This pattern held years later, long after neglected children had moved to a typical home environment.

OT’s diverse roles may be understood as a series of evolutionary co-options or expansions. Mother-infant bonds constitute the ancestral context for OT’s psychological functions. But, scholars argue, this hormone has been co-opted and repurposed from this ancient role in mammals to perform functions involving other types of social bonds (Carter, 2014; Crespi, 2015; Feldman, Monakhov, Pratt, & Ebstein, 2015).

Interdependent social relationships in humans exist in diverse contexts, including sexual pair-bonds, kinship bonds, and friendships. As the breadth and complexity of social relationships (and social brains; Dunbar & Shultz, 2007) expanded across evolutionary time, the functionality of the OT system too was modified and expanded (e.g., Numan & Young, 2016).

Pair-bonding and OT

Like the mother-infant bond, sexual pair-bonds exist within the context of reproduction and involve a coordination of social behaviors between members of a dyad.

In sexual pair-bonds, partners develop selective preferences for each other, cooperate with each other to raise offspring, and in general, form a bond that indicates psychological 'closeness' (Young & Wang, 2004). Not surprisingly, then, the sexual pair-bond is seen as another domain into which OT has extended.

Seminal studies in this domain focused on prairie voles – specifically, a comparison of two closely related vole species with contrasting mating systems. Prairie voles form enduring sexual pair-bonds, characterized by a strong partner preference that is facilitated by physical contact (and copulation in particular). Their sister species, montane and meadow voles, mate polygynously and do not form mating pair-bonds. Based on this observation, scholars used voles as a model through which to investigate the biological factors influencing monogamy. In a series of experiments, vole researchers published several findings (Insel & Shapiro, 1992; Williams et al., 1994; Cho et al., 1999) establishing that OT receptor density in the brain differs substantially between monogamous and polygynous voles. In prairie voles only, OT production during mating leads to subsequent partner preference behavior. And OT antagonists block the formation of pair-bond behavioral and sexual preferences.

Inspired by these studies, psychologists have examined the role of OT in establishing and maintaining human mating pair-bonds. OT is implicated in many of the hallmark prosocial elements of human romantic bonds. OT administration leads to more engaged, constructive communication about relationship conflicts (Ditzen et al., 2009), and more intense orgasms and greater contentment after intercourse with a partner (Behnia et al., 2014). Success of emotional support relationship interventions is related to OT levels (Holt-Lunstad et al., 2008), as is overall relationship satisfaction (Holt-

Lunstad, Birmingham, & Light, 2014; but see Smith et al., 2013). Schneiderman et al. (2012) measured OT levels at the beginning of a romantic relationship and found that new lovers had elevated OT compared to singles. Furthermore, OT levels at the outset of the relationship predicted relationship success six months later.

Studies in other pair-bonding primates provide comparative evidence consistent with human findings. In male common marmosets, OT levels rise after reunion with a mating partner (Seltzer & Ziegler, 2007). And black-tufted marmoset pairs engaged in increased rates of huddling and partner-seeking behavior after OT administration (Smith et al., 2010). Concordant findings in rodents, non-human primates, and humans collectively suggest that OT facilitates the process of sexual pair-bond formation and maintenance in monogamous mammals.

“The OT Paradox”

Against this background of research that generally supports a role for OT in the formation and maintenance of social bonds, contradictory findings have also accumulated. First, studies examining the circumstances in which OT is elevated have not consistently found them to involve successful bonding. Instead, OT has been found in some studies to associate with greater relationship distress (Taylor, Saphire-Bernstein, & Seeman, 2010) and greater anxiety regarding romantic relationships (Marazziti et al., 2006; Weisman et al., 2013). Tabak et al. (2011) found that women’s OT increased when they thought about relational distress. Elmadih et al. (2014) found higher levels of OT in low sensitivity mothers, compared to high sensitivity mothers.

Second, OT administration studies have found that, under some circumstances, OT promotes behaviors thought to be detrimental to relationship formation. Hence, while OT increases trusting behavior in some experimental economic games (Kosfeld et al., 2005), it may decrease it in others (Bartz et al., 2011). OT might also prompt envy and gloating in some situations (Shamay-Tsoory et al., 2009). And though OT administration promotes in-group favoritism, it also may foster out-group derogation (though perhaps to a lesser degree; De Dreu et al., 2011).

The juxtaposition of findings consistent with the idea that OT promotes bonding and those seemingly incompatible with this proposal has been dubbed *the oxytocin paradox* (Bethlehem et al., 2014). A number of scholars have recently attempted to resolve this paradox. Can an overarching conceptualization of OT's psychological effects simultaneously explain the disparate array of OT findings? Below, I list several (non-mutually-exclusive) proposals that have been advanced in the literature.

Proposal 1: OT has Anxiolytic Effects. In one view, OT's psychological effects are outcomes of a generalized dampening of anxiety or stress responses (e.g., Churchland & Winkielman, 2012; Neumann & Slattery, 2016). OT administration specifically dampens reactivity of the hypothalamic-pituitary-adrenal (HPA) axis to threats and, hence, suppresses cortisol responses to stress (Heinrichs et al., 2003; Windle et al., 1997). And some research has found that OT reduces amygdala activity and fear responses (e.g., Kirsch et al., 2005). The effects of OT on interpersonal trust, perceived trustworthiness of others, willingness to cooperate with in-group members, and interest in affiliation with others, in this view, all stem from OT's suppression of threat-sensitivity; under the

influence of OT, people simply see others as less threatening (Churchland & Winkielman, 2012).

This view faces empirical challenges (see Bethlehem et al., 2014). First, it is not obvious how the anxiolytic impact of OT explains some observed effects of OT, such as situation-specific decrements in trust or derogation of out-group members (e.g., De Dreu et al., 2011). Second, OT does not consistently suppress responses to threat. OT administration has been observed to potentiate episodic memory for aversive events (Striepens et al., 2012), anxiety responses to unpredictable events (Grillon et al., 2013), emotional intensity in response to conflict with partners in men (Ditzen et al., 2012), and Pavlovian fear conditioning (Eckstein et al., 2015). Physiologically, OT is released concordantly with corticotropin-releasing hormone (CRH), suggesting that OT might help mobilize the body for challenges, including threats (Carter et al., 2008; Carter, 2014). Consequently, some scholars have attempted to reconcile conflicting findings through modified conceptualizations of OT's effects on threat responses. Eckstein et al. (2015), for instance, argue that OT has targeted anxiolytic effects – in particular, it facilitates the extinction of responses to threat (see also Neumann & Slattery, 2016). When the conditions conducive to extinction are lacking (e.g., when social support is absent), OT may not have anxiolytic effects (e.g., Heinrichs et al., 2003) or may even potentiate threat responses.

Proposal 2: The Social Salience Hypothesis. In light of widespread social effects of OT administration of various kinds, a number of scholars have proposed that OT acts to heighten the salience of social cues and information (e.g., Bartz et al., 2011; Striepens et al., 2012; Shamay-Tsoory & Abu-Akel, 2016). This proposal explicitly expects that the

impact of OT on perceived safety or threat will be context-dependent. In safe, minimally threatening social situations, OT administration should bolster individuals' sense of safety and act in trusting, cooperative ways. By contrast, in circumstances in which threat is present, OT should augment perceptions of pertinent threats, and potentially respond with fear or aggression. Neurologically, the impact of OT on social salience, in this view, is largely mediated through OT's effect on dopaminergic reactivity, especially in mesolimbic regions (see Shamay-Tsoory & Abu-Akel, 2016).

Bethlehem et al. (2014) argue that effects on social salience cannot explain a number of psychological effects of OT. In particular, OT has been claimed to promote ethnocentrism, regardless of the appraisal of the in-group and out-group (DeDreu et al., 2011). The social salience hypothesis would seem to suggest that appraisals of the groups should matter. Striepens et al. (2012) instead proposed that OT administration facilitated approach behavior, but coupled with increased caution.

Proposal 3: OT Enhances Self-referential Processing. Focusing on neurobiological findings and contextual moderators of effects from OT administration studies, Hurlemann and Scheele (2016) review evidence supporting an argument that OT enhances emotional interoception—a consciousness of one's own subjective emotional state. This argument shares similarities to the social salience hypothesis, in that OT is claimed in both hypotheses to amplify psychological appraisals that an individual already possesses. In Hurlemann and Scheele's (2016) view, this conceptualization helps explain why OT might elicit anxiety in depressed patients (Macdonald et al., 2013), enhance in-group favoritism (De Dreu et al., 2010), and have blunted effects on the pleasantness of social touch in those with autistic traits (Voos et al., 2013).

As Hurlemann and Scheele note, a bias towards self-referential processing does not obviously square with findings that OT facilitates focus on bond partners. The resolution, they argue, lies in evidence that representations of the self often include close social partners (Aron & Fraley, 1999); in other words, a bias towards one's own emotional state can actually lead to increased empathy. This idea helps distinguish Hurlemann and Scheele's (2016) hypothesis from the social salience hypothesis: while the latter predicts a generalized increase in social cue sensitivity, the former predicts that this increased sensitivity is biased toward close social partners (who are seen as part of the 'self').

Proposal 4: OT Modifies Reward Sensitivity. The dopaminergic mesolimbic regions (e.g., the ventral tegmental areas and the nucleus accumbens) are richly populated with OT receptors. These regions are widely acknowledged to importantly regulate reward sensitivity: Detection of rewarding stimuli, tracking and reinforcement of behaviors leading to rewarding stimuli, and attention to discriminative cues upon which reinforcement is contingent. One major proposal, then, argues that OT exerts psychological effects through modification of reward circuits (for reviews, see Bethlehem et al., 2014; Numan & Young, 2016).

OT also interacts with the opioid system. These effects too may affect reward sensitivity, as opioids themselves interact with mesolimbic structures (see Bethlehem et al., 2014; Numan & Young, 2016). Whereas dopaminergic pathways may be particularly involved in the "wanting" component of reward (potentiation of reward seeking), opioid pathways may be especially involved in the "liking" component of reward (the experience of pleasure and reinforcement of acts leading to reward; Berridge et al., 2009).

How, precisely, does OT affect reward sensitivity and, as result, behavior? At this point, there exists no definitive answer. Some suggest that OT potentiates *social* rewards (see Bethlehem et al., 2014), and dampens the reward value of non-social rewards. Indeed, as already noted, the social salience hypothesis argues that, through effects on the mesolimbic system, OT increases the salience of social information (Shamay-Tsoory & Abu-Akel, 2016). These effects may be secondary outcomes of modification of mesolimbic reward sensitivity (Bethlehem et al., 2014).

Proposal 5: Nonlinear effects. The effects of OT might be moderated by dosage. Panksepp, Nelson, and Bekkedal (1997) raised this possibility in the early stages of behavioral OT research, speculating that “mild arousal of the oxytocin system may facilitate gregariousness, while higher doses have opposite effects” (p.92). Panksepp et al. posit that, through alleviation of separation distress, OT promotes ‘social confidence.’ While low levels offer sufficient confidence to facilitate social interactions and not enough to eschew them, high levels may prompt independence and a lack of gregariousness. A series of experiments in rats support these claims.

Dose-response relationships may depend on nature of outcome. Bales et al. (2007) reported that, in female prairie voles, low and moderate (1-4 mg/kg) levels of OT facilitated future alloparental behavior (more frequent pup retrieval and lower latency to retrieval) and selective partner preferences, whereas high dosages (8 mg/kg) led to preferences for strangers over partners. By contrast, Windle et al. (1997) found a consistent negative linear relationship between OT dose and corticosterone response to stressors in rats. Future studies that vary OT dosages across natural physiological ranges will be necessary to clarify its dose-dependent effects in humans.

Choosing Among Competing Theoretical Models

The five aforementioned proposals all attempt to make sense of an unclear literature. Many of the proposals overlap to some extent, and need not be mutually exclusive. All have some degree of empirical support. However, I focus on a different kind of conceptualization, one that does not rely on administration studies, unlike each of the aforementioned proposals. First, I make the case for this choice, by considering the context of past OT research and theory.

As noted above, OT's effects on social behavior in mammals likely debuted evolutionarily in the context of maternal-infant interactions, particularly during lactation. OT still importantly affects behavior in that context. Though its psychological effects may have been co-opted and modified to function in other social contexts, it should not have been modified in ways that disrupt its functionality within the maternal-infant relationship. OT's effects likely evolved because they promoted maternal care for and protection of an infant, and those effects should still do so.

Consider, then, some of the above proposals concerning how OT affects behavior. The social salience hypothesis argues that OT renders social cues salient, whereas non-social cues are less salient. One particular version of the reward sensitivity hypothesis claims that OT potentiates social rewards and dampens the potency of non-social rewards. How would these effects function within the context of the maternal-infant relationship? Specifically, how would these effects promote maternal care for an infant? OT might facilitate proficient maternal care if it extracted social cues emitted by the infant, or promoted the social reward value of cues of infant responsiveness and well-being. It is also plausible, however, that generalized salience of social cues or generalized

potentiation of social rewards could degrade the quality of maternal care (e.g., if mothers' attention were drawn to other social figures at the expense of attentiveness to their infants). One can ask similar questions about the role of OT in promoting pair-bonding. Attention to social cues emitted by a partner or potentiation of rewards in the context of the pair-bond may facilitate bond formation. Attention to social cues emitted by others or potentiation of rewards garnered from other social relationships might disrupt pair-bonding.

For OT to function within the context of particular social relationships, then, one might expect that its effects should be targeted toward those particular relationships. That is, the salience of social cues or modification of social rewards should be “tagged” to specific partners. While social cues emitted by a targeted individual might be rendered more salient by OT, the salience of social cues from others may be diminished. Consistent with this perspective, much experimental work examining the effect of OT on maternal behavior in rodents in fact assumes that maternal motivations are specially affected. OT facilitates maternal care (e.g., pup-carrying, attentiveness to pups, feeding of pups, maternal protective aggression; Numan & Young, 2016; but see Elmadih et al., 2014).

But how do social attention and motivation become targeted in this way? In species where OT has been co-opted to function in multiple social contexts (e.g., pair-bonding as well as maternal care), OT's effects should not be tagged to phenotypically defined classes of social targets, such as the features distinctly associated with infants. Individuals in such species, like humans, require flexibility in responses to individuals defined by other phenotypic features (e.g., adult pair-bond partners). A more sensible

functional design, then, might target OT's effects toward social relationships that otherwise exert potent motivational effects within the context in which an OT response occurs. In the context of a maternal care, the potent relationship figure is, naturally, the infant. In the context of pair-bonding, the potent relationship figure is the actual or potential pair-bond partner.

This analysis has two implications. First, the specific effects of OT will depend on the exact nature of the circumstances in which the OT response occurs. Second, a full understanding of OT's functionality requires an understanding of the contexts in which OT responses naturally occur. The upshot of these claims is that one cannot fully understand the functionality of the OT system through experimental administration studies alone. In administration experiments, OT's effects are examined within contexts chosen by the experimenters, not contexts in which OT secretions and projections naturally occur. To take one example, Eckstein et al. (2015) administered OT to participants before placing them into an fMRI where they perform a learning task. In studies such as this, the context surrounding a surge of OT does not resemble anything naturally selected over our evolutionary history. If crucial effects of OT in many natural circumstances are contingent on the presence of a particular potent relationship partner, OT administration studies that rely on effects generated without these contextual factors can only tell us so much about its functions. Therefore, conceptualizations that draw heavily from administration studies, such as the social reward hypothesis or the anxiolytic hypothesis, may partially be characterizing effects that have little to do with OT's evolved functions.

Natural Circumstances Producing OT Responses in Romantic Relationships

Among conceptualizations that focus on the circumstances producing an OT response, there are multiple views regarding what kinds of circumstances should do so. Several studies report positive relationships between endogenous OT and romantic relationship quality, consistent with a *Calm and Connect* model (Uvnas-Moberg, 2003). In this model, relationship bonding (expressed by touch or social cues) leads to the production of OT, which then reinforces warm, nurturing behaviors to further facilitate connection between bond partners. By contrast, multiple studies have found associations between OT and distress and anxiety regarding one's relationship (e.g., Taylor, 2006; Taylor et al., 2010; see also Tabak et al., 2011). The model used to explain these negative findings, *Tend and Befriend*, proposes that distress or anxiety within relationships leads to OT release, which in turn increases 'appetite' for social affiliation outside of the distressful bond (Taylor, 2006). There is no clear support for one of these models over the other (e.g., Smith et al., 2013).

A New Proposal: Orientation toward Valued, Vulnerable Relationships

Grebe, Emery Thompson, and Gangestad (2016) proposed a view that forms the basis for many of the predictions laid out in the current project. In this view, important events that prompt motivation to attend and respond to a relationship partner lead to OT release. In particular, cues that a valued relationship is threatened constitute such important events. OT, in turn, then functions to re-orient psychological resources toward the threatened relationship. Within valued romantic relationships, relationship threats may manifest via reports that individuals themselves are highly invested in their relationships, yet their partners are less invested or attentive to them. To test this model,

Grebe et al. asked romantically involved women and men to think about ways their relationship partners were responsive to them or not, and measured the change in OT as a function of this task. They also administered a battery of measures of relationship involvement to both members of the couple. The key analysis regressed individual's OT response to the task on both self- and partner- relationship involvement. Consistent with findings suggesting prosocial functions for OT, they found positive associations between self-reports of relationship involvement and OT. Reflecting the other end of the 'paradox', however, they found *negative* associations between an individual's OT and their *partner's* reports of investment. That is, peripheral OT release was predicted by the discrepancy between one's own investment, and one's partner's investment. Such a discrepancy, in which a relationship is valued but vulnerable, prompts motivation to attend to the relationship, which OT purportedly functions to do. Grebe et al. (2016) refer to this model as Identify and Invest – OT leads an individual to be attuned to a particular relationship (“Identify” a relationship partner) and be motivated to protect that relationship (“Invest”).

Features of Identify and Invest. The Identify and Invest model provides one resolution to opposing findings in the literature on OT and romantic relationships—and therefore, a resolution to a specific manifestation of the OT paradox. Depending on which individual within a bond a researcher examines, the same OT concentration might be associated with variables that imply prosocial bonding, *or* distressed bonding. Indeed, findings arguing for OT fostering strong bonds tend to rely on self-reports (e.g. Holt-Lunstad et al., 2008; Schneiderman et al., 2012), while findings that associate OT with distress focus on the behaviors from partners (e.g., Taylor et al., 2006; Taylor et al.,

2010). The key variable may be the vulnerability of the relationship overall, rather than just one member's perspective.

The Identify and Invest hypothesis, additionally, proposes a function for OT in relationships that reflects and complements its ancestral roles in the context of maternal care. In mother-infant bonds, relationships with infants are vulnerable not because infants might abandon mothers, but because infants' well-being is highly dependent on maternal attention. Common across both types of bonds, however, is the argument that OT should lead individuals to pay particular attention to the reactions and needs of a specific, highly-valued social partner.

Grebe et al. (2016) interpret relationship discrepancies as representing one manifestation of 'vulnerability' in valued pair-bond, which is the cue for OT production. However, one can conceive of alternative interpretations. More generally, OT might be secreted in situations where a relationship demands attention, whether to ensure stability or to render it a more satisfactory relationship for the individual. This latter interpretation might be particularly relevant for romantic pair-bonds in which partners are not reciprocating levels of involvement.

Finally, Identify and Invest bears similarity to the Tend and Befriend model in that relationship 'threat' or 'distress' evokes OT responses in both. Whereas Tend and Befriend proposes that threat may motivate individuals to affiliate with relationship partners outside of the threatened relationship, Identify and Invest proposes that threat motivates individuals to attend to the threatened relationship. The Identify and Invest model is highly compatible with the idea that OT functions regulating maternal care

constitute the foundation from which the OT system was co-opted to function in other relationships, including pair-bonds. One can question whether a mother should respond to threats toward her relationship with her infant by redirecting a desire for affiliation outside that relationship. Perhaps OT should instead function to lead mothers to attend to their infant's needs and protect them in the face of threats. It may make more sense, then, that OT's effects—co-opted to pair-bonding—should lead to attention to the threatened relationship, not the desire to forge new relationships.

Life-History Theory and OT

To survive and reproduce, organisms harvest energy from the environment and allocate that energy to fitness-enhancing activities. As the budgets from harvested energy have limits, organisms must inevitably decide how to allocate a finite pool of resources; energy allocated to particular activities cannot be allocated to other activities. Certain systematic ways of allocating energy promote the organism's fitness, given its ecological niche, better than alternative ways of doing so. Hence, allocation decision-making should evolve through natural selection. Specifically, natural selection extracts, out of all the possible allocation "strategies" organisms could use, those that maximize relative fitness. Other limited resources of an organism—e.g., micronutrient building blocks, time, neural or other tissue-specific resources—may also be subject to allocation decisions. Life history theory is a branch of theoretical biology that seeks to understand how selection shapes organisms' allocation decisions (Del Giudice, Gangestad, & Kaplan, 2015).

As how an organism can best use limited resources depends on life circumstances, optimal allocation strategies are highly contingent. When below an optimal body size, an

organism may allocate much energy to growth, but an organism should not do so once optimal body size is achieved (e.g., Charnov. 1993). When an organism is infected with pathogens or comes face-to-face with a predator, its allocation decisions regarding growth and behavior differ from those when it is germ-free or safely away from threats (e.g., Reznick et al., 2004; Wolf et al., 2007). Presented with a mating opportunity, an organism might fuel activities that would not be worthwhile in absence of that opportunity. Because energy and other resources are limited, any decision to allocate additional energy *toward* certain activities (e.g., growth, immune function, defense or flight, mating display or intrasexual competition) inevitably requires, simultaneously, decisions to take energy *away from* alternative current or future activities. For instance, an infected individual reduces muscular activity to, in part, afford greater allocation of energy to immunological activity.

Endocrine Hormones Within a Life-History Framework

Endocrine hormones are chemical signals that communicate “messages” to multiple internal sites simultaneously. They are released by a gland (e.g., the gonads, the pituitary) and then bind to receptors at multiple other sites. Hormone binding initiates a chain of reactions that affect activity in a way specific to the site (e.g., activating some sites, inhibiting others, both immediately and through processes that unfold over time [e.g., genomic programming]). Hormonal signals can simultaneously regulate multiple processes of different kinds, and at different time scales.

This feature of endocrine systems inspires a straightforward interpretation of their evolved function, broadly construed. Endocrine systems constitute major avenues through which selection has shaped organisms to coordinate simultaneous shifts of

energetic and other limited resources from one set of activities to another, contingent on life circumstances (e.g., Finch & Rose, 1995; Ketterson & Nolan, 1999; Lancaster & Sinervo, 2011). While life history theory seeks to understand the adaptive logic of allocation attunements—*why* they make the allocation decisions they do—an understanding of *how* organisms coordinate adaptive attunements requires an appreciation of how endocrine systems work.

In theory, selection has shaped these endocrine systems to modulate energy and resource allocation in response to particular circumstances that lead to hormonal release into the bloodstream in ways that enhanced fitness ancestrally. In particular, selection shapes (a) the mechanisms that dictate the circumstances under which a hormone will be released (and then “shut off”), (b) the distribution of receptors that receive endocrine signals, and (c) how tissues respond to receiving endocrine signals. Ultimately, through these actions, endocrine hormones function as key mediators determining life-history strategies, and their constituent trade-off decisions. This framework presents a starting point through which to conceptually integrate the diverse findings across the OT literature.

Hormones affect the brain too. Within the brain, there exist receptors for a host of hormones. Hormones hence can affect how neural resources are utilized: the stimuli that an organism attends to, the appraisal of those stimuli, potentiation of particular rewards and punishments (patterns of “liking” and “wanting”), and so on. Hormonal effects can take place over time courses ranging from nearly immediate to weeks (e.g., through effects on gene transcription, which can affect the molding of neural systems over time).

Conditional Responsivity and Internal Regulatory Variables

Allocation decisions should be a function of circumstances. Hence, life-history theorists argue that, in humans especially, the “perception, interpretation, and evaluation of life circumstances” generated from psychological processes may “ultimately guide many allocation decisions” (Del Giudice et al., 2015, p. 12). The concept of ‘internal regulatory variables’ offers one way to think about these processes (Tooby et al., 2008; Del Giudice et al., 2015). Internal regulatory variables are gauges that rely on incorporated environmental information, representations of information regarding environmental predictability, exogenous mortality risk, and the state of social relationships (among other things) into neutrally instantiated parameters. Hormone production and release, then, is a function of these appraisals, leading to coordinated behavioral and physiological actions that function to allocate limited resources.

An Example: Cortisol as a Response to Energetically Demanding Events

Consider a simple example: the release of cortisol in the classic ‘stress response’. An event is perceived, appraised, and judged to require the rapid mobilization of energetic resources. Projections from brain regions lead to the release of ACTH from the pituitary gland into the bloodstream, which stimulates release of cortisol from the adrenal glands. Within seconds, circulating cortisol causes increases in blood glucose levels, energy available to muscles and neural systems. It promotes insulin resistance in the liver, dampening the rate at which glucose is stored as fat. At the same time, cortisol suppresses other activities, such as inflammatory responses (e.g., by suppressing IL-6’s participation in inflammation; Waage et al., 1990) and somatic repair (Jenkins, Van Houten, & Bovbjerg, 2014). Cortisol release, then—in response to particular

circumstances (including but not limited to threat per se)—not only releases stored energy for potential use but also modulates how energy is to be utilized, increasing its availability for some specific activities, and diminishing its availability for other activities. (For similar analyses of the actions of testosterone and estrogen, see, e.g., Bribiescas, 2001; Ellison, 2003).

OT Responses and Modulation of Effort

Within a life history framework, I offer a conceptualization of how OT functions within social relationships. In this view, again, the OT system is sensitive to threats to specific valued social relationships. OT release leads energetic and other resources to be dedicated to protection of the threatened relationship; OT's psychological responses are “tagged” to the figure whose relationship with an individual is threatened. This model is compatible with the prototypical maternal-infant context in which OT's psychological effects initially evolved; mothers adaptively respond to cues from their infants or cues that their infants' well-being is threatened— i.e., threats met by an OT response are identified with (“tagged to”) the infant. I suggest that, when co-opted to deal with threats to other social relationships, the OT response remained tagged to specific targets (e.g., in pair-bonding, the pair-bond partner).

Dedication of psychological resources—attention and motivational attunements—to address threats in the context of specific relationships may draw resources away from efforts to build or foster other relationships. This outcome may not necessarily occur because social cues pertinent to the latter relationships elicit negative responses, or because the latter relationship figures are out-group members. Rather, they may occur because attention and motivation attuned to specific relationships results in lack of

attunement to other relationships. That is, just as energy is a limited resource with its allocation modified by endocrine hormones, so too psychological resources are limited, with allocation modulated by OT.

In accord with the proposed perspective, a common element of ‘anti-social’ OT findings is the use of a peripheral social target—an anonymous stranger (Bartz et al., 2011), an out-group member (De Dreu et al., 2010; 2011), or a competitor in an economic game (Shamay-Tsoory et al., 2009), for example. In the parlance of social network researchers, OT may foster targeted ‘bonding social capital’, but suppress the development of ‘bridging social capital’ (Putnam, 2001). Since the nascent days of social OT research, some scholars have argued there is little evidence for OT as a general-purpose gregariousness hormone (Panksepp et al., 1997).

Notably, the phenomenon whereby hormones modulate allocation of psychological resources toward some efforts to the detriment of others may be widespread. Cortisol may lead to vigilance to imminent threat cues, but potentially at the expense of long-term memory retrieval (see Het, Ramlow, & Wolf, 2005). Similarly, estradiol may enhance attention to mating-relevant stimuli (Roney, 2015), but result in less attention to feeding-relevant stimuli (Fessler, 2003).

For the current study, this conceptualization implies that there should be negative relationships between measures of involvement in romantic bonding, and measures of investment in bonds with other, less close social partners. And furthermore, this trade-off might be mediated by OT. Pair-bond relationships, in other words, might grow at the expense of other social bonds. Relationship scientists have noted this phenomenon; for instance, Savolainen (2009) concludes that romantic relationships tend to grow in

bonded-ness and commitment “when the partners prioritize union stability over involvement in other activities, such as career, friends or hobbies” (p. 291).

“Tend and Befriend” Versus a Bonding Trade-Off

At this point, it is useful to further sharpen distinctions between a ‘life-history Identify and Invest’ view and Tend and Befriend (Taylor et al. 2000). First, while both propose that the OT system has been designed to respond to threats, Taylor et al. view OT as a particular constituent of the female response to threat. In response to threats, whereas males may ready for combat or escape, they argued, females may more likely to attend to the well-being of offspring (“Tend”) or rely on social support, especially offered by other females (“Befriend”). In contrast, based on reviews of OT’s functions (see Carter, 2014), Identify and Invest predicts that OT’s social functions are similar between the sexes. In this view, threats come in more than one variety, each of which elicits different kinds of hormonal responses. The kinds of ‘threats’ that elicit an OT response—as I argue, cues of relationship vulnerability—may differ from those that elicit a classic stress response—indications of impending, energetically-demanding events.

Second, as mentioned earlier, Tend and Befriend proposes a re-orientation of bonding motivation from the distressed relationship to other social partners: Relationship distress generates an OT response, which increases an appetite for affiliation with others (Taylor, 2006). In contrast, Identify and Invest predicts the opposite—that relationship distress, if occurring in the context of a valuable relationship, requires *more* resources dedicated toward it, not fewer. Furthermore, appetite or motivation for affiliating with others should *decrease*, not increase, if a valued relationship is vulnerable.

Cross-Cultural Mating Psychology and the Influence of State Welfare

One major goal of the current project is to replicate the main “Identify and Invest” finding from Grebe et al. (2016). Beyond a replication, however, is an effort to extend this research to also examine social and cultural variables in Norway that differ substantially from the US. As two post-industrial Western populations composed primarily of individuals of European descent, Norway and the US do not differ as starkly as many other cross-cultural comparisons in psychological research. However, the differences that do exist may be meaningful. If life-history decisions are sensitive to ecological conditions (and appraisal of these conditions), and hormones mediate the processes of coordinated trade-offs, it is then reasonable to ask whether cultural variables with implications for life-history decisions might impact the links between OT and romantic relationships. This is a general premise that could be used to compare any number of societies; however, as Grebe et al. (2016) studied an American sample, whereas the current project recruited Norwegians, I frame this section in terms of comparisons between Norway and the US.

Norway occupies a unique place in today’s world. The Human Development Index (HDI; United Nations Development Programme, 2014), which measures a nation’s average level of income, life expectancy, and educational attainment, ranks Norway first among the 188 nations surveyed. The United States is not far behind, ranking 8th on the HDI. In contrast, however, Norway maintains this top position when adjusting for social inequality, whereas the United States drops to 27th (United Nations Development Programme, 2014). Similarly, while Norway ranks 9th on the Gender Inequality Index, the US is far below at 55th (i.e., the US possesses markedly more gender inequality than

Norway). While both Norway and the US possess a richness of resources within their respective nations, those resources are available to a larger number of people, and are distributed more equally throughout the population, in Norway.

Much of this can be attributed to the “Nordic Welfare State” (Pedersen, Samuelsen, & Wichstrøm, 2003; Grøntvedt & Kennair, 2013) model, an umbrella term generally meant to identify Scandinavian countries by their publicly-funded economic commitments to child care, universal access to services such as education and healthcare, gender equality in professional and social spheres, and support to individuals who need income subsidization (e.g., the unemployed, sick/injured, those with disabilities, the elderly, new mothers and fathers). Funding and commitment to these types of welfare is significantly lower in the US (Putnam, 2002). Burtless and Jencks (2003) note that this difference in policy is starkly reflected in popular opinion: “In most rich countries, sizeable majorities 'agree strongly' that the government ought to guarantee each citizen a minimum standard of living. Only one American in four agrees strongly with this proposition.” (p. 43)

For one aspect of the current project, I make use of a Norwegian sample to investigate a particular question: how might distinctive features of Norwegian mating and society impact OT responses generated from thinking about one’s romantic partner? I investigate these characteristics at the level of individual bonds, and at the level of national policy. First, I overview some of what evolutionary psychologists have learned about cross-cultural variation in mating behavior as a function of economic development and egalitarianism. Second, I briefly discuss how welfare policies might directly influence life-history decisions.

Cross-Cultural Mating Variation

Cross-cultural studies (e.g., Buss et al., 1999; Schmitt et al., 2004; Schmitt, 2005) represent one of evolutionary psychology's major contributions to a scientific understanding of mating. However, two caveats are worth considering for the purposes of the current project. First, when compared to the total range of variation examined in cross-cultural studies, Norway and the US possess quite similar socio-ecologies. Thus, overall associations between measures of development and mating psychology may not accurately capture differences between Norway and the US. Comparisons of similarly rich nations differing on levels of gender or income equality—like Norway and the US, even if those are not the two specific nations examined—provide more meaningful information for this project. Second, much of the work within cross-cultural evolutionary psychology has focused on sex differences in mating behavior across nations (e.g., Buss et al., 1992; Buss et al., 1999). As sex differences in OT functionality are not predicted in my project, cross-national sex differences in mating behavior are somewhat oblique to the research questions of interest. Nevertheless, sex differences are one of the most-studied aspects of cross-cultural mating psychology, and these findings can still help inform an understanding of associations between sociocultural forces and mating behavior.

Relationship Commitment and Investment

General levels of romantic commitment and investment within a culture might be one factor particularly relevant for predicting elicitation of the OT system in relationship contexts. Norms of romantic bonding and relationships—which differ substantially, even between Western societies like Norway and the US (e.g., Ramsøy, 1994; Træen, Holmen,

& Stigum, 2007)—could affect how individuals respond hormonally when considering their own relationships.

Are Norway and the US likely to differ on measures of relationship investment?

Studies of romantic relationships vary substantially in their operationalizations of what it means to be ‘committed’ or ‘attached’ to a partner. Sociosexuality (Simpson & Gangestad, 1991) speaks to one aspect of commitment: a willingness (or conversely, hesitance) to engage in uncommitted sexual relationships. Evolutionary psychologists have attempted to identify how environmental conditions varying across cultures might calibrate sociosexuality. On one hand, Developmental-Attachment Theory (Belsky et al., 1991) predicts that resource-poor environments calibrate developmental processes to favor insecure attachment and less committed sexual relationships. Conversely, Strategic Pluralism Theory (Gangestad & Simpson, 2000) predicts that greater developmental harshness magnifies the importance of biparental care; these conditions should thus associate with less restricted sociosexuality. A test of these competing predictions across 48 nations found support for Strategic Pluralism Theory in both sexes—HDI ratings covaried positively with less restricted sociosexuality—though associations were significantly stronger for women than men (Schmitt, 2005). Again, one might argue that Norway and the US do not differ substantially on the HDI; levels of inequality are what distinguish the two nations. Perhaps more relevant, then, is a specific comparison between the US and Finland (perhaps the nation sampled within the study most similar to Norway in gender and economic equality). Indeed, Finns report less restricted sociosexuality than Americans ($d = .46$; data extracted from Schmitt, 2005).

While more developed and/or egalitarian nations might be more permissive of uncommitted sexual relationships, that does not necessarily mean that monogamously partnered individuals report less investment in more developed cultures. On the contrary, nation-level averages of emotional investment in relationships (as defined by Schmitt & Buss, 2000) correlate positively with the HDI *and* measures of gender equality (Schmitt et al., 2009). Comparisons of romantic investment across two cultures with differing levels of development and gender equality (Chinese and North American) find no differences in relationship commitment, but lower intimacy among Chinese individuals (Gao, 2001; Marshall, 2008). Finally, self-reports of attachment styles in romantic relationships indicate similar levels of secure attachment in the US and Finland ($d = .10$, with Americans possessing slightly lower levels; data taken from Schmitt et al., 2004). While cross-national research suggests that more developed and egalitarian nations are more permissive of uncommitted sexual relationships, they appear to also be more invested within committed relationships. However, there is little indication that Norwegians and Americans specifically differ in their average investment within established romantic relationships.

Jealousy

Are Norway and the US likely to differ on measures of jealousy? Comparisons of romantic jealousy might also inform predictions on cross-cultural differences in OT functioning. Evolutionary psychologists posit that romantic jealousy is an emotion evolved to motivate behavior that aids in mate retention. Whether it manifests in more benign ‘attentiveness’ toward partners, or more aggressive mate guarding / ‘proprietaryness’, it is thought that romantic jealousy protects the bond between partners,

as well as the resources partners deliver (Bendixen et al., 2015). Jealousy, then, might have mating functions that overlap with OT. Romantic jealousy can be elicited by cues that a partner has been emotionally and / or sexually unfaithful. While studies have shown significant overall national differences in the relative jealousy evoked by certain cues of infidelity over others (Buunk & Hupka, 1987; Geary et al., 1995), a comparison of the US to the Netherlands (a country similar to Norway in geographic region and economic equality) shows only modest differences in average levels of jealousy evoked by various cues of partner infidelity (Buunk & Hupka, 1987). Averaging across men and women, there appears to be little reason to expect propensity toward jealousy to differ between Norway and the US.

Are sex differences in jealousy likely to differ between Norway and the US?

Perhaps sex differences in jealousy, not average levels, are more relevant for examining cross-cultural differences. Buss et al. (1992) proposed that while both sexes are sensitive to cues of infidelity, men and women differ in their reactions to types of these cues. Males in most species face the adaptive problem of paternity uncertainty. For men, who invest heavily in offspring, cuckoldry carries the substantial cost of investing in a child not one's own. Women, of course, do not face the same doubts regarding their maternity. However, while both men and women faced the adaptive problem of a partner investing resources in other mates, this problem was perhaps more salient for women, who depend on paternal care and investment, more strongly than females of most species, including closely related primates (Fernandez-Duque et al., 2009). Buss et al. (1992) predicted and found evidence that men, compared to women, are more distressed by indications of a female partner's sexual infidelity (as it decreases paternity certainty of future offspring),

whereas women, compared to men, are more distressed by indications of a male partner's emotional infidelity (as it may indicate his investing resources in another woman). Buss et al. (1999) later examined cross-cultural reactions towards these types of infidelity cues, showing that these sex differences extended across US, Korean, and Japanese samples. Since then, two meta-analyses have been published, each reaching somewhat opposite conclusions. On one hand, Carpenter (2012) argued that expected sex differences in jealousy are not supported in samples outside of the US, as his meta-analysis indicated that men tended to find emotional infidelity more upsetting than sexual infidelity in nations other than the US (Carpenter 2012, Table 2). However, this conclusion rests on a particular reading of Buss et al.'s predictions. In Carpenter's view, men should be more upset by sexual versus emotional infidelity to support predictions from evolutionary psychology; in other words, any crossover *within* gender runs contrary to predictions. However, Buss et al. (1992) focus on differences *between* the sexes—whether men, *more so than women*, are more upset by sexual versus emotional infidelity. When reframing the effect of interest to reflect this prediction, sex differences in jealousy reliably emerge in a meta-analysis across cultures (Sagarin et al., 2012; Frederick & Fales, 2016).

Sex differences in jealousy across cultures are not uniform, however (Sagarin et al., 2012). One might ask whether sex differences in jealousy should shrink or even disappear in countries where paired individuals—but women in particular—are less dependent on resource provisioning from a romantic partner. In such cases, perhaps cues of emotional infidelity carry less weight. Consistent with this prediction, Buunk et al. (1996) find a larger 'emotional versus sexual jealousy' sex difference in an American sample, compared to either a Dutch or German sample. In contrast, multiple studies from

Nordic countries have found sex differences in self-reports of jealousy by infidelity types (Bendixen et al., 2015; Kennair et al., 2011; Wiederman & Kendall, 1999), with effect sizes *larger* than those from US samples (Kennair et al., 2015). This is also in contrast to findings on sociosexuality, where sex differences shrink as a function of the HDI and gender equality (Schmitt, 2005).

Why might men and women become more psychologically dimorphic, at least in some respects, in societies with increased gender equality? Buss et al. (1992) suggested that sex differences in jealousy should increase as a function of paternal investment: compared to less investing bonds, women stand to lose more from a male partner disinvesting from her and her offspring, and men pay more for raising another man's offspring. Perhaps in societies where men and women more evenly split duties of child care, male abandonment is more distressful, and thus women exhibit greater emotional jealousy (Bendixen et al., 2015). Consistent with this perspective, sex differences in emotional investment are strongest in gender egalitarian nations, and this is disproportionately driven by women's increased investment (Schmitt et al., 2009). Guimond et al. (2007) suggest an alternative explanation based on social comparisons and stereotypes. By their formulation, in societies with relaxed gender roles, men and women create (and subsequently follow) stereotypes of gendered behavior based on between-gender comparisons. In societies with stricter gender roles, individuals are more likely to only assess within-gender comparisons, and thus do not create stereotypes that separate genders. Finally, some contextualize these findings as an example of the 'Gender Equality Paradox' (Eia & Ihle, 2010), where efforts to minimize sex differences instead magnify them, as increased freedom permits individuals to express their inherent, sex-

differentiated behaviors. Debate continues over the best explanation for positive relationships between gender equality and sex differences (Lippa, 2010). However, there is at least some indication that increased egalitarianism can increase individuals' propensities to experience sex-typical romantic jealousy. Whether this effect generalizes, such that Norwegians are broadly highly attuned to indications of relationship threat, is a question relevant to the current study.

Effects of State Welfare on Mating Decisions

Cross-national associations between indices of economic / social development and mating behavior could be due to numerous factors that collectively make up the 'typical' socio-ecology an individual experiences within a given country. One such underlying factor might be the presence and / or robustness of state-delivered welfare benefits. State-run welfare schemes provide resources to increase the fitness of oneself and one's kin—resources that would otherwise need to be acquired through other means (e.g., one's own labor, partner provisioning). Life-history decisions reflect the expectations of future budgets for various classes of activities. Perhaps the relative certainty and strength of state-delivered resources (which informs the need for resources originating from other sources) impacts life-history strategies. Little research has explicitly examined welfare benefits under a life-history framework from evolutionary biology. However, economists, demographers, and sociologists have extensively studied whether welfare schemes, and public policies in general, might influence processes highly consequential for life histories, such as marriage and family planning.

Do welfare benefit levels influence fertility? The question of whether welfare benefit levels influence decisions to have children has long been a topic of interest among

demographers and economists—and a politically charged issue in the US. Most famously, in the 1990s, legislators and scholars debated whether welfare systems created ‘perverse incentives’ for women (especially single women) to have children. More generally, scholars have tested predictions from economic models such as Becker (1991), who proposed that welfare increases the desired number of children though its effects on income. From a life-history theory perspective, the question can be framed in terms of the effects of welfare benefits on the age-schedule of fertility. Despite dozens of cross-sectional and longitudinal analyses (see Moffitt, 1998 for a review), no clear conclusion has been reached: one can find several pieces of evidence to support either no relationship (e.g. Acs, 1996), a positive relationship (e.g., Whittington, 1992), or even a negative relationship (e.g., Rank, 1989) between benefit levels and fertility. In his narrative review, Moffitt (1998) summarizes that “a neutral weighing of the evidence still leads to the conclusion that welfare has incentive effects on marriage and fertility, but the uncertainty introduced by the disparities in research findings weakens the strength of that conclusion” (Moffitt, 1998, p. 75).

Jencks (1997) argues that negligible or inconclusive influences of welfare support on fertility might partially be due to the minimal benefits mothers receive from the US government. Perhaps, then, in nations with stronger welfare schemes, effects of welfare benefit levels would be more noticeable. Brewer, Ratcliffe, and Smith (2012) offer one of the few longitudinal pieces of evidence in a non-American sample, finding that UK increases in child-contingent benefits predict increases in fertility rates (by approximately 15%) among paired women, though not among single women. Milligan (2005) reported a fertility increase of similar magnitude (17%) after benefit increases among Canadian

women. In an archival study comparing fertility rates and age-schedules between East and West Germany during the Cold War, Kreyenfeld (2004) found that the more comprehensive state-run welfare system in East Germany predicted markedly higher fertility rates, and lower age at first birth, compared to West Germany.

Welfare benefits and fertility in Norway. Over the past 25 years, Norway's fertility rate has been among the highest in Europe, and Norway has also surpassed its Scandinavian neighbors (with Iceland being an exception; Kravdal, 2016). To what extent is this attributable to the robustness of welfare policies? Little research has empirically examined this issue. Aassve and Lappegård (2009), in one study of welfare benefits and fertility in Norway, compared two groups of mothers: those who elected to send their first child to state-run daycare, and those who instead took cash payments to subsidize caring for their child themselves. The authors asked whether this cash benefit increased the rate at which mothers had second and third children. Indeed, those who took the cash payment were quicker to have more children. As it is difficult to interpret which option represents a 'higher' benefit level, it is unclear whether this result is consistent with fertility increasing along with the magnitude of benefits. However, Lappegård (2010) provides a finding that *is* consistent with such a prediction: mothers and fathers who take advantage of a specific welfare benefit—parental leave—are more likely to have another child than those who do not. Furthermore, Kravdal (2016), in his review of potential explanations for Norway's relatively high fertility rate, suggests at multiple points that Norway's welfare policies impact fertility: discussing the situation for Norwegian mothers, he writes that “even if a relationship is dissolved ... there is a

welfare state to rely on” (p. 21); later, he speculates directly that “[generous] welfare arrangements ... probably affect fertility positively” (p. 24).

Do welfare benefits influence partner choice? Just as welfare benefits may influence fertility and the decision of whether to have children, they may also influence one’s choice regarding a partner for these decisions. Welfare systems typically provide financial resources for individuals as well as their dependents. Thus, it might be expected that higher levels of benefits predict less prioritization of financial prospects in partner choice, or that higher levels predict greater rates of single parenthood (Becker & Becker, 2009). Hoffman and Duncan (1995), finding inconsistent evidence that welfare benefits increase the likelihood of divorce among mothers, reject the notion that welfare benefits influence marital decisions. However, Moffitt (1998) interprets the overall literature somewhat differently, concluding there are real but unstable effects of welfare benefits on marriage formation and dissolution. I was able to find no research directly examining how welfare benefits associate with characteristics desired in a romantic partner. The current project, then, is the first to examine such factors.

The available evidence on welfare benefits and family planning decisions is valuable, but its applicability to the current project may be limited. Archival research analyzing large-scale demographic patterns tells one little about the psychological processes that might underlie any relationships between welfare benefits and life-history decisions. Again, perceptions may be paramount for understanding life-history predictions, as noted by evolutionary biologists (Del Giudice et al. (2015; see quotation above) and demographers alike. Kreyenfeld (2004) notes that “indicators of how women and men perceive the compatibility of childrearing and employment” (p. 308) can help

clarify how welfare benefits influence life-history decisions. Therefore, one unique extension of the current project is the addition of measures asking participants their perceptions regarding the importance of state welfare benefits (see Measures).

Conclusion

The goal of this section was to review two distinct literatures: cross-cultural mating psychology, and effects of welfare policies on life-history decisions. Both literatures highlight how particular aspects of socio-ecological variation might influence mating behaviors or decisions—but despite this common motivation, opposing predictions emerge. As citizens of a rich, egalitarian country, cross-cultural evidence suggests that Norwegians should possess less restricted sociosexual orientations, but also high levels of commitment and investment within monogamous bonds. On the other hand, Norwegians also enjoy a high standard of welfare benefits, which, according to some demographic evidence, predicts greater odds of both relationship failure and non-formation—but again, the robustness of this link is unclear. Similarly, whereas some mating psychologists have argued that increasing egalitarianism might lead individuals to experience more distress at the prospect of losing a partner's investment (Bendixen et al., 2015), others suggest that egalitarian societies help relieve this distress (Buunk et al., 1996). In spite of some apparent contradictions, below are a few general conclusions I draw from the literature. These broad themes inform the predictions advanced for the current study.

- 1) The available cross-cultural evidence strongly suggests that Norwegians, as citizens of a highly developed and egalitarian country, should be highly committed in their romantic relationships. And, despite robust welfare benefits

compared to the US, Norway has a total fertility rate equal to the US, and a higher proportion of children raised by both parents (OECD, 2011), contradicting the idea that welfare benefits should decrease the demand for committed relationships.

- 2) There are theoretical and empirical reasons to predict that Norwegian welfare support impacts individuals' decisions regarding pair-bonding and reproduction. From this literature, one might predict that attunement to levels of partners' relationship involvement would be relatively low in Norway. Perhaps Norwegians should be relatively more inclined to 'go it alone', knowing that they can rely on governmental support instead of a partner. Despite this, empirical findings from Norwegian samples do not fully support these predictions. For instance, rather than Norwegians being less attuned to indications of a partner's disinvestment in a relationship than Americans, some evidence is more consistent with the opposite, at least in women. Thus, predictions in either direction for OT responses are plausible: In Norway, impacts of welfare support might strengthen OT responses to partners, or weaken them.
- 3) As Gauthier (2007) notes, associations between demographic outcomes and public policies can be difficult to interpret. Much more research is needed to investigate how welfare impacts life-history decisions. One way to begin to unravel these complex associations might be via asking about subjective appraisals of welfare. Certain individuals within a society may perceive the importance of welfare benefits more acutely than others; assessing this may have implications for the life-history consequences of welfare policies.

The Current Study

In the current study, I look to replicate recent empirical findings on OT (Grebe et al., 2016), while also extending theoretical arguments about overarching functions of OT in social bonding (e.g., Gangestad, 2016; Gangestad & Grebe, 2016). As an additional extension, I examine how a highly salient characteristic of Norwegian society—the ‘Nordic Welfare State’—might influence individuals’ orientations toward life-history decisions, and thus the expected associations between OT and relationship features.

Predictions

- 1) The main findings from Grebe et al. (2016) will replicate. OT increases across the writing task for men and women will associate with high involvement in the relationship, controlling for reports of partner’s involvement (as measured by dimensions such as love/bonding, trust in one’s partner, and sexual passion/responsiveness). However, a perceived lack of involvement from one’s partner will also be positively associated with an individual’s OT response, controlling for self-reports of involvement. Considering these variables jointly, a *positive difference* score on relationship involvement (where self-reports exceed reports on one’s partner, representing relationship vulnerability) will covary positively with an OT response. These predictions reflect the effects observed in Grebe et al., but use reports on one’s partner, instead of reports from one’s partner.
- 2) OT changes, while corresponding to greater involvement in the bond with a relationship partner, will associate with less participation in social activities with strangers or acquaintances, lower levels of extraversion, as well as less interest in

having a large number of friends. As an allocator of limited psychological resources for social bonding, large OT changes represent a bias of these resources towards relationship partners, which necessitates orientation away from other kinds of social bonding effort.

- 3) OT responses to primes regarding one's partner will be moderated by the extent of consideration of state welfare in life-history decisions. In the context of sex differences in jealousy, Buunk et al. (1996) speculate that "women in more sexually egalitarian cultures are more self-reliant for resources" (p. 363). I follow this line of reasoning, but modify it somewhat to square with theory in the OT literature: I predict that individuals (both men and women) who more strongly weigh the importance of state welfare will be less sensitive to cues of relationship vulnerability, and will thus show a weaker link between relationship discrepancy and an OT response. This does not imply, however, that OT responses in general will be stronger or weaker in Norway, compared to the US. Dynamics of the individual relationship are expected to *interact* with cultural factors to predict OT responses.

Methods

Participants

148 students (115 women and 33 men; mean age = 22.93, SD = 2.84) from two campuses at the Norwegian University of Science and Technology (NTNU) were recruited to participate in a study entitled "Oksidativt Stress, Hormoner Og Relasjoner"

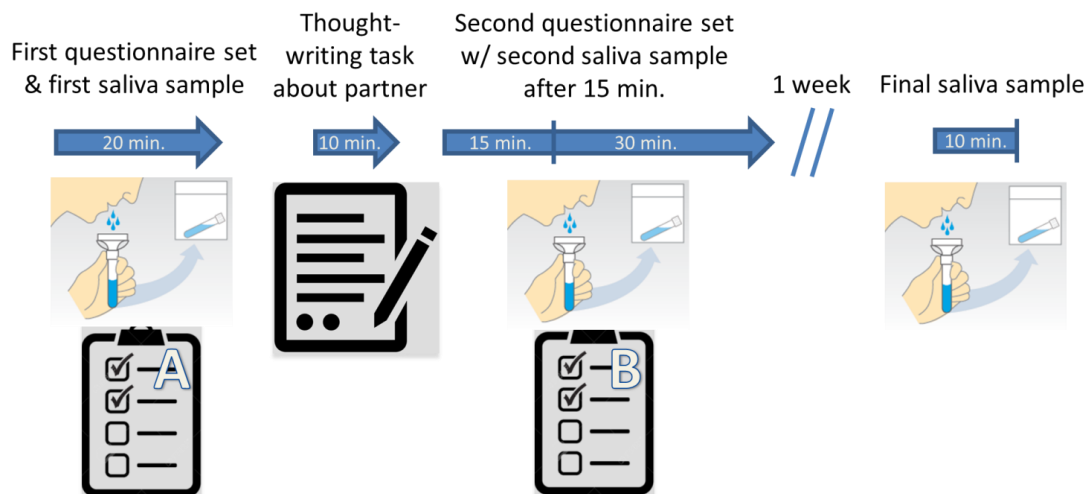
(Oxidative Stress, Hormones and Relationships).¹ While I did not restrict participation to any particular department, participants were most commonly recruited through Facebook posts, fliers, and study groups affiliated with the Department of Psychology at NTNU.

Procedure

Individuals arrived at a study room in the Department of Psychology building at NTNU-Drøgtvoll, and were assigned to semi-private cubicles separated by partitions. Up to 4 participants performed procedures simultaneously. In the following order, participants 1) were given informed consent (as approved by REK-West, a regional ethics committee in Norway); 2) completed a series of background questionnaires to complete, during which they provided a first saliva sample; 3) spent ten minutes completing a writing task about the ways they are accepted by and connected to their romantic partners; 4) completed a second set of questionnaires and, 15 minutes after beginning them, provided a second saliva sample; and 5) had a facial and full-body photo taken. They were then given a kit with all the necessary materials for a second follow-up sample, to be returned one week after the first study session. The initial study session lasted, on average, approximately 90 minutes. Upon return, participants dropped off their samples and received compensation (a certificate valid for one free movie ticket at the local cinema). The total time of the lab sessions equaled approximately 95 minutes. Figure 1 provides a schematic of the laboratory session.

Figure 1. Schematic of laboratory procedure.

¹ The title of the study also reflects the collection of questionnaire data and biological samples (e.g., urine) for analyses that do not directly pertain to my dissertation project.



Questionnaire Measures

All participants completed measures in the Norwegian language. While some standardized measures were already available in Norwegian, most measures had to be translated for the purposes of this study. To ensure precise wording and meaning was maintained in the translation process, all English-language measures were translated to Norwegian by two native speakers, then back-translated.

In the initial questionnaire set, participants provided demographic details, health histories for both themselves and their families, information regarding lifestyle and levels of physical activity, the Perceived Vulnerability to Disease Scale (Duncan, Schaller, & Park, 2009), retrospective questions asking about their timing of puberty relative to peers, and for women only, a measure assessing usage of hormonal contraceptives, and position within the ovulatory cycle.

Thought-writing Task

The thought-writing task, completed after the first questionnaire set, was a direct Norwegian translation of the task used in Grebe et al., (2016). Participants were given a piece of paper with the following instructions:

“Please spend a few minutes thinking about your relationship with your partner. Then write about ways that your partner responds to you in ways that show that your partner truly accepts and connects with you, or how you wish your partner would respond to you in ways that show that your partner truly accepts and connects with you.

In total, you’ll have about 10 minutes for this task. So you have a few minutes to gather your thoughts before writing.”

In the second questionnaire set, participants completed Simpson et al.’s (1996) questionnaire on avoidant and anxious attachment in relationships, and the NEO Five Factor Inventory (NEO-FFI; Costa & McCrae, 1992). Participants also provided detailed information on specific aspects of their own romantic relationships by completing the Relationship-Specific Investment Inventory (Ellis, 1998), which consists of self and partner reports of relationship investment on the subscales of emotional nurturance, antagonism, commitment, sexualizing others, giving of time social neglect, dishonesty, and sexual responsiveness. In addition, participants completed—self-reports only—Tancredy & Fraley’s (2006) Attachment Bond Strength questionnaire, and a measure of infatuation with the partner (adapted from an unpublished measure from Helen Fisher; see Eastwick & Finkel [2012]). Grebe et al. (2016) developed two additional measures for their study that I also include: a 12-item measure of Desired Closeness with the

partner (e.g., “I want to be emotionally close, in ways I’ve never felt before”); a 12-item measure of Desired Closeness Lacking with the partner (e.g., “I want much, much more to be able to know my partner like I’ve known no one before”).

Composite measures of ‘self’ relationship involvement or investment were created through a factor analysis of the aforementioned 12 relationship measures. ‘Partner’ relationship involvement composites were computed through a factor analysis of the 8 PSII subscales; the remaining four measures did not assess reports on one’s partner.

For the ‘self’ measures, a scree plot suggested four factors, accounting for 65% of the variance. A parallel analysis (computed using the nFactors package [Raiche & Magis, 2010] in R 3.2.5) also suggested four factors. The first factor contained strong loadings (>.45) for bond strength, commitment, emotional nurturance, and closeness lacking (reverse-loaded). The second factor possessed a strong loading only for antagonism. The third factor was defined by strong loading for social neglect only. The final factor had strong loadings for emotional nurturance, infatuation, and desired closeness to partner. To ease interpretation of relationship ‘involvement’, I also extracted a single higher order factor from these four factors as a ‘general’ composite of relationship involvement, following the procedure in Grebe et al. (2016; loadings = .63, -.32, -.48, .84 for the four factors, respectively; 49% of variance explained). The loadings on this general factor were interpretable as a measure of overall involvement: strong positive loadings on bonding, commitment, and desiring connection; strong negative loadings on antagonism and social neglect.

A factor analysis of the 8 ‘partner’ subscales yielded a three factor solution. For these factors, the subscales loaded onto factors in patterns and magnitudes somewhat similar to the ‘self’ factors above; however, the direction of loading was opposite (see Appendix A for pattern loadings for both self and partner factors). I extracted another ‘general’ composite, this time of partner investment, from the three factors, which was structurally similar to the ‘self’ composite. I then reversed the scores on the partner composite, such that the interpretation was consistent across both composites: higher levels correspond to greater relationship involvement. As the self and partner individual factors are not composed of the same scales, I focus on the two general investment factors in the results.²

Consideration of state welfare in life-history decisions. For this study, I developed a set of survey questions that assess participants’ perceptions of two related but distinct forces: first, the extent to which they perceive the benefits of state welfare as impactful on certain life-history decisions; and second, assuming welfare benefits do have an impact, how participants believe they would do so.

Participants completed five items asking the extent to which they perceive state welfare as important for their overall well-being, as well as its particular impact on deciding whether to have children, when to have children, who to choose as a partner, and what to choose as a career. Next, participants completed four questions asking *how* welfare benefits might hypothetically influence these choices. Participants chose their preferred response along a seven-point Likert scale for each item, indicating whether

² Another way to create a ‘general’ factor of investment would be to extract the first principal component from a factor analysis of all the relationship measures; unsurprisingly, this method of creating general factors highly correlated with the method I use: $r = .97$ and $.91$ for self and partner, respectively.

state welfare would hypothetically influence them towards one choice or another. For instance, participants could indicate that state welfare benefits would alter their preferences towards having children *earlier in life* (1), *later in life* (7), or would have *no effect* (4). For full list of items and response scales, see Appendix B.

Interest and participation in social bonding with those other than the pair-bond partner. I also created several measures to assess participants' investment and interest in social bonding with those other than close partners. Participants indicated their level of agreement with two statements: "I would rather have a lot of friends than just a few, very close friends" and "I consider it more important to have a few very good friends who I can trust, than to have many friends". Additionally, participants reported the number of 'close' social partners in their lives, other than their partner (the criteria used to define 'close' is provided in Appendix C); they then reported their desire to either decrease this number, increase this number, or keep it the same. Finally, I created a brief measure to assess participation in social groups and activities. This measure may quantify some common varieties of investment in social relationships with more peripheral social partners (i.e., not close social partners). For each of four classes of social activities—clubs, intramural sports, small gatherings with mostly strangers or acquaintances, and large gatherings with mostly strangers or acquaintances—participants completed three items: whether or not they recently participated in these types of activities; an open-ended field asking for the name or specific variety of the respective activity; and the number of days in the past month they participated in the activity. I focus on the third question, days per month, as this provides information regarding the degree of participation in these activities. A number of participants indicated no participation in one or more of these

types of social activities, and non-zero responses were highly skewed. I therefore log-transformed the frequency of participation variables with the formula $X_{new} = \log (X_{old} + 1)$, which preserved zero values. I performed the same transformation on the sum of the four frequency variables to calculate an overall score of ‘peripheral sociality’. See Appendix C for full measure.

OT Assays

The process for collecting saliva samples was identical to the procedure used in Grebe et al. (2016). In brief, at each of the three collection points, participants were instructed to provide approximately 5 mL of saliva, split evenly between two test tubes. All samples were frozen at -20°C before being shipped on dry ice to UNM’s Hominoid Reproductive Ecology Laboratory, where I performed assays for OT. Before assaying, samples were mixed by vortexing, and centrifuged for 15 minutes. From the supernatant saliva, I withdrew a 1.5 mL portion (or the maximum amount possible, in cases where less was available), which was then dried down in a vacuum concentrator at 4°C and reconstituted with 250 μL of assay buffer immediately prior to assay, resulting in a 6:1 concentration.

OT concentrations were measured using an ELISA kit from Enzo Life Sciences (ADI-901-153A; Farmington, NY). Enzo reports a 15 pg/mL sensitivity for this assay. The mean intra-assay coefficient of variation (CV) was 7.1%, and the mean inter-assay CV was 14.7%. The assay instructions for OT recommend an extraction step, which is designed to eliminate interfering substances from the sample matrix that might also react with the assay antibody and lead to biased measures of OT concentration. However,

recent evidence indicates that the vast majority of OT in the bloodstream is bound to purportedly ‘interfering’ substances eliminated by extraction (Carter, 2014), perhaps making unextracted measurements a better estimate of circulating OT levels.

Additionally, interference from the sample matrix may be trivial for saliva samples once they are dried and reconstituted with sample buffer. Some notable previous studies, including the study containing the finding I aim to replicate, have assayed OT in unextracted samples (Grebe et al., 2016; see also Schneidermann et al., 2012; Taylor et al., 2010) Two recent validations determined that intranasal OT produced reliable increases in OT from unextracted saliva collected 30-90 minutes after administration (Daughters et al. 2015), continuing for up to 7 hours (van IJzendoorn et al., 2012). All assays for participants were thus performed on unextracted samples.

Results

Analysis

I created a series of general linear models in SPSS 22.0 and R 3.2.5 to test each of the predictions for the current study. OT change was the dependent measure in all primary analyses. An OT change score was available for 147 participants; I eliminated one unrealistically high change score that was likely assayed or recorded incorrectly (this participant’s OT increased nine-fold during the task, more than 5 SD above the average; the next highest increase was less than four-fold), leaving 146 change scores. First, I focused on effects for each of the general investment factors, controlling for either self or

partner investment as applicable, sex, and the logarithm of relationship length;³ I mean-replaced one report of relationship length (375 months) that was greater than the participant's age. Following Grebe et al., (2016) I then calculated a difference score between these two investment composites and used this difference score as a predictor of OT change. Next, I examined whether these effects were moderated by any of the state welfare perception variables, and whether OT changes associated with decreased reports of social bonding investment in peripheral social partners. Finally, I performed exploratory analyses on these same welfare and social bonding variables to investigate their associations with established measures of personality and behavior.

OT Change

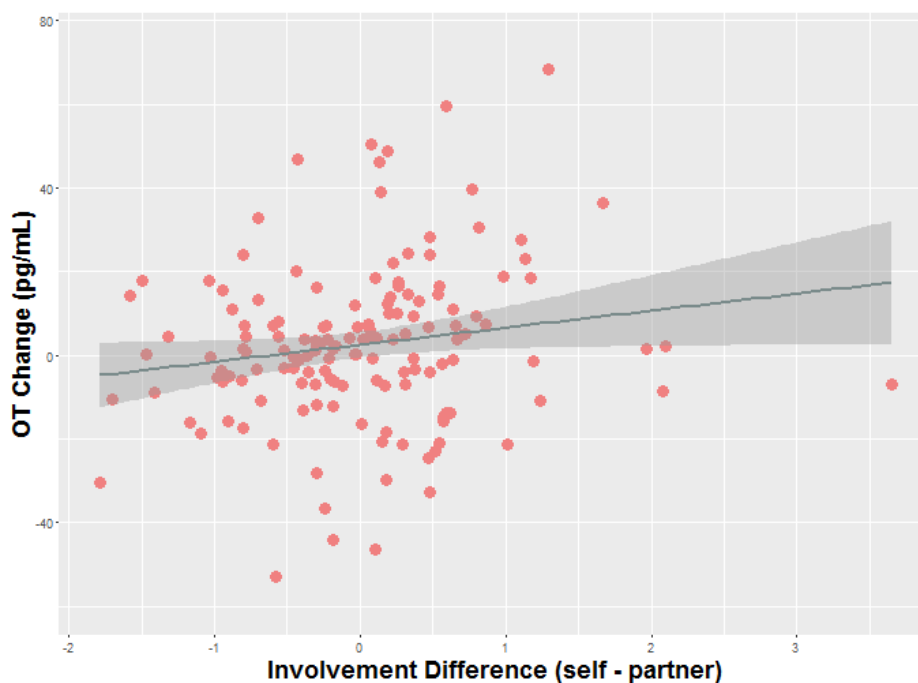
I first present analyses that test one set of major predictions. Specifically, I predicted that, consistent with previous findings, a discrepancy in relationship involvement would predict OT change. Considered separately, self-reports of involvement positively predict this OT change, while partner-reports negatively predict it.

Involvement Discrepancy. Following Grebe et al. (2013) and Grebe et al. (2016), I calculated a discrepancy score for relationship involvement by subtracting partner involvement from self involvement. This discrepancy, in which individuals reported more involvement than their partners, positively predicted an OT response, $F(1,142) = 4.16$, $\beta = .20$, $p = .043$, partial $\eta^2 = .028$. See Figure 2. A sex x involvement discrepancy

³ Past work emphasizes the potential importance of *new* relationships for OT (e.g., Schneiderman et al., 2012) Perhaps there is an asymptotic effect of relationship length, in which new relationships have a more pronounced effect. I log-transformed relationship length so the variable reflects the effects of a proportional change in time. Using the untransformed relationship length variable did not affect interpretation of results.

interaction was not predicted, and indeed, had almost no effect, $p = .979$.⁴ Winsorizing one outlier on involvement discrepancy (seen on the right end of Figure 2) slightly strengthened the effect, $F(1,142) = 5.05$, $p = .026$, partial $\eta^2 = .034$.

Figure 2. General involvement difference and OT change across the task.



Self and partner-reports of involvement, considered separately. Controlling for reports of partner involvement, higher self-reports of involvement non-significantly predicted a higher OT change, $F(1,141) = 2.50$, $\beta = .18$, $p = .116$, partial $\eta^2 = .017$. The effect of partner reports on the OT change, controlling for self-reports, was significant in the opposite direction, $F(1,141) = 3.98$, $\beta = .21$, $p = .048$, partial $\eta^2 = .027$, such that reports of lower partner involvement predicted a stronger OT response. See Table 1 for a summary of effects.

⁴ Sex interactions in the other sets of analyses are similarly non-significant. As sex interactions were not expected, and not found in this main analysis, I do not include them in reporting other analyses.

Table 1. Associations of Relationship Involvement with OT Change as a Function of Relationship Thoughts

Model	Involvement Discrepancy			Self and Partner		
	β	F	p	β	F	p
Sex	.001	<.01		.02	.02	
Relationship length (log)	-.04	.24		-.04	.26	
Self Rel. Involve.				.18	2.50	.116
Partner Rel. Involve.				-.21	3.98	.048
Discrepancy	.20	4.16	.043			

Moderation by welfare consideration. Adding the interaction of one's overall perceived dependence on welfare with relationship discrepancy to the above model did not yield a significant moderation effect, $F = .31, p = .577$. A composite of the four individual items assessing level of consideration showed a marginally significant interaction with relationship discrepancy, $F(1,139) = 2.21, p = .096$; greater welfare consideration, summing across the four items, *increased* the association between relationship discrepancy and an OT change. See Table 2. However, the follow-up items assessing the *direction* of influence for welfare consideration yielded consistently non-significant interactions, all $p > .190$.⁵ In other words, there was no indication that *how* participants viewed the influence of welfare altered the link between relationship involvement discrepancy and an OT response.

Table 2. Expanding the Relationship Discrepancy Model to Include Moderators of Welfare Benefits

⁵ These items were examined individually, as a composite sum would not be interpretable, and similarly, an exploratory factor analysis of the 4 questions did not reveal an obvious shared dimension among the items.

Model Effect	Overall Dep. Item			Sum of 4 Ind. Items		
	β	F	p	β	F	p
Sex	-.02	<.01		<.01	<.01	
Relationship length (log)	-.03	.24		-.03	.17	
Discrepancy	.21	4.71	.032	.24	4.84	.014
Welfare Dep.	-.04	.33		.05	.44	
Discrepancy x Welfare Dep.	.05	.33		.15	2.81	.096

Other kinds of social bonding investment. I predicted that individuals who had a greater OT change across the task (generated from thinking about their partner) would indicate less investment in other kinds of social bonds. I collected four different measures that I interpret to provide some information regarding non-partner social investment: 1) the NEO-FFI dimension of extraversion, defined by some psychologists as “the quantity and intensity of energy directed outward into the social world” (Borkenau & Ostendorf, 1993); 2) interest in having many friends, versus a few close friends; 3) ‘peripheral sociality’, the extent of participation in social activities with those other than close social partners (measure described in Methods); 4) the reported number of close social partners other than the pair-bond partner. Consistent with predictions, extraversion showed a negative zero-order correlation with the OT change, $r(145) = -.27, p = .001$. Including extraversion in the *Involvement Discrepancy* model (see Table 3) showed that, controlling for relationship discrepancy, sex, and relationship length, those with a higher OT response scored lower on extraversion, $F(1,140) = 4.84, \beta = -3.59, p = .030$, partial $\eta^2 = .033$. Similarly, those with a stronger OT response viewed having many friends as less

important, $r(145) = -.17, p = .037$; this was marginally significant in the *Involvement Discrepancy* model, $F(1,141) = 2.71, \beta = -.13, p = .102$, partial $\eta^2 = .019$.

Turning to the peripheral sociality variables, stronger OT responses predicted marginally less participation in large social gatherings in a bivariate correlation, $r(143) = -.16, p = .055$. However, none of the other participation variables, including the composite measure of peripheral sociality, predicted an OT change (all $p > .548$), and none were significant predictors in the *Involvement Discrepancy* model. See Table 3.

Table 3. Expanding the Relationship Discrepancy Model to Include Other Kinds of Social Investment.

Model	Extraversion			'Many Friends'			Peripheral Soc.		
	β	F	p	β	F	p	β	F	p
Sex	.01	<.01		<.01	<.01		<.01	<.01	
Rel. Length (log)	-.06	.62		-.06	.61		-.02	.07	
Discrepancy	.20	4.43	.037	.19	3.02	.085	.21	4.86	.029
Non-Partner Soc. Inv.	-.17	4.83	.030	-.13	2.71	.102	.09	.23	

Finally, participants did not vary in their OT change as a function of the number of 'close' social partners that they reported, $r(144) = .03, p = .704$, or as a function of their satisfaction with their number of close partners, $r(144) = -.03, p = .696$.

Exploratory Analyses

Social bonding investment. The peripheral sociality measures were developed for this study in expectation that they would negatively predict an OT response, but they mostly failed to do so. Perhaps these reports of social activities reflect stable personality

traits, rather than transient patterns arising due to aspects of one's romantic relationship. To investigate this, I examined associations between peripheral sociality and the NEO-FFI. Controlling for sex, overall peripheral sociality related negatively to neuroticism $r(144) = -.15, p = .080$, positively to extraversion, $r(143) = .20, p = .018$, and positively to openness to experience, $r(144) = .30, p < .001$. No relationship emerged with either agreeableness ($p = .917$) or conscientiousness, ($p = .345$). Each of the individual participation variables correlated similarly to personality dimensions, with the exception of intramural sports, which associated negatively with neuroticism ($r = -.20$), but did not associate significantly with extraversion ($r = .11$) or openness to experience ($r = .09$).

Interest in 'having many friends'. In addition to possessing a stronger OT response, individuals who reported less interest in having many friends also had larger relationship involvement discrepancies, $r(144) = -.19, p = .023$. This association is consistent with the hypothesis that a trade-off exists between investing in vulnerable relationships and investing in social affiliation outside the pair-bond. Additionally, one interpretation of significant associations between relationship discrepancy, OT change, and orientation toward large friendship networks is a causal mediation model: relationship discrepancy leads to a larger OT response when one considers this relationship, which mediates less interest in maintaining a large group of friends. I tested the feasibility of this interpretation with a mediation analysis. Inconsistent with full mediation, the direct effect of relationship discrepancies on 'many friends' (i.e., controlling for OT change) remained significant, $r(143) = -.17, p = .046$, and was not substantially reduced from the total effect. While this result is, in principle, consistent with partial mediation as described by Baron and Kenny (1986), an analysis of the

indirect effect (measuring the extent of mediation) with Hayes' (2013) PROCESS macro for SPSS indicated a small effect size, $R^2 = .008$, 95% CI: [.002, .034].

Discussion

The study presented in this manuscript was designed to replicate a previous finding on OT and romantic relationships, and also extend a model of natural OT production to explore previously unexamined predictors. Below, I discuss the study's results individually in terms of their support for the predictions I advanced, and how these results might be interpreted within theoretical frameworks for OT.

Replication of Grebe et al. (2016)

The replication of Grebe et al. (2016) is arguably the clearest effect from the current study. I found that a greater relationship discrepancy, in which individuals report more involvement than their partners, predicted a larger OT response, in line with Grebe et al. (2016). First, I discuss this main finding in the context of the current climate surrounding behavioral OT research.

The Value of Replication. What is the contribution of a replication to the scientific body of knowledge regarding OT? Flatow (2016) refers to replication studies as “the green leafy vegetables of the research world: not the most exciting thing ... despite their healthy reputation”. Indeed, the widespread phenomenon of publication bias is likely driven, in part, by an incentive structure in academia that disproportionately rewards finding novel effects over pursuing replications (Pashler & Wagenmakers, 2012).

However, this structure is changing. Seminal papers such as Simmons, Nelson, and

Simonsohn (2011) that draw scientific attention to widely-used practices that can elevate false positives in the published literature, and highly-cited examples of failures to replicate published findings, such as the Open Science Collaboration's (2015) Reproducibility Project, have placed the necessity of replication front and center. Prominent psychology journals such as *Perspectives on Psychological Science* now dedicate space to registered replications (with some high-profile unsuccessful replications already emerging; e.g., Wagenmakers et al., in press), and heavyweights like *Nature* and *Science* now explicitly welcome replication efforts of studies they previously published.

One of the many lessons resulting from this 'reproducibility crisis' is that scientists must shift their perspective on replications. Often, successful replications may be seen as not noteworthy, perhaps because researchers feel that the existence of an effect was never in question; after all, it was published in a peer-reviewed journal. Unsuccessful replications, on the other hand, are sometimes seen as lifting the veil from a false positive masquerading as a real effect. In reality, replications are not just votes in one direction or another regarding the 'truth' of an effect. They can provide new knowledge regarding the nature of an effect—for instance, its strength, boundary conditions, or sensitivity to context (Maes et al., 2016).

What does the current replication help reveal? At a fundamental level, it does provide additional evidence against the possibility that Grebe et al. (2016) was a false positive. A wave of recent research (e.g., Open Science Collaboration, 2015; Baker, 2016) has, at the very least, made the case that established effects can be more elusive than expected. Observing a statistically significant effect across two independent samples is not trivial; it already places the amount of evidence supporting this effect above a large

proportion of published research. Additionally, the effect emerges across samples from two different (albeit both Western) cultures. Despite variation in numerous social norms and policies—including welfare benefits—young adults in Norway, like young Americans, appear to produce more OT when thinking about their partner if their pair-bonds are vulnerable.

The specific effect I replicate—a naturally-generated OT response conditional upon context—can also speak to the state of behavioral OT research in general, which is itself under scrutiny because of reproducibility concerns. For instance, early findings in the OT literature indicated that OT administration can increase trusting behavior (e.g., Kosfeld et al., 2005, Mikolajczak et al., 2010), empathetic capacities (Domes et al., 2007; Hurlemann et al., 2010), or simply make people more prosocial interaction partners (Zak et al., 2007). While one meta-analysis indicated that OT does increase trust (Van IJzendoorn & Bakermans-Kranenburg, 2012), another review found no overall effects of OT administration on trusting behavior (Nave, Camerer, & McCullough, 2015). Relatedly, researchers have drawn attention to publication bias in OT administration studies by ‘opening their file drawers’ and arguing that null effects of OT on prosociality are far more common than one might expect (Lane et al., 2016). These published critiques often focus on issues of statistical power (many OT administration studies test only a handful of participants) or uncertainty regarding administration mechanisms (e.g, since OT does not cross the blood-brain barrier, it is unclear how nasal sprays reach the central nervous system to have neuromodulatory effects). These critiques are valuable; I offer yet another one. In my view, the current state of uncertainty regarding OT administration work is partially a product of findings outpacing theoretical development.

Again, experimental administration studies are powerful in that they allow targeted investigations of effects. However, these studies also give substantial power to researchers to select the contexts in which they have participants receive a surge of OT. Perhaps some of these situations speak to circumstances that ancestrally utilized the OT system, but many others (e.g., learning tasks in an fMRI) likely do not. In studies with a lack of adaptive fit between circumstance and biological response, there are issues of interpretation with OT administration. How does one know, for instance, that an observed effect is due to OT, and not one of the many other hormones (e.g., progesterone, estradiol; see below) with which it interacts in the brain and / or circulation? More fundamentally, as I argue in the Introduction, effects of OT are tied to the circumstances that elicit it. If researchers are not pairing administration with these contexts, it is difficult to generate a consistent functional interpretation. This may lead to the proliferation of conceptualizations that sound plausible, but because of their shaky theoretical grounding, are not borne out by replication attempts.

Qualifying Identify and Invest in the Current Study

I focused on Identify and Invest (Grebe et al., 2016) as the main theoretical conceptualization of interest in the current study. Even considering a successful replication, Identify and Invest is still a preliminary framework; its premises, operationalizations, and predictions should be further developed and clarified. How does the current project speak to this issue?

Tend and Befriend versus Identify and Invest. As mentioned in the introduction, one prominent model for the natural production of OT is the Tend and Befriend

perspective (Taylor et al., 2010). This view in some ways resembles Identify and Invest, the view I have favored throughout this manuscript. Both see OT as a response to threats, and therefore predict that cues of relationship disengagement should predict increased OT. It is valuable, then, to consider the current study's results in terms of these two conceptualizations. Consistent with Tend and Befriend, a lack of partner involvement predicted a stronger OT response—and in fact, this was a stronger predictor than self-reports of high involvement. However, Tend and Befriend also proposes that OT increases potentiate the desire to seek affiliation outside the distressed relationship. Identify and Invest predicts just the opposite: OT increases orient bonding resources *back toward* the valued relationship, and perhaps away from other social partners. In this respect, the results of the current study are consistent with Identify and Invest, but run contrary to Tend and Befriend: OT changes correspond to less desire to have many friends, and less extraversion (which some psychologists define as “the quantity and intensity of energy directed outward into the social world” [Borkenau & Ostendorf, 1993]). Measures from the current study were not designed to directly test predictions from Tend and Befriend. However, the results I obtain are nevertheless inconsistent with what one might expect under a Tend and Befriend framework.

Reports from one's partner versus reports of one's partner. The relationship discrepancy effect, found in both the current study and Grebe et al., was appreciably weaker in a Norwegian sample—a β coefficient of .20—compared to Grebe et al. (2016), where the effect had a β of .30. Some of this difference may be due to sampling variability, but some could arise from differences in design. How might variation in measures impact the framing of an effect within Identify and Invest? In the current study,

relationship discrepancy was determined solely via self-reports. Grebe et al. (2016) also focused on the reports from an individual's partner, arguing that perceptions of a partner's involvement might be biased by one's own feelings regarding the relationship. Indeed, in Grebe et al., reports on one's partner did not significantly predict OT responses (though the effect was in the predicted direction). In this study, however, only reports on one's partner were available. And, contrary to Grebe et al., these reports strongly predicted OT changes—even more so than reports on oneself. This provides an obstacle to interpretation. Why are the results inconsistent in this way between Norway and the US (again, sampling variability notwithstanding), and which kind of partner-reports are to be favored? It is my position that reports from a partner are still preferable. Reports from one's partner may be less prone to bias (as Grebe et al. argue), and dyadic data analyses allow for the modeling of responses from both perspectives in the relationship, while accounting for their non-independence (Kenny, Kashy, Cook, & Simpson, 2006). Partners were not recruited in the current study, primarily due to logistical constraints, but having both members of the couple is advantageous, all else equal. I speculate that, were partners recruited in this study, their reports would have predicted actor OT changes more strongly than the available reports on them.

Vulnerability, or something else? Another issue, briefly mentioned in the introduction, concerns the best interpretation of the relationship discrepancy effect. Grebe et al. (2016) argue for a conceptualization of such relationships as 'vulnerable', in part because this interpretation readily extends to putative ancestral functions of OT. In theory, the OT system was co-opted over evolutionary time to function in pair-bonds, but it should have done so within the bounds of its evolved roles in mother-infant bonding.

Like mothers' bonds with their infants, romantic relationships with unequal reports of involvement can be characterized as vulnerable. To be consistent with Grebe et al., I adopted this characterization in reporting the results from the current study. However, one might wonder if this is the most appropriate interpretation. Of course, 'vulnerable' is only one way to characterize a pair-bond where involvement of the individual members is unequal. While many relationships with a discrepancy may be vulnerable, one can also imagine relationships where there is a discrepancy in involvement, but the bond is still stable—for instance, when available alternatives are even less attractive (Rusbult, 1980; Buss et al., 2017). In addition, if a discrepancy is truly capturing vulnerability, one might expect worries about partner abandonment or infidelity should also predict an OT response. In this study, they do not (all $r < |.07|$). What alternative conceptualizations might be worth considering?

One alternative starts by questioning the adaptive logic of being highly involved in a relationship with a partner who does not reciprocate. In dyadic relationships, including romantic bonds, a partner who fails to meet one's own level of involvement is also, from the perspective of the more involved individual, failing to cooperate. At some point, if humans evolved adaptations to continuously assess the costs of remaining in such a relationship relative to any benefits, individuals should sometimes elect to 'walk away' from uncooperative pair-bond partners (Aktipis, 2004; Buss et al., 2017). Of course, not all individuals have the same tipping point; some may be very sensitive to discrepancies, and choose to quickly jettison an uncooperative partner, whereas others might be relatively averse to leaving a relationship, even as discrepancies in involvement become severe. One might argue that the sample from this study is more likely to capture

the latter kind of individual, since the former would have already moved on. If this is the case, then this might provide an alternative functional account for my results. The effect of OT might be the same—to orient resources toward a relationship—but perhaps discrepancies predict an OT response simply because the study examined people who are more likely to attend to partners perceived as uncooperative, rather than abandoning them. Again, the relationship need not be vulnerable, *per se*.

How might one identify individuals unlikely to abandon an uncooperative partner? Physically unattractive individuals tend to have lower standards for mates (Buss & Shackelford, 2008), and might thus be less inclined to leave a relationship. And in general, those with lower mate value than their partners, because they are less likely to find alternatives, might respond to involvement discrepancies with a greater OT response. Self and partner mate value was assessed in the current study, but the interaction between relative mate value and relationship involvement discrepancy did not significantly predict an OT change ($p = .365$). Targeted research questions in future studies are needed to more clearly test this alternative—based on tendencies to stay with uncooperative partners—against a view focusing on vulnerability.

The above perspective still falls under an Identify and Invest view, but attributes effects to something other than vulnerability. Several variations on this argument are possible. For instance, relationship novelty is another circumstance tied to increased OT (Schneiderman et al., 2012)—are new relationships necessarily vulnerable? Perhaps it is simply uncertainty, not vulnerability, generating an OT response to attend to that relationship. The same could be applied to discrepancies in involvement, or other situations that generate an OT response (e.g., events requiring maternal aggression;

Bosch et al., 2005). In general, Identify and Invest might imply a number of different labels for OT's eliciting circumstances besides 'vulnerable', without sacrificing the core premise that OT is tied to specific, ancestrally-salient cues from valued relationship partners.

Framing the effect from the current study and Grebe et al. is not just an exercise in semantics. The same is true for many other results in the OT literature. How one interprets the outcomes of these empirical tests drives future predictions and research programs, as can be seen clearly from a review of the various proposals for OT's effects. Identify and Invest, like other frameworks for OT, is built upon a specific interpretation of past research. For Identify and Invest to advance understanding of the psychological functions of OT, future studies must attempt to distinguish between closely related, but distinct, conceptualizations.

Extensions of the Current Project

While sampling variability may be one factor (or even the only factor) explaining smaller OT responses in the current study, it was one goal of this project to identify moderating factors that might lead OT responses to differ between two samples from different countries. Thus, I asked whether there are meaningful intervening variables that could explain a difference, and attempted to identify one such set of variables: welfare benefits, and individual differences in perceptions of these benefits. In addition, to identify potential trade-offs that could result from increased involvement in a vulnerable pair-bond, I examined reports of participation and investment in social bonds with those other than the partner. Here, I turn to these results.

Welfare Considerations. I predicted that particular aspects of the Norwegian welfare system would act upon OT responses in the current study, due to previous research suggesting that welfare benefits can influence important life-history decisions, such as when and whether to have children. However, welfare consideration, whether assessed via conscious perceptions or hypothetical appraisals, did not make a consistent difference on the extent of OT responses to vulnerable relationships. Participants who viewed welfare benefits as more impactful showed some faint suggestion of a stronger link between OT and relationship discrepancy. However, the crucial follow-up question—assessing the direction of this influence—showed no similar interaction. I do not place much stock in the robustness of this single marginally significant effect. Several factors may help explain why no consistent effects were observed, though it is ultimately difficult to defend any particular interpretation of null results. One simple explanation is based on the observation that subsidization by the state is an evolutionarily novel circumstance. A defining characteristic of human life-histories is an extreme reliance on social partners for provisioning of necessary resources, protection from dangers, and assistance in raising offspring (Sugiyama, 2004; Hrdy, 2009). These bonds are so integral to one's fitness that it may be difficult to calibrate one's attunement away from them, even if there is some level of conscious recognition regarding the purpose of state welfare. This is consistent with my results, as participants do, on average, believe that welfare encourages greater fertility and more freedom in partner and career choices. I investigated perceptions of welfare support in hopes of addressing whether an institution can, in some way, 'stand in' for social partners in its effects on individuals' life-history decisions. In a broad demographic sense, it may do so. However, from the perspective of

an individual, perhaps a non-social entity does not carry the same motivational salience as a valued social partner. Thus, perhaps it is not surprising that elicitation of an OT response, including within romantic bonds, is not appreciably modified by considering an entity with which humans have not co-evolved.

Alternatively, it may be that Norwegians do perceive welfare benefits in terms of their effects on life-history decisions, and do instantiate this information, but the effects are too small to significantly influence a physiological OT response in one direction or the other. The total cost of raising a child to adulthood in Norway averages 1,300,000 NOK (approximately \$150,000; SIFO, 2016). These costs perhaps swamp the expectations of welfare benefits when considering life-history decisions, even when one can expect relatively high levels of financial support. Or, perhaps the student sample was too young to reveal an effect of welfare consideration. In Norway, first time fathers average 31 years old, and mothers 29 years old (Statistics Norway, 2015). Student participants in the current study were, on average, still several years away from making the life-history decisions described in the measures, perhaps rendering the questions too abstract for them to capture any influence that might exist.

Yet another interpretation could be that these null results are due to a misplaced emphasis on adaptive calibration. Zietsch (2016) proposes that adaptive calibration—the optimization of the level of a trait to relevant environmental or contextual factors—is unlikely to explain much psychological variation between individuals. In making this point, he challenges the robustness of adaptive calibration effects in several domains, including extraversion and facial masculinity preferences. While I predicted that individual differences in welfare support consideration would alter the extent to which

individuals generate OT responses when thinking about a vulnerable relationship, my results are arguably more consistent with a simpler explanation: OT responses are best explained by a combination of relationship discrepancy and random genetic variation; perceptions of state-delivered resources, as a kind of instantiated environmental information, has little impact. Still, other explanations are plausible, too. Perhaps young Norwegians live with a relatively constant expectation of state welfare support, as they all experience relatively similar environmental cues of support, and they were not alive to remember a time when welfare benefits were less comprehensive. One could then speculate that Norwegian students experience an appreciable, but relatively invariant, amount of adaptive calibration in their mating psychology, and thus their hormonal responses. I note that this last possibility is consistent with the smaller OT-relationship discrepancy effect I observed in Norway, but more research is needed to determine whether this smaller effect can in any way be attributed to welfare policies.

Peripheral Social Investment. In this study, individuals in more vulnerable relationships were less extraverted, reported less desire to have many friends, and reported less participation in social events with ‘peripheral’ partners. Of these three measures of social bonding outside the pair-bond, two—‘many friends’ and extraversion—also negatively predicted OT changes generated from thinking about a pair-bond partner. While not reliable across all measures, multiple results are consistent with a trade-off between peripheral social investment and pair-bond investment. For ‘many friends’, the pattern of correlations is also consistent with an OT-mediated trade-off of psychological resources for social bonding; however, the extent of mediation is small. Future tests are needed to determine whether social investment measures,

especially those developed for the current study, are robustly predictive of OT and pair-bonding investment. These significant results are a promising basis for future investigation, but constructs like extraversion are admittedly ad-hoc proxies of social bonding, and entail much more than investments in certain types of relationships. Social network analysis may be one way to further explore these preliminary findings in future research.

Social network researchers such as Putnam (2001) speak of an individual's total social capital as the sum of "bonding social capital" (tightly-knit, emotionally close relationships) and "bridging social capital" (relationships with the potential to provide new perspectives and resources). This distinction resembles the trade-off I propose between 'close' and 'peripheral' relationships. One possibility is that OT fosters the development of the former, but suppresses development of the latter via influences on social dispositions. One popular measure of these social dispositions, extraversion, was associated with lower OT changes in the current study. How does extraversion, then, predict social capital? If bonding resources are in fact limited and must be adaptively allocated, one might expect extraverts—who enjoy greater marginal benefits from investment in wide social networks—to have higher bridging social capital, but lower bonding social capital. Indeed, two studies provide evidence consistent with each of these predictions (the first in a study of Finnish students [Kotkavuori, 2015], and the other a sample of Portuguese Facebook users [Venkatanathan et al., 2012]).⁶ In the current study,

⁶ Interestingly, some scholars argue that although an average individual's bonding and bridging capital have decreased in Western countries, including the US, over the past several decades, this drop has been markedly slower in Sweden (Putnam, 2002). Perhaps Norway, another Scandinavian country with similar social structures, is a particularly valuable setting to investigate the factors that predict different kinds of social capital.

I asked participants to self-report on their number of ‘close’ social partners (one proxy of their bonding social capital) and found no relationship to OT. However, these self-reports may not perfectly correspond to formal analyses of one’s social network. Individuals might over or under-perceive the quantity of their bonding social capital, perhaps due to errors in meta-perception (e.g., Kenny & DePaulo, 1993) or variations in personality itself (e.g., extraverted people also tend to have higher self-esteem; Robins et al., 2001). A better understanding of an individual’s social network may help lead to further insights regarding trade-offs between types of social investment.

One specific prediction pertaining to a social bonding-trade-off—whereby the level of participation in social activities with ‘peripheral’ partners in particular should correspond to lower OT responses—was not borne out by the data. Despite this, there are reasons to believe the assessment of peripheral social investment is worth exploring further. First, the measure appears to possess some degree of construct and discriminant validity. Considered aggregately, peripheral sociality associates positively with extraversion and openness to experience, but negatively with neuroticism. This suggests that, as intended, the measures I developed capture meaningful individual differences. In addition, activities that are arguably more likely to be pursued for reasons other than social interaction—in this case, intramural sports—do not associate with these personality dimensions in the same manner. And though they relate to established personality dimensions, I believe these measures of overt participation reflect something distinct. One’s participation might not just reflect personality, but also how much effort one expends on a certain activity. Furthermore, the marginal benefits of effort might differ substantially between individuals; in other words, perhaps interactions between

participation and other psychological traits are important to examine. Participation helps get at one's *investment*, which may necessitate fewer resources invested in other social activities, like shoring up the bond with one's romantic partner. In general, perhaps these measures failed to predict OT responses not because they are irrelevant to the OT system, but because other individual difference variables, or other hormonal mechanisms, are necessary to understand any link between different varieties of social investment (see below).

Future Directions

The current study, along with Grebe et al., (2016), takes an initial step toward building a life-history framework for OT (see also Gangestad & Grebe, 2016). However, much remains to be investigated. Below I list two potential avenues for future development.

Physiological functions of OT. Ultimately, this project investigates the psychological/neuro-modulatory functions of OT. Even if one's interests lie in this domain, though, an understanding of non-psychological functions is beneficial. If one's goal is to explain how a given hormone allocates energy and resources—and this is the perspective I adopt for OT—then physiological effects can provide information about the potential mechanisms through which this is accomplished. Gangestad & Grebe (2016) develop this argument at length. Here, I focus on a few aspects of OT's physiological functions that are particularly worth considering in light of my results.

One major physiological role of OT appears to involve energy balance—specifically, OT may reduce energy intake and increase expenditure. Several studies

indicate that OT decreases food intake in both rodents and humans (reviewed in Blevins & Baskin, 2015; Gangestad & Grebe, 2016). OT knockout mice develop obesity even without a change in food intake, suggesting a role in expenditure (Takayanagi et al., 2008). Muscle cells in heart tissue increase glucose uptake after OT administration (Gutkowska & Jankowski, 2012). OT also stimulates lipolysis in adipocytes (reviewed in Chaves et al., 2013).

OT inhibits pro-inflammatory cytokines (Clodi et al., 2008), but also facilitates processes such as wound healing (Detillon et al., 2004). Perhaps OT modulates immune function towards processes of tolerance / repair and away from active resistance, in effect limiting the extensive allocation of resources to immunity (Gangestad & Grebe, 2016).

Along with potential psychological functions, physiological effects of OT like those listed above help create a framework for how OT mediates the broad re-orientation of energy and effort within an organism. I have proposed that OT affects motivational priorities, directing them toward close social partners. While one might expect this leads to fewer psychological resources for other activities, other motivations may need to be curtailed as well. Feeding might be one competing motive; if OT depresses this motivation, it could facilitate pursuit of social bonding goals (for a related argument focusing on estradiol, see Fessler, 2003). In a complementary fashion, OT downregulates energy dedicated to energetically expensive forms of immune responses. On the other end, OT might potentiate certain other physiological states that aid in pursuit of its evolved functions. For instance, it may prime the cardiovascular system to increase throughput specifically in response to emotionally salient cues (Gamer & Büchel, 2012), such as those from a partner. And, OT might generally increase energetic resources

available via lipolysis. While some aspects of this model resemble the classic ‘stress response’, the events that lead to an OT response, and the resulting cascade of physiological and psychological changes, are likely distinct from an HPA response to threat (see Introduction). The current study did not examine these physiological factors, but future research integrating them will aid in the development of a more powerful explanatory framework (see also Gangestad & Grebe, 2016).

Interactions with other hormones. Hormones do not act alone, and their effects may not be additive. If an endocrine hormone fundamentally operates as an allocator and coordinator of resources, one efficient way to accomplish this could be via affecting the functionality of other hormones. This could be carried out in number of ways, via positive or negative interactions on the production of a hormone, reception of a hormone at specific tissue sites, or both. Theoretical arguments about the importance of interactions are backed by molecular evidence. Gimpl & Fahrenholz (2001) provide an extensive review of the OT receptor and its interactions with several hormones. I briefly outline interactions of two hormones—estradiol and progesterone—with the OT system, in order to provide some specific instances of what physiologists have revealed as a complex web of hormonal interaction. Estradiol appears to strongly potentiate the activity of OT within the brain, through both increased production and receptor density (e.g., Quinones-Jenab et al., 1997; Rissman, 2008). In contrast, interactions between progesterone and OT are less straightforward. Peripherally, high levels of progesterone, such as during the late stages of pregnancy, appear to function in opposition to OT (Gimpl & Fahrenholz, 2001). Progesterone binds directly to uterine OT receptors, inhibiting their function (Grazzini et al., 1998). Neuromodulatory effects may show

different patterns. At low doses, OT may stimulate progesterone release, and progesterone may mediate OT responses to certain stressors (Brown & Brown, 2015). OT might jointly rely upon priming by estradiol and progesterone to potentiate mating behavior in rodents (Schumacher et al., 1989). At the same time, centrally administered progesterone blunted lactation-induced OT increases in rats (Thomas, Crowley, & Amico, 1995), suggesting that progesterone *withdrawal*, not priming, permits OT functionality in the context of nursing.

Again, these examples offer only a small glimpse at the network of physiological interactions between hormones. Some theoretical models, such as the steroid-peptide theory of social bonds (van Anders et al., 2011), suggest that OT's interactions with other hormones, as well as contextual factors, can shape psychological responses. Certain eliciting cues lead to the production of multiple hormones, and this combined production may accomplish different adaptive goals from those achieved by either hormone in isolation. OT and testosterone (T), for instance, are claimed to have opposing effects on pair-bonding behaviors from studies that usually examine these hormones independently. Indeed, nurturing contexts appear to increase OT, but decrease T (van Anders et al., 2011). However, in some situations one should expect OT and testosterone to function synergistically—during interactions with a pair-bond partner that contain elements of both nurturance and sexual desire, as one example. In turn, elevated OT and T may function to serve one kind of bonding goal—pertaining to a sexual partner—whereas a state of elevated OT, but lowered T, serves another—pertaining to offspring or other kin. Two studies find that OT and T positively covary in men (Jaeggi et al., 2015; Grebe et al., 2016), though in the latter study, the interaction of OT and T changes did not predict

relationship involvement or discrepancies in involvement (Grebe et al., unpublished data). T was not measured in this study, though remaining saliva samples permit future hormone assays. This single example, which shows how an assessment of T may be valuable for drawing additional insights regarding the bonding functions of OT, perhaps extends to several interactions between OT and other endocrine hormones.

Conclusion

It is not hard to understand the widespread interest in OT over the past twenty years. In the early stages of psychological OT research, the apparent far-reaching effects of this hormone in the processes of maternal, sexual, and social intimacy provided convincing evidence that OT was a major proximate mechanism behind the diversity of intense social bonds humans form with other individuals. It was, in other words, love distilled into biochemical form. This simplistic view has since fallen out of favor, and the current zeitgeist of OT research has spent the past several years looking for ways forward. In this dissertation, I have attempted to contribute to this effort through multiple channels: by questioning assumptions and interpretations of existing models, framing OT in terms of its fundamental functions as an endocrine hormone, and rigorously testing a newly developed proposal through replication and extension. The success of these efforts was mixed, and even the conclusions I draw in line with expectations are preliminary. However, the results I obtained provide several promising avenues for future empirical and theoretical development in behavioral OT research.

Appendix A: Pattern Loadings for Self and Partner Relationship Involvement Measures

Self				
Factor	1	2	3	4
bond	.590	.090	-.094	.334
want	-.004	.042	.037	.747
gotwant	-.461	.211	-.079	.172
sdhon	-.221	.212	.325	-.057
sen	.446	-.295	.398	.516
sant	.013	.701	-.046	.008
scom	.664	.243	-.208	.083
ssexr	-.047	-.428	-.201	.102
stime	.323	-.045	-.383	.222
ssocng	-.018	.037	.617	-.012
infat	-.065	-.119	-.164	.561

Partner			
Factor	1	2	3
pen	-.497	-.443	-.026
pant	-.186	.811	.407
pcom	-.670	.054	.049
psexr	-.076	-.467	.082
psexo	.053	-.027	.564
ptime	-.641	.013	-.164
psocng	.381	.144	.110
pdhon	.049	.023	.675

9. To the extent that you take into account the state welfare when choosing careers, does it lead you to a greater propensity toward a more lucrative career, or to a career where you can realize your personal desires and does not need to be profitable?

1 2 3 4 5 6 7
More lucrative **No change** **More self-realizing**

Appendix C: Non-Partner Social Bonding Investment Items (English Translation)

Here are five statements describing close social partners; they can be friends, family, boyfriend, or others. Read through all five statements before continuing:

- She / he is totally honest and truthful with me.
 - She / he is really sincere in their promises.
 - I feel that I can trust that he / she will help me in every situation.
 - I can tell him / her anything.
 - I completely trust her / him.
1. How many people in your life fulfill all those statements, and (as you see it) feel the same about you?
 2. On a scale from 1 to 7, do you want the number of people that meet these criteria to be greater, lesser, or the same?

1	2	3	4	5	6	7
Lesser			The same			Greater

The next questions deal with different kinds of activities and how often you participate. Some designations are subjective concepts (small groups, larger groups) - use examples and discretion about these concepts.

1. Have you ever been a member of a club, through university or elsewhere? (Eg. Student organizations, film clubs, quizlag etc.)
2. If yes : What kind of club?
3. If yes : How many days per month?
4. Do you participate actively in sports through student sports teams or with other students from your educational institution?
5. If yes : What kind of sport?
6. If yes : How many days per month?
7. Do you go to social events with *small* groups of strangers? (Eg. Intimate concerts, lectures (outside school hours) etc.)
8. If yes , what kind?
9. If yes : How many days per month?

10. Do you participate in social events with *larger* groups of strangers? (Eg. Greater concerts in Olavshallen / Great Hall of the Union, sport events, Byåsen Handball / RBK etc.)

11. *If yes* : what kind?

12. *If yes* : How many days per month?

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