Trait Social Anxiety as a Conditional Adaptation:
A Developmental and Evolutionary Framework

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Abstract

Individuals with *trait social anxiety* are disposed to be wary of others. Although feeling social anxiety is unpleasant, evolutionary psychologists consider it to be an adaptation. In current models, social anxiety is described as functioning to have helped our prehistoric ancestors avoid social threat by warning individuals when their interactions with other group members were likely to be negative and motivating them to act in ways to prevent conflict or limit its damage. Thus, trait social anxiety is thought to have evolved in our species because it allowed our ancestors to preserve their relationships and maintain their positions in social hierarchies. While we agree with this conclusion drawn by existing evolutionary models, we believe that there is an important element missing in these explanations: the role that individual *development* has played in the evolution of trait social anxiety. We propose a new model, which argues for trait social anxiety to be considered a *conditional adaptation*; that is, the trait should develop as a response to cues in the early childhood environment in order to prepare individuals to face social threat in adulthood. Our evolutionary model can provide new insights into how trait social anxiety has persisted in our species and how it functions in the modern world.

Keywords: trait social anxiety; social anxiety disorder; developmental systems theory; evolutionary psychology; conditional adaptation

Trait Social Anxiety as a Conditional Adaptation: A Developmental and Evolutionary Framework

Anxiety is an unpleasant experience. In times of stress, individuals may feel somatic symptoms of anxiety (e.g., increased heart rate, shallow breathing, etc.) resulting from arousal of the sympathetic nervous system and suppression of the parasympathetic system (e.g., Kreibig, 2010). They may also have anxious thoughts (e.g., worry and apprehension) focused on the stress (e.g., Ingram & Kendall, 1987). Still, anxiety serves an important function: it makes us vigilant to potential threats in our environment (e.g., Nesse, 2005). Social anxiety is meant to serve the same function, but in a specialized context; that is, when threat is *social* in nature (e.g., Green & Phillips, 2004). In evaluative settings, like in a job interview or a class presentation, feeling anxiety can be a reminder to proceed with caution (e.g., to think more carefully about what to say before speaking, to listen closely to questions being asked, etc.). In situations in which making a good impression seems to be an unlikely outcome, social threat may still be avoided by deferring to others or by not interacting with them at all (Arkin & Shepperd, 1990). Thus, feeling social anxiety can be a valuable defense mechanism that helps individuals avoid damaging their relationships and reputations (Leary, 2010).

Unfortunately, social anxiety can also be triggered in situations that contain no real threat (e.g., Pozo, Carver, Wellens, & Scheier, 1991). Having the tendency to feel anxious in most social contexts, threatening or otherwise, is the mark of *trait* social anxiety (Leary & Kowalski, 1995). Individuals with the trait often cope by limiting their interactions with others or by being closed off when interacting, but this can sometimes lead to the very rejection and exclusion that they feared in the first place (Maner & Kenrick, 2010). For some, trait social anxiety is debilitating, interfering with their relationships, work, and mental health to a point that would be considered disordered. With such poor outcomes, it may be difficult to see trait social anxiety as anything but a flaw in a system that is otherwise designed to protect. Considering how that system was designed over the course of evolution, however, may provide some clarity.

In the ancestral environment, social threat likely had an effect on an individual's ability to survive and reproduce; violence from others could result in physical harm and poor evaluation could result in loss of status, rejection by allies, or even ostracism from one's group, all of which would have meant less access to resources and mates (Gilbert, 2001). If being vigilant to social threat increased our ancestors' ability to avoid conflict in their social groups (e.g., by knowing when to show submission to more dominant group members and so avoid attack), the genes associated with that vigilance could have been passed down through generations to persist in our species. In this way, social anxiety may be considered an evolutionary *adaptation* (e.g., Baumeister & Tice, 1990; Gilbert & Trower, 1990; Green & Philips, 2004).

Missing from the existing evolutionary models of social anxiety, however, is a clear integration of developmental processes. Developmental research has found trait social anxiety to be rooted in early childhood and to be caused by interactions between genetic

(e.g., amygdala reactivity) and environmental (e.g., parenting) factors (Degnan & Fox, 2007; Schmidt, Polak, & Spooner, 2005). Here, we propose that an evolutionary approach that considers the *developmental systems* in which trait social anxiety evolved would be better able to account for individual differences than the existing models. Specifically, we propose that trait social anxiety should be considered a *conditional adaptation* in which the early childhood environment provides cues for the level of social threat an individual is likely to experience as an adult. When the future environment is predicted to be high in social threat, the development of trait social anxiety could be seen as advantageous.

This paper begins at the proximate level with an overview of what is known about the development of trait social anxiety. We define the construct and describe its range of severity, the genetic and environmental factors associated with its development, and the implications for individuals' socioemotional functioning. Then, at an ultimate level, we outline three existing evolutionary theory-based frameworks that emphasize the adaptive function of social anxiety in helping our ancestors face social threats (i.e., the threat-detection, social competition, and social exclusion approaches). We then introduce a new evolutionary framework – one that builds on the existing models yet interweaves the developmental evidence described in the first section. Specifically, we suggest that trait social anxiety can be considered to be a conditional adaptation that prepared children to avoid social threat in adulthood.

The Development of Trait Social Anxiety

At the broadest level, the experience of social anxiety can be described as feeling uneasy, tense, or afraid while in (or imagining being in) the presence of others (McNeil, 2010; Schlenker & Leary, 1982). When individuals feel social anxiety, it is often triggered by a belief that their words, actions, or appearance will be evaluated by others, especially if they expect that evaluation to be negative or to go against the particular, ideal image that they want to present of themselves (Arkin, Appelman, & Burger, 1980; Clark, 2001; Leary, 2010; Watson & Friend, 1969). Individuals are more likely to experience an intense socially anxious state when their relationships are at-risk (Baumeister & Tice, 1990; Leary, 2010). For example, one individual may feel anxious while giving a presentation to her colleagues because she believes that they will perceive her as disorganized if she does not do well, and another may worry that talking about negative emotions with his friend will make him less likeable.

Although almost everyone experiences social anxiety at one time or another in their lives, some individuals are *disposed* to be socially anxious and will feel anxiety in a wide variety of social situations; these individuals can be said to have *trait social anxiety* (Leary & Kowalski, 1995). Individuals with trait social anxiety tend to interact with others with a particular style that is marked by inhibited and avoidant behavior, such as letting others initiate conversation, making less eye-contact, disclosing little information about themselves, and speaking less, in general, than their non-anxious peers (Cheek & Buss, 1981; Davila & Beck, 2002; Leary & Buckley, 2000; Sparrevohn & Rapee, 2009). When interacting, socially anxious individuals may also act in *innocuously sociable* ways (e.g.,

nodding along and making noises of agreement) to show they are engaged, while not actually contributing to the conversation (Leary & Kowalski, 1995).

Because individuals with social anxiety may be described as ‘shy’ in everyday language and research alike, the terms should be distinguished for conceptual clarity. Shyness can be defined as both feeling social anxiety and displaying inhibited or avoidant behaviors (e.g., Coplan & Armer, 2007; Leary & Buckley, 2000). High correlation has been found between (self-report) measures of shyness and social anxiety, and the constructs appear to load on a single, underlying, factor (Anderson & Harvey, 1988; Brook & Willoughby, 2017). Despite these findings, caution should be taken when using measured shyness to inform research on social anxiety. For example, some researchers believe anxiety to be sufficient but *not necessary* for a ‘shy’ label to be applied (e.g., Hopko, Stowell, Jones, Armento, & Cheek, 2005). Similarly, the colloquial use of the term ‘shyness’ often refers only to shy *behaviors*, which may affect how individuals interpret items on shyness measures (e.g., Harris, 1984; Henderson & Zimbardo, 2010). In contrast, social anxiety *cannot* be defined by behavior alone; an individual who feels highly anxious in the presence of others but does not show inhibited behavior as a result should still, necessarily, be described as socially anxious (e.g., Leary, 1983). For the same reason, individuals who behave in inhibited ways or avoid social interaction because they prefer to be alone (i.e., *introversion*: Carlyn, 1977) or lack motivation to interact (i.e., *social disinterest*: Coplan, Prakash, O’Neil, & Armer, 2004) should not be considered socially anxious. It can be especially difficult to differentiate between shy behaviors caused by anxiety from those caused by social disinterest in early childhood (Coplan & Armer, 2007; Rubin, Coplan, & Bowker, 2009). In the current review, research on shyness has been included only when the methods clearly contained social anxiety as part of the operational definition of shyness, and this same criterion was used when incorporating research on other, similar, constructs (see McNeil, 2010).

The place of *social anxiety disorder* (or *social phobia*) in social anxiety research has been widely debated. The DSM-5 criteria for diagnosing social anxiety disorder include a persistent fear of social situations that is out of proportion to the actual threat posed by public scrutiny, an avoidance of social situations or intense anxiety when enduring them, and clinically significant distress or impairment in daily functioning (American Psychiatric Association, 2013). The most recent version of the International Classification of Diseases (i.e., ICD-11, currently in draft form) incorporates these criteria into its definition as well (World Health Organization, 2018). Given that these criteria show similarity to components of *trait* social anxiety, it should be asked whether the disorder is merely an extreme form of the trait (i.e., one end of a *continuum* of severity), rather than a separate ‘disease entity’ (McNeil, 2010; Rapee & Heimberg, 1997; Rapee & Spence, 2004). Although some have argued against this continuum model of social anxiety (e.g., Chavira, Stein, & Malcarne, 2002; Turner, Beidel, & Townsley, 1990), a more recent study by Ruscio (2010) found evidence for the model: data from a large survey of individuals with social fears fit a dimension model, ranging in severity, better than a categorical one.

Thus, trait social anxiety should not be considered to be a separate construct from social anxiety disorder, but rather *becomes labeled* as disordered when it interferes with daily life, which is a threshold that can vary from person to person (e.g., if an individual’s

social anxiety is most severe in public speaking situations, but she hardly ever has to engage in public speaking at her job, her social anxiety would not be considered disordered: APA, 2013). As Spence and Rapee suggested in their 2016 review, social anxiety disorder, “reflects an interaction between social anxiety and life impairment... [which] is likely to be heavily environmentally determined” (p. 52). Environmental factors can also increase the *severity* of trait social anxiety, which will make it more likely to cause life impairment. For example, childhood trauma (e.g., abuse and neglect) has been found to be associated with social anxiety disorder (e.g., Bruce, Heimberg, Blanco, Schneier, & Liebowitz, 2012; Chartier, Walker, & Stein, 2001; Simon et al., 2009). The position adopted in the current review is that social anxiety disorder is an extreme version of trait social anxiety, extending from the same developmental pathway to reach a degree that is non-functional for individuals’ personal circumstances. Ideas about the disorder have thus been incorporated throughout the paper, in order to fully understand the evolution of the trait.

Early Development

There is a reliable link between trait social anxiety and an inhibited temperament in infancy (e.g., Chronis-Tuscano et al., 2009; Schwartz, Snidman, & Kagan, 1999). Inhibited infants will show high motor activity (e.g., movement of the limbs and arching of the back) and high negative affect (e.g., crying or fretting) in response to unfamiliar stimuli at four-months-old and will act cautiously around unfamiliar people, objects, and events at two years (Kagan & Snidman, 1991). Behaving in a cautious, passive, reserved, or disengaged way around novelty (i.e., *behavioral inhibition*) is a characteristic of an inhibited temperament that is likely to persist throughout the lifespan (Kagan, Reznick, & Snidman, 1988; Leary & Buckley, 2000). ‘Behavioral inhibition’ in this context may be distinguished from inhibitory control (i.e., the ability to suppress approach behaviour toward pleasurable outcomes: Derryberry & Rothbart, 1988) in being a response to the unfamiliar (Kochanska & Knaack, 2003).

Individuals with an inhibited temperament are likely to display reticent behavior in preschool and to be shy in later childhood (e.g., watching others’ activities instead of either interacting with them or engaging in solitary activity; Fox & Henderson, 2000; Volbrecht & Goldsmith, 2010). They are also likely to be socially anxious in adolescence, to be non-assertive and low in positivity as adults, and to be at increased risk of developing social anxiety disorder within their lifespan (Caspi et al., 2003; Clauss & Blackford, 2012; Schmidt et al., 1997). The degree of stability in inhibition when measured at infancy is fairly low, however, and social anxiety in middle childhood, adolescence, and adulthood is more strongly predicted by behavioral inhibition at preschool age (Hirshfeld-Becker et al., 2007; Karevold, Ystrom, Coplan, Sanson, & Mathiesen, 2012; Prior, Smart, Sanson, & Oberklaid, 2000). Further, when infants show distress and behavioral inhibition in the presence of unfamiliar people, it is not necessarily a *social* fear, but rather due to a heightened reactivity in their sympathetic nervous systems to novelty of any form (e.g., Kagan, 2010). An inhibited temperament in the early years is not caused by social anxiety nor is it an early form of the trait; in fact, individuals only begin to show fear of negative evaluation in later childhood and adolescence (Westenberg, Drewes, Goedhart, Siebelink, & Treffers,

2004; Weems & Costa, 2005). Rather, an inhibited temperament in early childhood should be seen as a *predisposition* for developing trait social anxiety.

Genetic Inheritance

Behavioral inhibition shows a moderate to high degree of heritability. Smith and colleagues (2012), for example, found that behavioral inhibition scores of preschool-age same-sex twins were more highly correlated in monozygotic than dizygotic pairs. Moderate heritability has also been found for trait social anxiety; a meta-analysis of twin studies estimated that genetic factors account for 58 percent of the variance in social anxiety symptoms over the course of the lifespan and 27 percent of the variance in diagnosis of social anxiety disorder (Scaini, Belotti, & Ogliari, 2014). The heritability estimates of behavioral inhibition and subsequent trait social anxiety may actually be measuring an inherited *sensitivity* to the childhood environment. Evidence for such sensitivity has been found in an adoption study by Natsuaki and her colleagues (2013) in which toddlers whose birth mothers met the diagnostic criteria for social anxiety disorder showed less behavioral inhibition around an unfamiliar adult when they had highly responsive adoptive mothers and more behavioral inhibition when they had unresponsive adoptive mothers.

One inherited biological characteristic associated with trait social anxiety that may cause individuals to be more sensitive to their environments is a heightened reactivity of the amygdala. The main function of the amygdala is to initiate the fight, flight, or freeze responses that keep an organism safe in times of threat, and these responses are accompanied by somatic symptoms (e.g., elevated heart rate) that can be interpreted as fear or anxiety (e.g., Davis, 1992). Thus, the more easily an individual's amygdala reacts to environmental stimuli, the more often he or she will feel anxious. Heightened amygdala reactivity has been found to be associated with the inhibited temperament type in infancy, behavioral inhibition throughout the lifespan, and trait social anxiety (Kagan, 2010; Kagan, Snidman, Kahn, & Towsley, 2007, but see: Fu, Taber-Thomas, & Pérez-Edgar, 2017). Adults who had inhibited temperaments as infants have been found, using fMRI measures, to show greater amygdalar activation in response to novel faces compared to those who had been uninhibited as infants, yet there is no difference in activation in response to familiar faces (Schwartz, Wright, Shin, Kagan, & Rauch, 2003). Similarly, adults with social anxiety disorder have been found to show greater amygdalar activation, specifically in the right amygdala, in response to angry, fearful, or disgusted faces, compared to non-anxious controls (Phan, Fitzgerald, Nathan, & Trancer, 2006).

Amygdala reactivity is associated with other bodily processes. Elevated levels of cortisol in baseline measures, for example, have been found to be associated with greater amygdalar sensitivity in young children and have been found in shy preschoolers who had been inhibited as infants (Schmidt et al., 1997; Tottenham, 2012). The thickness of specific areas in the prefrontal cortex may also affect how the amygdala reacts to threatening stimuli; cortical thickness in these areas has been found to differ in adults who were inhibited as infants from those who were uninhibited (Kagan, 2010). The parasympathetic nervous system may also play a role in inhibition and later trait social anxiety as inhibited children have been found to show poorer biological regulation, which likely makes it

harder for them to calm themselves after experiencing a threatening event (Hastings, Kahle, & Nuselovici, 2014; Marshall & Stevenson-Hinde, 1998).

Thus, trait social anxiety appears to be predicted by a particular pattern of activation within the body's threat-detection system. It is important to recognize, however, that trait *social* anxiety is not the only outcome predicted by this activation pattern; *all types* of trait anxiety can be linked to heightened amygdala reactivity and related processes (Fakra et al., 2009; generalized anxiety disorder: Monk et al., 2008). The developmental context determines whether an individual who is predisposed to being particularly sensitive to threat will develop trait social anxiety. That is, the interaction between genetic and environmental factors produces trait social anxiety, through multiple developmental pathways (Degnan & Fox, 2007; Detweiler, Comer, Crum, & Albano, 2014; Rubin, Coplan, & Bowker, 2009; Schmidt, Polak, & Spooner, 2005). In addition, the likelihood that an individual will develop trait social anxiety will increase with each environmental factor present during development (e.g., Simon et al., 2009).

Environmental Factors

Anxious parents can pass their anxiety on to their children beyond their shared genes, such as through modelling anxious behavior and imposing overprotective limits on their children's interactions (Calkins, 1994; de Rosnay, Cooper, Tsigaras, & Murray, 2006). The effects of parental control will depend, in part, on its context: in goal-oriented tasks, control can be an appropriate form of *guidance*, whereas in free-play situations, it may be taken by children as a sign that the situation is actually threatening (Rubin, Cheah, & Fox, 2001). Such *intrusively* controlling behavior by parents has been found to be associated with trait social anxiety, childhood anxiety disorders of various types, and social anxiety disorder (Bögels, van Oosten, Muris, & Smulders, 2001; Greco & Morris, 2002; Hudson & Rapee, 2001; Knappe, Beesdo-Baum, Fehm, Lieb, & Wittchen, 2012; Lieb et al., 2000). The effects of intrusive control on children's anxiety, however, may be limited to children with inhibited temperaments (e.g., Lewis-Morrarty et al., 2012; Rubin, Burgess, & Hastings, 2002). Shy behavior by children can also *evoke* overprotective reactions in parents, especially parents who are anxious themselves, which can result in a transactional cycle that maintains anxiety in children (Hiebert-Murphy et al., 2011; Ollendick & Benoit, 2012; Rubin, Coplan, & Bowker, 2009).

Two other parenting factors associated with trait social anxiety are a lack of emotional warmth towards the child and rejection. Parents show warmth through expressions of unconditional love, by directing positive affect, affection, support, praise, and approval towards their children (e.g., Kerr & Stattin, 2003; Markus, Lindhout, Boer, Hoogendijk, & Arrindell, 2003). Parental rejection is a related concept; it describes a tendency to use cold punishments for misbehaviors (e.g., the silent treatment) and to be excessively critical and less accepting of the child (Van Zalk & Kerr, 2011). In middle childhood, perceived parental rejection has been found to be positively associated with social anxiety symptoms (Grüner, Muris, & Merckelbach, 1999). In a longitudinal study by Van Zalk and Kerr, high scores in social fear in adolescence were found to predict higher scores in perceived parental rejection and lower scores in perceived warmth one year later

(2011). Finally, social anxiety disorder in adolescence and anxiety disorders of various types in childhood have also been found to be associated with rejection and low warmth by parents (Knappe, Beesdo-Baum, Fehm, Lieb, & Wittchen, 2012; Lieb et al., 2000; Hudson & Rapee, 2001).

Parents are not the only external influence on children's social adjustment; peers also play a role in the development of trait social anxiety. There is some evidence that early social exposure (e.g., daycare) can decrease behavioral inhibition in early childhood (e.g., Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). When preschool children are ignored or rejected by their classmates, they are likely to become more inhibited over a two-year period (Asendorpf, 1990). In adolescence, relational victimization (e.g., intentional exclusion) has been found to predict increased social anxiety symptoms in girls, while overt victimization (e.g., physical aggression) predicts increased symptoms in boys (Ranta, Kaltiala-Heino, Fröjd, & Marttunen, 2013; Siegel, La Greca, & Harrison, 2009). Trait social anxiety is also associated with neglect from peers on sociometric ratings (Inderbitzen, Walters, & Bukowski, 1997). Developmental changes that occur in the brain during adolescence may make it a period of particular sensitivity to social exclusion (Somerville, 2013; Vijayakumar, Cheng, & Pfeifer, 2017). The fact that mood and anxiety disorders often emerge in adolescence can, in part, be explained by these maturational changes (Nelson, Leibenluft, McClure, & Pine, 2005). The relation between trait social anxiety and negative experiences with peers is likely reciprocal; typical coping methods for social anxiety reduce the number of opportunities that individuals have to learn and practice social skills, which may lead them to interact awkwardly and garner negative evaluation from others (Gazelle, 2006; Heerey & Kring, 2007; Leary & Buckley, 2000; Luchetti & Rapee, 2014; Miers, Blöte, & Westenberg, 2011; Spence & Rapee, 2016).

Anxious Relational Schemas

The environmental factors associated with trait social anxiety affect individuals who are genetically predisposed to the trait by altering how they *process* social interactions; that is, trait social anxiety is characterized by *anxious relational schemas*, which are cognitive representations that prime individuals to see themselves as socially incompetent, to see others as evaluative, and to see their social interactions as negative (Baldwin, 1992; Daleiden & Vassey, 1997; Ingram & Kendall, 1987). Socially anxious individuals are also prone to setting unrealistic standards for themselves and ruminating on past failures, both of which can lead them to expect poor outcomes from their social interactions (Clark, 2001). Thus, anxious relational schemas amplify feelings of social anxiety in individuals prone to experience it and also work to maintain the trait by biasing them to focus on aspects of their social interactions that seem to confirm the need for that anxiety (e.g., reflecting on past comments that may have made them appear 'stupid' to others; Calvete, Orue, & Hankin, 2013; Hofmann, 2007).

One way that relational schemas are created is through the sensitivity and consistency of the caregiving that is received, typically discussed in terms of the parent-child attachment system. *Anxious* relational schemas are often the result of insecure attachment to parents (i.e., when the child does not expect to receive consistent support

from the caregiver). Preschool children showing insecure attachment styles are more likely to have childhood anxiety (both social and non-social) than securely-attached children (Shamir-Essakow, Ungerer, & Rapee, 2005). Insecure-ambivalent attachment (i.e., the child feels uncertain about what support the caregiver will provide) specifically has been found to be associated with behavioral inhibition in toddlers, social anxiety in middle childhood, and anxiety disorders of all types in adolescence (Brumariu & Kerns, 2008; Calkins & Fox, 1992; Warren, Huston, Egeland, & Sroufe, 1997). Finally, adults with social anxiety disorder tend to be classified as either securely- or ambivalently-attached, but show greater levels of anxiety and an increased likelihood of being either single or divorced if they are ambivalently-attached (Eng, Heimberg, Hart, Schneier, & Liebowitz, 2001). Thus, when infants come to expect their parents to be unresponsive or inconsistently responsive to their needs, they may carry that expectation into all of their future relationships with others.

Anxious relational schemas can bias individuals to attend to threatening stimuli in their environment (Daleiden & Vassey, 1997). The onlooking behavior (i.e., reticence) that is characteristic of children who later develop trait social anxiety, in which they appear too preoccupied with watching others play to engage in solitary activity (as well as too anxious to join in) may be a consequence of not being able to shift their attention away (e.g., Henderson, Marshall, Fox, & Rubin, 2004). Five-year-old children observed to have been behaviorally inhibited in preschool have been found to be less accurate, on average, in identifying a target stimulus when it was presented on the opposite side of the display from a threatening (e.g., angry) face shown immediately prior (i.e., the 'dot-probe' task; Pérez-Edgar et al., 2011). Within the group of inhibited children in this sample, those who showed this threat bias were more likely to also be socially withdrawn. A recent study by White and her colleagues (2017) found a more complicated relation between the ability to shift attention from threat and inhibition, in that children in their sample who had been behaviorally inhibited in preschool were more likely to have anxiety problems (social and non-social) at 7-years-old if they showed an attention bias toward threat, but having that threat bias at 5-years-old was *not* related to anxiety at either time point. Socially anxious adults, those with the disorder and those with less extreme forms of the trait, have been found to show a negative bias toward threat, as well (e.g., Amir, Elias, Klumpp, & Przeworski, 2003; Buckner, Maner, & Schmidt, 2010; Pishyar, Hararis, & Menzies, 2004).

Anxious relational schemas can also bias individuals to interpret their interactions with others as negative, causing them to feel dissatisfied or fearful in their relationships with others (e.g., Rapaport, Clary, Fayyad, & Endicott, 2005). Shy children, for example, have been found to consider their friendships to be of poorer quality than as rated by objective measures, and socially anxious children tend to expect ambiguous social situations (e.g., inviting peers to their birthday party) to end badly (Fordham & Stevenson-Hinde, 1999; Muris, Merckelbach, & Damsma, 2000). Adolescents with social anxiety disorder have been found to rate negative social events (e.g., walking into class late) as more costly and more probable than their non-anxious peers, and adults with the disorder will interpret ambiguous social situations (e.g., your friends stop talking when you approach) as distinctly negative (e.g., they were gossiping about you; Amir, Foa, & Coles, 1998; Rheingold, Herbert, & Fanklin, 2003). Adults with social anxiety disorder have been

found to misattribute the mental states of others and will assign negative labels (e.g., 'upset') to individuals that non-anxious controls describe neutrally (e.g., 'pensive'; Hezel & McNally, 2014).

Context-Specific Outcomes

The difficulties, perceived or otherwise, that individuals with trait social anxiety may have in their personal relationships can lead to internalizing problems, such as loneliness, low self-esteem, and depression (e.g., Eng, Heimberg, Hart, Schneier, & Liebowitz, 2001; Fordham & Stevenson-Hinde, 1999; Jackson, Fritch, Nagasaka, & Gunderson, 2002; Jones, Rose, & Russell, 1990; Riggio, Throckmorton, & DePaola, 1990; Stein et al., 2001). Negative outcomes associated with trait social anxiety are not universal, however. When cultures value social cohesiveness and behavioral control (e.g., some collectivist cultures) there is more acceptance of the inhibited behaviors associated with trait social anxiety. For example, behavioral inhibition was initially found to be accepted and encouraged more by Chinese mothers than Canadian mothers and to be associated with greater peer liking and higher school achievement in young Chinese children (e.g., Chen, Chen, Li, & Wang, 2009; Chen et al., 1998). Yet, after there was a cultural shift in China towards a more capitalistic economy and individualistic values, shy behavior in Chinese children was found to be associated with more negative outcomes, like peer rejection and depression (Chen, Cen, Li, & He, 2005; Yang, Chen, & Wang, 2015). Similarly, university students from western countries have been found to rate outgoing individuals as more likeable and having better career prospects than shy individuals, while students from relatively collectivist East Asian countries are more equal in their ratings (Rapee et al., 2011). Finally, while there is increased prevalence of trait social anxiety in collectivistic cultures (Heinrichs et al., 2006; but see: Schreier et al., 2010), some of the lowest prevalence of social anxiety *disorder* have been observed in East Asian countries, suggesting that social anxiety interferes less in daily life in cultures that are more accepting of inhibited behavior (Hofmann, Asnaani, & Hinton, 2010).

Outcomes may also differ in relation to gender. Inhibited temperament in girls is more likely to lead to later trait social anxiety, and girls report more social anxiety than boys in middle childhood (La Greca & Stone, 1993; Schwartz, Snidman, & Kagan, 1999). Women report feeling more social anxiety than men in a variety of social situations (e.g., interacting with the opposite sex and with strangers, public speaking: Caballo et al., 2014), and social rejection appears to cause more biological stress for women than men, which may lead to a heightened motivation to avoid it (Stroud, Salovey, & Epel, 2002). There may, however, be a greater *acceptance* for socially anxious (i.e., inhibited and avoidant) behavior in girls, and it may also be more *expected* of girls to be concerned with how they are being evaluated by others (Doey, Coplan, & Kingsbury, 2014; Keenan & Shaw, 1997). Together, these findings suggest that trait social anxiety may be more functional for women, but the evidence for this idea is mixed. Social anxiety disorder, for example, has been found in some studies to be represented equally in women and men, distinguishing it from other anxiety disorders which are more prevalent in women, but there is also evidence that men

are more likely to seek treatment for the disorder and for less severe symptoms (Asher, Asnaani, & Aderka, 2017; Caballo et al., 2014; McLean, Asnaani, Litz, & Hofmann, 2011).

Interim Summary

At the proximate level, trait social anxiety has its developmental roots in an inhibited temperament in infancy. Heightened reactivity in the sympathetic nervous system (e.g., the amygdala) can thus be considered a genetic predisposition for social anxiety. Inhibited children who receive overly controlling or rejecting parenting, who lack early social exposure, or who are victimized or excluded by their peers, are likely to form anxious relational schemas, which will amplify their feelings of anxiety during social interactions and promote the development of the trait. Although social anxiety can lead to negative individual outcomes (e.g., depression), the trait is more likely to be accepted, and even admired, in certain cultures (e.g., collectivistic ones) and may also be expected of girls. These context-specific outcomes suggest that social anxiety can serve important social functions. We will explore such functions at the ultimate level in the next section. After we have outlined existing evolutionary theories of social anxiety, we will integrate the research on the development of the trait to propose a new evolutionary framework that emphasizes the role that development played in preparing our ancestors to face social challenges in adulthood.

Social Anxiety as an Adaptation

Many evolutionary theorists posit that trait social anxiety persisted in our species because it served a distinct function in increasing individuals' fitness (i.e., their ability to survive and to reproduce viable offspring). That is, social anxiety has been proposed to be an evolutionary *adaptation*. Like other complex traits (e.g., depression, aggression, inhibitory control, etc.), social anxiety is thought to have evolved to meet specific challenges that our prehistoric ancestors faced in their social groups (Allen & Badcock, 2006; Bjorklund & Harnishfeger, 1995; Bjorklund & Kipp, 1996; Campbell, 2005; Durisko, Mulsant, & Andrews, 2015; Volk et al., 2012). There are three main categories of evolutionary approaches that have been taken to trait social anxiety – threat-detection, social competition, and social exclusion – which differ in emphasis but not in conclusion. That is, all three approaches propose that social anxiety evolved to protect our ancestors from the increased risk of *social threat* that they encountered when they began to live in larger social groups.

Estimates about the size and structure of ancestral groups have been made using various sources of evidence, including fossil records, observations of existing hunter-gatherer societies, and comparisons to other social species, particularly our closest primate relatives. Group size at different time points in prehistory, for example, can be gleaned by estimating the average size of the neocortex in adult members of a particular ancestral species from skull size of existing fossils and by comparing that estimate to the average neocortex size of modern primates (Dunbar, 2007). Using this method, it is estimated that *Australopithecus afarensis*, our ancestors from approximately 3 million years ago, lived in

groups of around 70 individuals while archaic *Homo sapiens*, from 0.4 million years ago, lived in groups of around 125 individuals (Aiello & Dunbar, 1993). Opinions vary on the exact social structure of ancestral groups, but two main structures are likely to have each been present at some point during the evolution of our species (and may have been present concurrently, in different regions): hierarchical and egalitarian structures.

Very early in evolution, the ancestors we share with other primates likely lived in small groups, composed primarily of kin, that were dominated by one male member (i.e., the *alpha* of the group; Boehm, 2011). Although some theorists believe that our ancestors became primarily egalitarian when they shifted to living in larger groups (e.g., Erdal & Whiten, 1994), it is also possible that certain groups survived by living in dominance hierarchies, while others were able to put less emphasis on social rank and more on social cohesion. In modern primate species, such as chimpanzees, both of these social structures have been described as different ‘modes’ of living and are triggered by the resources available to the group. In *agonic* mode, resources are found at one central location and this promotes competition between group members that can best be solved (to avoid too high a degree of conflict) by basing decisions on social rank (i.e., forming a dominance hierarchy). In *hedonic* mode, resources are dispersed in the environment, so group members must forage in scattered ways that would make maintaining cohesion in the group difficult without engaging in more cooperative and affiliative activities (i.e., forming an egalitarian structure; Pierce & White, 1999). It is possible, even likely (e.g., Stamps, 2003), that the ancestral environment was marked by changing factors like weather and migration of prey, so it is feasible that the *agonic* and *hedonic* modes would have been activated at different and overlapping points in the evolution of our species. Thus, in the current paper, the evolution of trait social anxiety was considered to have evolved to be adaptive in both social structures.

Although larger group living provided many benefits to our ancestors (e.g., defense against predators, access to cooperative allies and mates, and the transmission of knowledge; Bowles, 2009; Tooby & Cosmides, 1996; Whiten & Erdal, 2012), it also presented new costs in the form of conflict between group members (Buss, 1990). In hierarchical societies, individuals with low rank were vulnerable to attack by more dominant group members and those with high rank could be violently challenged for their position in the social hierarchy (Gilbert, 2001; Öhman, 1985; Mann, 1986). In both hierarchical and egalitarian societies, the choices an individual made (e.g., attempting to take more than their fair share of resources) could have damaged their reputations, which would have lost them allies or made them less appealing to *potential* allies and mates (Cummins, 2000; Leary, 2010). In the case of dominance hierarchies, reputation damage would have resulted in status loss, which meant access to fewer resources (including, again, allies and mates; Cummins, 2000; Gilbert, 2001). In extreme cases of reputation damage individuals could have been ostracized from their group, which would have greatly decreased their chances for survival in the ancestral environment (Spoor & Williams, 2007; Wesselmann, Naime, & Williams, 2012). Rejection and exclusion on a smaller scale, from allies and potential mates, would have also decreased an individual’s fitness by taking away the benefits that those relationships typically provided (Kerr & Levine, 2008; Leary, 2010).

Existing Evolutionary Models of Social Anxiety

The ability to quickly identify and respond to social threat is an advantage when living in large groups. Based on what is known about trait social anxiety in modern environments – that socially anxious individuals are highly sensitive to cues of negative evaluation and tend to cope with their anxiety by avoiding or being behaviorally inhibited in social interactions – it would make sense that prehistoric individuals who were prone to experiencing social anxiety would have been more fit to respond to certain group contexts. That is, trait social anxiety likely evolved in our species as an adaptation for responding to social threat. Three existing evolutionary approaches take this stance.

Threat-detection. The threat-detection approach to trait social anxiety is the broadest of the existing approaches because it seeks to explain anxiety and fears of all types, not just social. From the threat-detection view, anxiety has evolved as a mechanism for *defense regulation* (Marks & Nesse, 1994). ‘Regulation’ here can refer to homeostasis (i.e., balance in bodily systems): when environmental change (e.g., the approach of a predator) threatens the life of an organism, a corresponding change in the body (e.g., elevated heart rate) can alert the organism that it needs to act (e.g., by fleeing, fighting, or freezing) in order to avoid the detected threat and restore balance to the affected system(s) (Nesse, 2005). Anxiety is one form of bodily imbalance that can motivate individuals to respond to threat (Miloyan, Bully, & Suddendorf, 2016).

Anxiety generally had a lower cost for our ancestors than the threats it served to signal (e.g., predation), so experiencing anxiety at times when no threat was actually present (i.e., a ‘false alarm’) would have often been an acceptable consequence of having an efficient threat-detection system, especially given that environmental cues are *limited* in how well they predict threat (e.g., a rustling in the bushes could be from a predator or a non-harmful organism; Nesse, 2005). There does come a point at which anxiety is *excessive*, and further vigilance for threat poses too high of a cost, by way of missed opportunities and the strain that stress puts on bodily systems, but this depends on the actual level of threat found in the surrounding environment (Bateson, Brilot, & Nettle, 2011; Brosschot, Gerin, & Thayer, 2006; Marks & Nesse, 1994). In harsh environments, threat-detection systems *need* to have particularly low thresholds in order to help organisms survive and compete with other members of their species; having the *trait* to experience anxiety rapidly and in response to subtle cues in the environment (e.g., an angry facial expression) can make an individual more fit in these contexts (Green & Phillips, 2004).

Specialization of threat-detection systems is thought to have evolved in order to allow organisms to defend themselves more efficiently and accurately against specific threats. An example is parental anxiety (i.e., increased vigilance by parents for potential threats to their offspring; Hahn-Holbrook, Holbrook, & Haselton, 2011), which is one factor that has been associated with the development of trait social anxiety in children (e.g., de Rosnay, Cooper, Tsigaras, & Murray, 2006). Different types of anxiety in *offspring* would have also helped to protect them from various threats over the course of their development, such as stranger and separation anxiety in infancy, which motivate offspring to stay in safe proximity to their parents, and social anxiety in adolescence, which helps

them to avoid rejection and exclusion when they first leave the safety of their parents to find their place in the larger social group (Boyer & Bergstrom, 2011).

Social competition. The social competition approach to trait social anxiety builds from the threat-detection approach to propose more specifically that social anxiety evolved in our species to detect threats from living in a status hierarchy (i.e., violence from other group members, loss of status, and, as a result of extreme status loss, ostracism from the group). Thus, this approach assumes that trait social anxiety evolved while our ancestors were in an agonistic mode of social structure, when there was a clear dominance hierarchy in the social group and those who were more dominant had greater access to resources (Gilbert & Trower, 1990). To survive and thrive in such a competitive environment, prehistoric individuals needed to have a *competitive mentality* (i.e., the ability to detect threats and process information relevant to social comparison, such as being able to identify the rank of interaction partners relative to the self; Gilbert, 2001). Individuals likely differed in the ease at which the competitive mentality was activated, based on genetic predispositions and the early environment in which they learned to interact (Irons & Gilbert, 2005). In individuals of low social rank, having an effective competitive mentality would have included being ready to make submissive displays (e.g., lowering gaze and avoiding eye contact) in order to appease more dominant group members and reduce the likelihood of receiving aggression; social anxiety could have served as that readiness, making subordinate individuals with the trait more fit to survive and maintain their position in the group (Gilbert, 2001; Öhman, 1985). Dominant members would have also been at-risk of physical and reputational damage as well if they were to be challenged by multiple group members, so acts of submission by subordinates would have actually helped to maintain dominance hierarchies (Trower & Gilbert, 1989).

The social competition approach sees individuals with trait social anxiety as starting from a position of defence. Just as our prehistoric ancestors likely were, modern individuals with trait social anxiety are less concerned with social enhancement (i.e., raising their social rank) than they are with limiting the damage for which they perceive they are at-risk (and thus maintaining their current position; Hofmann, 2007). It is of note that, in prehistory, climbing in social rank would have carried its own costs because a higher social position would have needed to be defended more often than a lower one (Gilbert, 2001). Social rank in prehistory may also have been affected by what Sloman and Dunham (2004) have called *adaptive* and *maladaptive cycles*. An adaptive cycle would begin whenever individuals experienced success in a competitive environment because the confidence they gained would have made them more likely to succeed at their next venture and their success would have been amplified by comparing themselves to less successful group members. In contrast, individuals who experienced failure would have had less confidence and may have been trapped in a maladaptive cycle, leading to trait social anxiety and depression. In Sloman's view, early experiences with parents can lead to individual differences in the ability to avoid maladaptive cycles, both in prehistory and in modern contexts: securely-attached individuals are more likely to accept their failures without losing confidence, and so are less likely to experience anxiety and depression as a result (2008).

Social exclusion. The social exclusion approach to social anxiety also builds off of the threat-detection approach, but highlights a different type of social threat than the social competition approach (MacDonald & Leary, 2005). Here, feeling social anxiety is a signal that the individual is at-risk of being rejected or excluded by members of their social group (either at the level of individual relationships or at the group level; Baumeister & Tice, 1990). This approach does not assume a dominance hierarchy; our prehistoric ancestors could have been at-risk of being rejected or excluded no matter their social rank if they behaved in socially undesirable ways (e.g., by not cooperating with an ally; Kerr & Levine, 2008). Thus, state social anxiety could have evolved when the social groups of our ancestors were structured in hedonic mode as protection against damage to their relationships of all types (Leary, 2010; Leary & Kowalski, 1995).

A key idea proposed by social exclusion theorists is the existence of the *sociometer*, an evolved internal system that monitors an individual's interactions for cues of social threat (e.g., an angry facial expression from a social partner) and then triggers a negative feeling, like anxiety, jealousy, or loneliness, in order to alert the individual that he or she is at-risk (Kerr & Levine, 2008; Leary, 1990; Leary & Baumeister, 2000). The primary function of the sociometer is to keep track of an individual's *relational value* (i.e., the degree to which a social partner perceives the relationship with the individual to be important, shown through displays of acceptance, love, respect, or warmth; Leary, 2001). The experience of social anxiety can then motivate the individual to behave in ways that would avoid their relationship being devalued (e.g., by acting innocuously sociable; Leary & Kowalski, 1995). Individual differences in social anxiety (i.e., the *trait*) are explained by this approach as reflecting a discrepancy in how much an individual wants to be valued by others and how much they perceive that they actually are; an individual lacking in socially desirable qualities, like physical attraction or special skills, would be more *susceptible* to experiencing social anxiety if they were also motivated to be well-liked by their peers (Leary, 2010).

Comparing the models. The three existing evolutionary approaches to social anxiety all take the stance that it evolved as a mechanism for avoiding the social threats that arose from living in larger groups. Where the social competition and social exclusion models differ is in the particular social threats that are emphasized. The social competition model focuses on the threats of status loss and physical harm by members of different rank, while the social exclusion model focuses on exclusion and rejection by any group member. In contrast, our proposed approach to social anxiety takes the stance that the trait evolved as an adaptation to *all* types of social threat. Feelings of social anxiety could be triggered by social rank cues in the context of domination (i.e., agonistic mode) and by relational value cues in the context of more personal relationships (i.e., agonistic or hedonic mode; Vertue, 2003; for a counterargument, see Leary & Kowalski, 1995). As discussed at the start of this section, the environments in which our prehistoric ancestors lived within their groups likely varied, by region and time, in the availability of resources, which makes it likely that our ancestors experienced both agonistic and hedonic modes of living during the evolutionary period. Schmidt and Poole (2019) make a further distinction between the types of social

threat in their recent evolutionary model of shyness. Specifically, they propose that two forms of shyness evolved in response to the different threats: 'fearful shyness' (i.e., a fear of social novelty) emerged first to protect our ancestors against physical harm by conspecifics, while 'self-conscious shyness' (i.e., a fear of negative evaluation) bifurcated from fearful shyness later, when our ancestors began living in larger groups and had to navigate more complex social interactions. Although our model focuses on social anxiety as a broader trait, we agree with Schmidt and Poole that it is likely that our ancestors first encountered threats of domination (e.g., physical) *earlier* in evolution than more complex threats to relational value (e.g., reputation damage).

All of the existing approaches to social anxiety provide explanations for how the trait would have increased our ancestors' fitness by making them more likely to survive in the face of social threat: social anxiety helped keep at-risk individuals from provoking attacks by more dominant group members, from losing the support of allies, and from being ostracized from their groups. Reproduction is also a part of the fitness equation, however, and it may be more difficult to see how trait social anxiety could have had a positive effect on individuals' ability to reproduce. It is possible that trait social anxiety increased reproductive fitness only *indirectly*. After all, survival and group affiliation are needs that would have had to be met *before* an individual could find a mate; loners who were ostracized from their groups had little chance of surviving *or* reproducing, so by just helping individuals to maintain their positions in their social groups, trait social anxiety would have increased their chances to mate (Buss, 1990; Kenrick, Griskevicius, Neuberg, & Schaller, 2010). Maintaining kin relationships was also important; prehistoric individuals would pass genes on to future generations if they helped their kin to survive and rear offspring (i.e., *inclusive fitness*; Daly, Salmon, & Wilson, 1997). Inclusive fitness would have been increased by trait social anxiety if it encouraged individuals to remain close to their kin (such as by avoiding ostracism from the social group, as a whole, or conflict with individual kin, on a smaller scale; Leary, 2010).

There are also several ways that trait social anxiety could have increased reproductive fitness *directly*. Individuals in danger of damaging their reputations would have increased their social desirability if they behaved in innocuously sociable and reparative ways, which are often motivated by feeling social anxiety (Leary & Kowalski, 1995). Dominant or narcissistic group members may have found expressions of social anxiety appealing in potential mates, as submissive displays would reassure them of their social control (Gilbert, 2001). Modern nonhuman primate research has also found that individuals in hierarchical groups do not always choose dominant mates; female chimpanzees in the wild, for example, have been found to mate with subordinate males in 'consortships' for short periods away from their groups (Tutin, 1979). In our evolutionary past, subordinate individuals would have been chosen as mates by individuals higher in the social hierarchy, despite their social disadvantages, when dominant individuals adopted low-gain, low-risk reproductive strategies (e.g., dealing with less competition while pursuing mates of low social rank; Dunbar, 1988; for similar arguments on trade-offs in the evolution of personality traits see Sih, Bell, & Johnson, 2004; Wolf, van Doorn, Leimar, & Weissing, 2007).

Finally, in discussing evolutionary models such as these, it is important to recognize that individual variation is a necessary component of natural selection, and most traits should be expected to show a range of functioning (Konner, 2010). Prehistoric individuals who fell at the extreme end of the range for trait social anxiety may have been less likely to benefit from their anxious feelings and may have even incurred fitness costs (e.g., of never mating; Gilbert, 2001). Thus, the genes associated with extreme social anxiety would not have been passed down to future generations, while more average forms of the trait would have been preserved. This idea reflects *stabilizing selection*, the process by which deviations from the norm are selected against and become increasingly rare in a species or population (Kutschera, 2009). The presence of extreme forms of social anxiety in modern individuals (which, in many contexts, would be labelled social anxiety disorder) could then be considered *noise*, appearing on occasion due to normal genetic variation (Hofmann, 2007; though see Gilbert, 2001 and Maner & Kenrick, 2010, discussed below, for environmental factors that may explain some instances of social anxiety disorder).

Notably, the existing evolutionary models of social anxiety focus on the adult phenotype, with little attention paid to *developmental* processes. In the next section, we propose a new approach to the evolution of trait social anxiety that incorporates what is known about the *development* of the trait. Our approach is not meant to counter the models just described, but rather to acknowledge, as Konner (2010) stated, that “Adult phenotypes do not evolve, life cycles do; life *is* development, and modifications of development are of the essence of evolution” (p. 741).

A Developmental Systems Approach to Trait Social Anxiety

A *developmental systems* approach to evolutionary psychology is one that recognizes the role that development played in the evolution of our species.¹ For individuals to pass on their genes, they need to first survive to adulthood, and this involves developing from a state of complete vulnerability and dependency on others to, hopefully, one prepared to navigate the environment more independently (Boyer & Bergstrom, 2011; Weems & Costa, 2005). Prehistoric individuals were able to succeed in the face of environmental challenges and so pass on their genes because the traits that they *developed* over their lifespan made them fit (Bjorklund, 2016a). The developmental systems approach is, thus, one that acknowledges the interconnection between evolution and development; evolved traits appear over the course of an individual’s development, and these traits evolved within the *context* of the development of each of that individual’s ancestors (Barrett & Kurzban, 2006; West-Eberhard, 2005).

¹There are a variety of ways that the developmental systems approach may be applied to evolutionary psychology (e.g., Witherington & Lickliter, 2016). The approach that we have taken in this paper would be considered a ‘soft’ version. That is, unlike a ‘hard’ developmental systems approach that views organisms and their environments as inseparable, a ‘soft’ approach treats organisms as distinct from their environments, while still recognizing them to be interconnected (Bjorklund, 2016b).

An important assumption of the developmental systems approach is that evolved mechanisms are not *destined* to occur in individuals that inherit the associated genes, but rather *predispose* those individuals to process environmental information in a particular way, which determines the traits they will develop through their experiences (Bjorklund, 2015; Elman et al., 1996). This assumption incorporates the idea from epigenetics that genes are always expressed in context (Zhang & Meaney, 2010). That is, the interaction between genetic and environmental factors causes individual traits to develop and, consequently, drives evolution (Bjorklund & Ellis, 2014). An individual with a predisposition towards a trait will develop that trait when exposed to environmental conditions that are similar to those in which the trait evolved. Even traits considered to be ‘universal’ *may* not develop if the individual is exposed to conditions that are not typical for that species (e.g., Gottlieb, 1991).²

The interaction between inherited genetic mechanisms and the environment in which the individual develops thus reflects a source of individual variation in evolved traits that goes beyond random mutation. It is rare for a single genotype to produce a single phenotype (West-Eberhard, 2005). Instead, most traits develop in response to particular environmental conditions along a range (i.e., *phenotypic plasticity*; Pigliucci, Murren, & Schlichting, 2006; Wilson, 1994). Stable environments are not likely to produce variation (e.g., human development does not need to make adjustments for gravity: Bjorklund & Ellis, 2014), but for aspects of the environment that are variable, phenotypic plasticity can allow individuals to develop in different, adaptive, ways. Because natural selection acts upon individual variation, phenotypic plasticity, as one major source of that variation, has an important role in evolutionary theory (Bjorklund, 2016a).

When individuals’ fitness is increased by their ability to adapt to environmental conditions, their offspring are likely to inherit that plasticity (Price, Qvarnström, & Irwin, 2003), but plasticity is not always adaptive. Adjustment of a phenotype to environmental conditions takes time and resources (e.g., energy), which may limit the fitness benefits that a plastic phenotype can provide in comparison to a fixed one and may even have fitness costs (DeWitt, Sih, & Wilson, 1998; Dingemanse, Kazam, Réale, & Wright, 2010). A major cost of phenotypic plasticity is the possibility for error (i.e., that the developed trait will not be suited for the environmental conditions; Fawcett & Frankenhuis, 2015). The adjustment of a trait to environmental conditions will be more adaptive at certain periods in development than others; in very early life, individuals will not have been exposed to enough features of the environment to make adjustment accurate, while adjustment too late in life will not provide much benefit (Fischer, van Doorn, Dieckmann, & Taborsky, 2014). Individuals who are exposed to a more homogeneous (and thus more informative) set of environmental features over the course of development will typically adjust earlier than individuals who experience an environment that is constantly changing (Frankenhuis & Panchanathan, 2011).

²We emphasize here that universal traits *may* not develop because it is always possible for traits to develop even in conditions that are atypical for the species. That is, in the absence of species-typical conditions, “all bets are off”; an outcome could develop across a range of conditions never experienced by a species. We thank an anonymous reviewer for providing helpful insights on this point.

Individuals who are biologically more sensitive to environmental conditions (i.e., have a wider *norm/range of reaction*; Konner, 2010; Stamps, 2003) will be both more likely to thrive in supportive environments and more vulnerable to threatening ones, while individuals with a narrower range of reaction will be less likely to be either harmed or enhanced by the environment (i.e., differential susceptibility: Belsky, 1997; Belsky & Pluess, 2009; Boyce & Ellis, 2005). Differential susceptibility also provides fitness advantages within single family units. That is, having one child who is more susceptible to environmental influences (including parenting) than another would make it more likely that at least one of them would survive to reproductive age and pass on their genes; if the susceptible child is well-suited to the future environment that child will thrive, but if the susceptible child is ill-suited, the unsusceptible sibling is still likely to be, moderately, fit (Belsky, 2005; Frankenhuis, Panchanathan, & Belsky, 2015).

Trait social anxiety as a conditional adaptation. In taking a developmental systems approach to the study of social anxiety, we propose that the trait should be considered a *conditional adaptation*. Conditional adaptations result from specialized evolved mechanisms that detect features in the early environment and set development on a course to make the individual as fit as possible in future environments (Belsky, Steinberg, & Draper, 1991; Boyce & Ellis, 2005). Environmental features that were often associated with survival or reproductive challenges in the ancestral environment now act as cues for the challenges the individual will face in adulthood, thus adjusting development to prepare the child for adult life (Bjorklund, 2015). Although the effects of conditionally adaptive evolved mechanisms are not always positive (e.g., if the future environment was not well predicted by early cues due to a major change in conditions), they persisted in our species because they were more likely than not to increase an individual's fitness during the prehistoric period (Frankenhuis & Del Giudice, 2012; Penke, 2011).

Although the term 'conditional adaptation' was introduced by Boyce and Ellis in 2005, Penke proposed an update to the theory by differentiating between two types of conditional adaptations. *Adaptative conditional adjustments* are considered short-term adaptations in that they occur quickly, do not cause lasting developmental change, and are typically reversible (e.g., adjusting preferences for mating given current conditions: Todd, Penke, Fasolo, & Lenton, 2007). *Adaptive developmental plasticity* maps onto Boyce and Ellis's original (2005) definition of the term 'conditional adaptation': development is entrained, and fundamentally altered, in early childhood. When using the term 'conditional adaptation' in our model of trait social anxiety, we will be referring to adjustment that causes lasting developmental change (i.e., adaptive developmental plasticity).

The model proposed here takes as an initial premise, from the existing evolutionary models of social anxiety, that the trait evolved to protect individuals from social threat (including status loss, physical harm by group members, rejection, and exclusion), which allowed them to retain the fitness benefits of living within groups. However, we additionally suggest a key role for development in the evolution of the trait. Within a conditional adaptation framework, trait social anxiety would be expected to develop as a response to cues of social threat in the early childhood environment in individuals who are sensitive to their conditions. That is, we borrow from the concept of differential

susceptibility, which implies that some individuals will be more likely to show conditional adaptations than others (Bjorklund & Ellis, 2014), to propose that some children will inherit mechanisms that are specifically suited to detecting *particular* (i.e., social) cues and this will make them more likely to develop trait social anxiety.³

If trait social anxiety is a conditional adaptation, then the environmental factors, described in the first section, that have been found to be associated with it would be considered early cues of social threat. Prehistoric parents living in high-risk environments, for example, would have needed to be highly controlling in order to ensure their offspring's survival (e.g., Hahn-Holbrook, Holbrook, & Haselton, 2011), so when parents in modern environments are intrusively controlling of their children, they may inadvertently provide cues that the social environment is unsafe (e.g., Rubin, Cheah, & Fox, 2011). Rejection, neglect, and cold responses by a prehistoric parent could have either reflected stress from social threat or an internal characteristic of the parent (e.g., poor emotion regulation) that itself could lead to social difficulties, so these factors could have signaled that offspring would inherit an unstable position in the social group (e.g., Sloman, 2008). Modern children who receive rejection and lack of warmth from parents may avoid similar reactions from others if they are cautious in future social interactions (e.g., Grüner, Muris, & Merckelbach, 1999). A third way that prehistoric parents may have protected their offspring in high-risk environments would have been to limit exposure to non-kin members of the group (including peers), who would be less trusted than kin to not do harm (e.g., Daly, Salmon, & Wilson, 1997). Lacking early social exposure in modern environments may thus be a cue that there will be high social threat outside of the home (e.g., Fox, Henderson, Rubin, Calkins, & Schmidt, 2001). While parents have a large impact on the child's early environment, peers can also provide cues of social threat in the form of rejection and exclusion (e.g., Asendorpf, 1990; Leary, 2010). That the presence of multiple environmental factors associated with trait social anxiety is more likely to lead to its development (e.g., Simon et al., 2009) would make particular sense if the trait were a conditional adaptation: an early environment with a higher number of cues of social threat would be considered a stronger predictor of a threatening future environment.

The genetic factors that are associated with trait social anxiety would be considered, from a conditional adaptation approach, to reflect individual differences in susceptibility to the social environment. From research with individuals in modern environments described in the first section of this paper, we know that an *interaction* between genetic and environmental factors is likely needed to produce trait social anxiety (e.g., Detweiler, Comer, Crum, & Albano, 2014). An inhibited temperament (which is associated with a highly reactive amygdala) may thus reflect a genetic predisposition for detecting and processing cues of social threat in ways that would promote the development of trait social anxiety. The finding that an inhibited temperament more strongly predicts social anxiety when it is present at preschool age than in infancy (e.g., Karevold, Ystrom, Coplan, Sanson, & Mathiesen, 2012) also makes sense from a conditional adaptation perspective. It is unlikely that our prehistoric ancestors had entirely stable social environments, so adjustment of the phenotype for trait social anxiety based on cues of social threat would

³We would like to thank an anonymous reviewer for suggesting that trait social anxiety may be best represented by a specific susceptibility to social cues.

not provide an advantage if it occurred too soon in development for the individual to have been exposed to an adequate number of cues to have an accurate representation of their environment (Fischer, van Doorn, Dieckmann, & Taborsky, 2014). Thus, having cues of social threat in infancy would not be considered as predictive of future environments as cues present *throughout* infancy and into preschool age. The interaction between genetic and environmental factors will also decrease the number of inhibited infants that later develop trait social anxiety, because some inhibited infants receive early cues of social support (e.g., Degnan & Fox, 2007).

Anxious relational schemas, described above as cognitive representations that prime individuals to expect negative outcomes from their social interactions, can be considered an evolved mechanism that produces trait social anxiety in response to early cues of social threat; individuals with anxious relational schemas are biased to attend to threatening stimuli in their environment and to interpret their social interactions in negative ways, which makes them more sensitive to cues of social threat (e.g., Muris, Merckelbach, & Damsma, 2000; Pérez-Edgar et al., 2011). Children form expectations regarding interactions (i.e., relational schemas) through early interactions with caregivers and learn to behave in ways that, during prehistory, would have made them more fit in particular social environments (Bowlby, 1969; Simpson, 1999). Thus, attachment with parents can be considered an evolved mechanism through which cues in the early environment adjust later development to affect how an individual approaches their interactions with others throughout life (e.g., Simpson & Belsky, 2008). The attachment system has also been implicated in the evolution of trait social anxiety by authors taking the social competition approach (i.e., Irons & Gilbert, 2005; Sloman, 2008) and in particular by Vertue (2003), whose argument would certainly fit with the conditional adaptation view of the trait. However, anxious relational schemas are not only formed through the parent-infant attachment system; negative experiences with others, such as peers, can also change the ways that individuals think about their social interactions. That individuals with secure attachments will sometimes develop trait social anxiety (e.g., Eng, Heimberg, Hart, Schneier, & Liebowitz, 2001) can thus be explained by the presence of early cues of social threat from sources other than parents (e.g., Fox, Henderson, Rubin, Calkins, & Schmidt, 2001).

The existing evolutionary approaches to social anxiety consider behavioral inhibition and avoidance of social interaction to be damage-limiting strategies for dealing with social threat. Our conditional adaptation model takes this same stance but adds that being prepared to learn these behaviors over the course of development provides a fitness advantage early enough in development to avoid significant damage from social threat. Offspring in prehistory likely made their first attempts at independence (i.e., away from the relative safety of their parents) within their social groups during adolescence, so adolescents who had developed a high sensitivity to social cues of rejection or exclusion and learned to display behavioral inhibition and avoidance when feeling anxious would have been better able to navigate high-risk social environments on their own (e.g., Baumeister & Tice, 1990; Boyer & Bergstrom, 2011; Gilbert, 2001). The fear of negative evaluation first appears in late childhood and early adolescence in modern environments (Westenberg, Drewes, Goedhart, Siebelink, & Treffers, 2004; Schmidt & Poole, 2019) and

corresponds with developmental changes in brain structures that make adolescents highly sensitive to social cues (Somerville, 2013), which in turn fits with the position that adolescence was a period of transition for prehistoric individuals (Boyer & Bergstrom, 2011).

Testing the conditional adaptation model of trait social anxiety would require examining the effects that early environments have on the development of the trait. Research with modern human populations, described in the first section, provides initial support for the model. Indeed, the environmental factors that are associated with the development of trait social anxiety (e.g., parenting that is overly controlling, rejecting, or cold, lack of social exposure, etc.) can be construed as cues for social threat in the future environment. Additionally, between-group differences in trait social anxiety have been observed, which may reflect variation in early childhood environments; for example, trait social anxiety has been found to be more prevalent in girls and in individuals who live in collectivistic cultures (e.g., Caballo et al., 2014; Heinrichs et al., 2006). However, a prediction from the conditional adaptation model that would require future research is that these groups would, on average, show either heightened susceptibility to environmental conditions or would be more likely to receive cues of social threat in early childhood (or both). Examining cross-cultural research from a conditional adaptation framework may also allow us to identify a broader spectrum of environmental cues for social threat or social support (e.g., Chen et al., 1998).

A conditional adaptation model would also predict that individuals may be *miscalibrated* in their development if the cues present in childhood do not match the adult environment (Frankenhuis & Del Giudice, 2012). In the case of social anxiety, this would mean that some inhibited children will develop the trait when there is little social threat for them to face in adulthood. Miscalibration in this direction may actually be common in modern environments because social threat is less likely to have the life-or-death consequences that it had in prehistory, and this mismatch may lead to social anxiety disorder (Gilbert, 2001; Maner & Kenrick, 2010). Alternatively, miscalibration may occur in the opposite manner; some individuals may face a high amount of social threat in adulthood that was not predicted by cues in childhood. One method to examine these aspects of the model would be to examine older children and adults (i.e., those who have already adjusted to cues present in their early environments) within populations that experience significant, sudden, changes in their social environments, such as refugees who have relocated to new communities (see Rasco & Miller, 2004 for related considerations).

Conclusion

In the first half of this review, we detailed developmental research on the genetic and environmental factors associated with trait social anxiety, its presentation over the lifespan, and how the trait may interact with culture to produce individual differences in socioemotional outcomes. We then turned to an evolutionary perspective to examine what function the trait may have served our ancestors and why it persisted in our species. Existing evolutionary frameworks view social anxiety as an adaptation that helped our ancestors to manage the unique survival and reproductive challenges they faced in the

form of social threat. These approaches largely focus on the function that social anxiety served our *adult* ancestors, without a clear explanation for the role that developmental processes played in the evolution of the trait.

We proposed an evolutionary framework that incorporates our knowledge of how the trait develops in modern contexts to better explain its function over prehistory. Specifically, trait social anxiety is presented as a conditional adaptation: the development of trait social anxiety evolved to prepare individuals for socially threatening future environments. The environmental factors that have been found, in developmental research, to be associated with social anxiety are thus considered to be cues in the early environment that would have predicted high levels of social threat in adulthood during prehistory. In individuals who are specifically susceptible to social contexts (i.e., those with an inhibited temperament in infancy), cues of social threat in the early environment promote the development of trait social anxiety as a protective, damage-limiting strategy. Social anxiety is not always protective, however; the predictive power of socially threatening cues in the early environment may be stronger for children living in certain modern contexts (such as collectivistic cultures) than others. By taking into consideration how social anxiety adapts to early conditions, we can achieve better understanding of how the trait functions in the modern world and when (and if) it is necessary to intervene.

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